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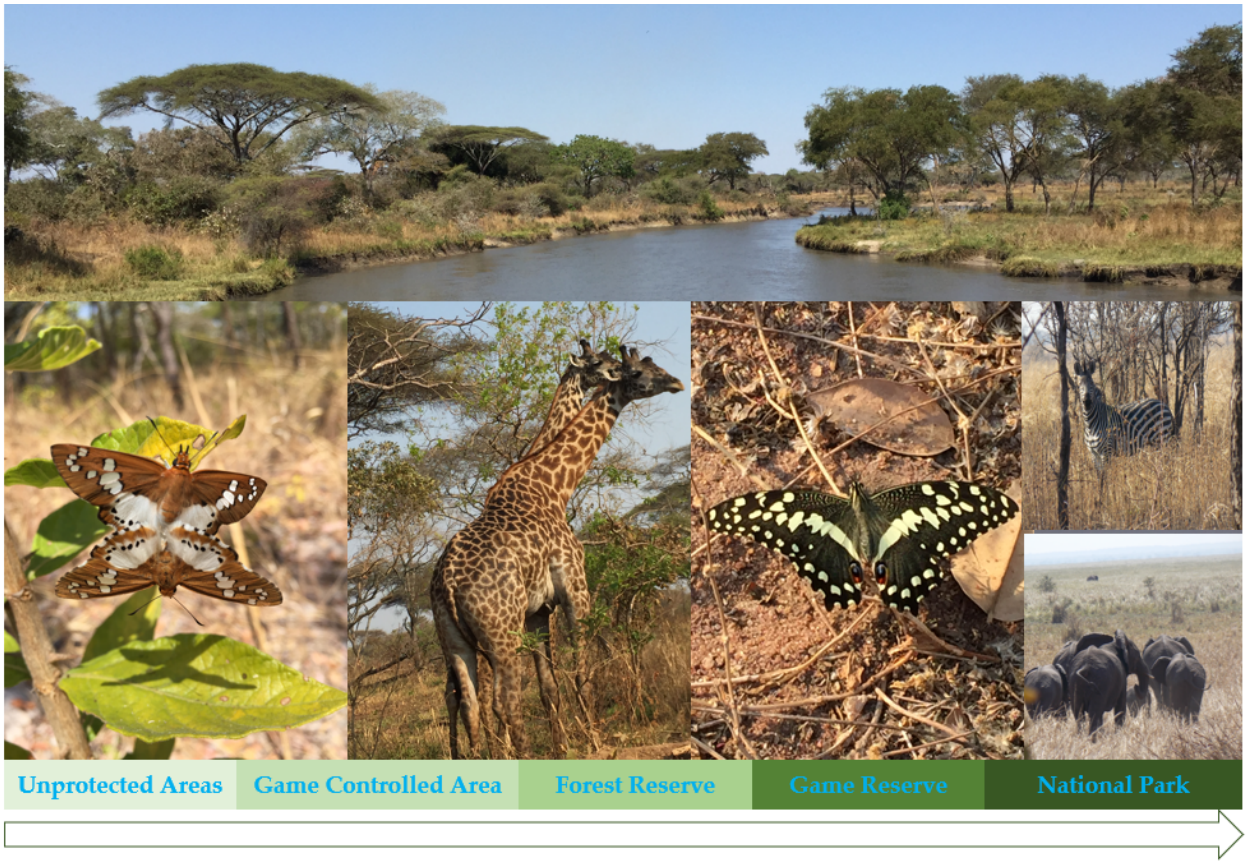
BIODIVERSITY RESPONSES TO A PROTECTION GRADIENT IN TANZANIA



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by

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To my beloved parents Alphonce Giliba whom I lost in 2011 & Macrina Bernard,

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Preface

This cumulative dissertation is submitted for the degree of Dr. rer. nat. at Leuphana University in Germany. It comprises of five chapters based on empirical research in Tanzania, conducted between 2019 and 2022. The research described herein was part of an interdisciplinary research project "Wildlife, values, justice: reconciling sustainability in African protected areas" funded through a Junior Professorship for research into the sustainable use of natural resources by the Robert-Bosch Foundation. Together, the empirical studies presented in this dissertation contribute to the understanding of the ecological effectiveness of different protection levels (from strict to less strictly protected: national park, game reserve, forest reserve, game-controlled area, and unprotected areas) and functional connectivity across a large protected area network in southwestern Tanzania. The empirical studies were designed within the context of protection gradient, land-use and land-use change, and conditions potentially influencing biodiversity patterns. One chapter (4) is published, one revision submitted (2) and two are in revision (3 and 5). A reference to the journal in which a chapter is published or in revisions as well as its status and co-authors are presented at the title page of each chapter. A bibliography is provided at the end of each chapter, and some chapters are followed by supporting information. Due to the standalone nature of the individual chapters, some reiteration in the text of this dissertation was inevitable.

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Abstract

Biodiversity is quickly diminishing across the planet, primarily owing to human pressures. Protected areas are an essential tool for conserving biodiversity in response to increasing human pressures. However, their ecological effectiveness is contested and their capacity to resist human pressures differ. This dissertation aimed to assess the ecological effectiveness of different protection levels (from strict to less strictly protected: national park, game reserve, forest reserve, game-controlled area, and unprotected areas) in protecting biodiversity (both mega diverse butterflies and mammals), maintaining habitat connectivity, and reducing anthropogenic threats at the wider landscape in southwestern Tanzania. To achieve this overarching goal, I employed an interdisciplinary approach. First, I analyzed butterfly diversity and community composition patterns across protection levels in the Katavi-Rukwa Ecosystem. I found that species richness and abundance were highest in the game reserves and game-controlled areas, intermediate in the forest reserves, national park and unprotected areas. Species composition differed significantly among protection levels. Landscape heterogeneity, forest cover, and primary productivity influenced species composition. Land-use, burned areas, forest cover, and primary productivity explained the richness of species and functional traits. Game reserves hosted most indicator species.

Second, I modelled the spatial distribution of six large mammal target species (buffalo *Syncerus caffer*, elephant *Loxodonta africana*, giraffe *Giraffa camelopardalis*, hartebeest *Alcelaphus buselaphus*, topi *Damaliscus korrigum*, and zebra *Equus burchellii*) across environmental and protection gradients in the Katavi-Rukwa Ecosystem. Based on species-specific density surface models, I found relatively consistent effects of protection level and land-use variables on the spatial distribution of the target mammal species: relative densities were highest in the national park and game reserves, intermediate in forest reserves and game-controlled areas and lowest in un-protected areas. Beyond species-specific environmental predictors for relative densities, our results highlight consistent negative associations between relative densities of the target species and distance to cropland and avoidance of areas in proximity to houses.

Third, I examined temporal changes in land-use, population densities and distribution of six large mammal target species across protection levels between 1991 and 2018. During the surveyed period, cropland increased from 3.4 % to 9.6 % on unprotected land and from ≤0.05 % to <1 % on protected land. Wildlife densities of most, but not all target species declined across the entire landscape, yet the onset of the observed wildlife declines occurred several years before the onset of cropland expansion. Across protection levels, wildlife densities occurred at much greater densities in the national park and game reserves and lowest in the forest reserves, game-controlled areas and unprotected areas. Based on logistic regression models, target species preferred the national park over less strictly protection levels and areas distant to cropland. Because these analyses do not support a direct relationship between the timing of land-use change and wildlife population dynamics, other factors may account for the apparent ecosystem-wide decline in wildlife.

Fourth, I quantified land-use changes, modelled habitat suitability and connectivity of elephant over time across a large protected area network in southwestern Tanzania. Based on analyses of remotely-sensed data, cropland increased from 7% in 2000 to 13% in 2019, with an average expansion of 634 km^2 per year. Based on ensemble models, distance from cropland influenced survey-specific habitat suitability for elephant the most. Despite cropland expansion, the locations of the modelled elephant corridors (n=10) remained similar throughout the survey period. According to ecological knowledge, nine of the modelled corridors were active, whereas one modelled corridor had been inactive since the 1970s. Based on circuit theory, I prioritize three corridors for protected area connectivity. Key indicators of corridor quality varied over time, whereas elephant movement through some corridors appears to have increased over time.

Overall, this dissertation underpins differences in ecological effectiveness of protected areas within one ecosystem. It highlights the need to utilize a landscape conservation approach to guide effective conservation across the entire protection gradient. It also suggests the need to enforcing land use plans and having alternative and sustainable forms for generating income from the land without impairing wildlife habitat.

Chapter 1

Chapter 1

Prospects for biodiversity conservation in human modified landscapes

Introduction

Almost 30 years after the Convention of Biological Diversity entered into force, biodiversity continues to decline at extraordinary rates due to human-induced pressures (IPBES, 2019; Mammides, 2020; WWF, 2020). Land-use change, direct exploitation of organisms, pollution, and invasive species associated with an increasing human population and per capita resource use are the underlaying drivers of biodiversity loss globally (IPBES, 2019). In sub-Saharan Africa land grabbing by big firms from other countries for large-scale agriculture (Balehegn, 2015; Williams et al., 2021), and widespread poverty, human population growth, and heavy dependence on natural resources pose serious threats to biodiversity (Coad et al., 2008; Fisher et al., 2005; Redford and Fearn, 2007). As a primary response to these manifold human pressures on species and ecosystems, protected areas are a key conservation instrument for conserving nature and safeguarding biodiversity and human well-being (Gaston et al., 2008). However, the effectiveness of protected areas is questioned, and their ability to endure multiple human pressures differs (Geldmann et al., 2019). To increase protected area effectiveness, understanding the drivers and responses determining their capacity to protect biodiversity is crucial (Burkmar and Bell, 2015; Mazor et al., 2018).

Despite the large and currently increasing coverage of protected area networks in Africa, empirical evidence indicated that large mammal populations have declined by more than 50% over the past decades (Craigie et al., 2010). Land-use change and direct exploitation are considered to be the foremost direct drivers, while human population growth and reduced functional connectivity (Fynn and Bonyongo, 2011; Riggio and Caro, 2017; Roever et al., 2013), underfunding (Coad et al., 2019), and subsequent failure to implement and enforce effective conservation measures (Henson et al., 2016; Lindsey et al., 2014; Muhumuza and Balkwill, 2013) are frequently mentioned as the underlying causes.

Among ecosystems with documented declines in large mammal populations are the Katavi-Rukwa Ecosystem (Caro, 2008; Mtui et al., 2017), the Ruaha-Rungwa ecosystem, (TAWIRI, 2013), and the Ugalla ecosystem (TAWIRI, 2010), all located in southwestern Tanzania. In spite of large coverage of protected areas with different designated (International Union for Conservation for Nature [IUCN], 2020; Riggio et al. 2019;), ranging from strictly protected (IUCN Categories I to V) to less strictly protected, permitting human activities and resource extraction to some extent (IUCN Category VI). Land-use change (especially the expansion of cropland) and overexploitation (often illegal harvesting) of species (Caro et al., 2013; Martin and Caro, 2012) elevated by a growing human population (Masanja, 2014) and an increasing demand for natural resources pose increasing pressure on protected areas and surrounding landscapes in southwestern Tanzania (Martin and Caro, 2012; WCMC-UNEP, 2016). However, insights on the extent of land-use change on biodiversity (especially large mammal populations) remain scarce (Kiffner et al., 2013). Apart from unprotected areas, different categories of protected areas exist in Tanzania, ranging from strictly protected (national park) to less strictly protected (game reserve, forest reserve and game-controlled area) permitting human activities and resource extraction to some extent (Caro and Davenport, 2016; Caro, 1999a). Few studies already investigated the ecological effectiveness of protected areas in protecting vertebrate biodiversity (especially large mammals) across Tanzania (Stoner et al., 2007), however this countrywide assessment only focused on national parks and game reserves and did not consider other protection levels that may also support wildlife populations (Caro, 1999a). Likewise studies on invertebrate biodiversity (especially butterflies) from the Katavi-Rukwa Ecosystem are rare, and mostly focused on the strictly protected national park (Fitzherbert et al., 2006), leaving out the less strictly protected game reserve (Gardner et al., 2007). To date, however, biodiversity patterns (especially butterfly species richness and abundance, and large mammal population densities) have neither been linked to land-use changes nor to different protection levels across an entire ecosystem at the wider landscape. Here, I integrate biodiversity patterns and land-use change analyses over time to assess the ecological effectiveness of five protection levels (national park, game reserve, forest reserve, game-controlled area, and unprotected areas) in safeguarding biodiversity and reducing human threats. Understanding how protection levels mediates biodiversity and human threats is crucial for effective planning and management of integrated protected areas system at the wider landscape (CBD, 2022; UNEP-WCMC; IUCN; and NGS, 2020). My dissertation provides evidence-based information on the ability of unprotected and protected areas with different management form to maintain natural habitat cover, butterfly species, and population densities of large mammal for making informed decision.

Accelerating loss and fragmentation of wildlife habitats outside protected areas through land-use change (in the East African context mainly expansion of cropland and settlement), progressively isolates protected areas in many ecosystems (Fynn and Bonyongo, 2011; Newmark, 2008, 1996). One effective approach to ensure that protected areas can meet their core conservation goals is to connect established protected areas through corridors (Gilbert-Norton et al., 2010; Sekhran et al., 2010; Simberloff et al., 1999). A feasible approach to maintain or reverse the loss of habitat connectivity is to identify, and then protect, or restore wildlife corridors (Bond et al., 2017; Jones et al., 2012). Even though the locations of the majority of wildlife corridors in Tanzania are widely recognized (e.g. Caro et al. 2009 ; Riggio and Caro 2017), their precise locations and present status are frequently unknown (Jones et al., 2009). In an ideal world, wildlife corridor locations are informed by the actual movement of the target species (Alavi et al., 2022; Zeller et al., 2012). However, such data are rarely available for an entire protected area network and over lengthy periods of time. As an alternative to animal movement data, presence data from periodically conducted aerial surveys serve as a suitable surrogate for space use over large areas (Pittiglio et al., 2012). Based on such presence data, species distribution models can be generated for target species (Tobgay and Mahavik, 2020; Torres et al., 2010), and the inverse of the habitat suitability can be used to predict movement corridors across the protected area network (Cisneros-Araujo et al., 2021a; Keeley et al., 2016).

Although wildlife corridors models based on available species distributions and remotely sensed data have been performed for large-scale conservation planning of wide-ranging large mammal species in eastern Tanzania (e.g. Cisneros-Araujo et al. 2021b). To this end, I aimed to conduct a comprehensive analysis of the protected area network connectivity in southwestern Tanzania by adding the following four crucial elements: First, I incorporate connectivity analyses over time to investigate temporal processes affecting habitat suitability and connectivity (Martin et al., 2019; Ntukey et al., 2022; Saura et al., 2019). Second, I include empirical data rather than relying solely on expert opinion (e.g. Van de Perre et al. 2014; Cisneros-Araujo et al. 2021b) and parameterize species distribution models with both natural landscape and anthropogenic features rather than using land cover (e.g. Cisneros-Araujo et al. 2021b) alone as input for modelling corridors. Third, I evaluate the relative importance of individual corridors in order to prioritize conservation actions on the ground, and validate corridor models by comparing them to independent data. Understanding functional connectivity at the wider landscape is imperative for large-bodied and wide-ranging terrestrial mammals to ensure well-connected and effective systems of protected areas (CBD, 2022; UNEP-WCMC; IUCN; and NGS, 2020). My dissertation provides spatially explicit information about wildlife corridors to precisely identify critical places for functional connectivity protection and restoration across a large protected area network in southwestern Tanzania. Further, my dissertation offers a framework to integrate several temporal data sources, ecological models and validation techniques to model spatially explicit wildlife corridors for effective protected area network conservation.

Mammals and insects as biodiversity focal taxa

Biodiversity covers different levels of organization from genes to ecosystems with different dimensions (i.e., taxonomic, functional, genetic and phylogenetic diversity; Chao & Colwell 2022). To this end I focus on distinct taxonomic and functional groups because different taxonomic groups may respond differently to land-use and land-use changes, and protection levels. In this dissertation, I use large mammals and butterflies as study taxa to understand how biodiversity respond to land-use and land-use changes; and protection levels in Tanzania. The two taxonomic groups provide important ecosystem services and all are facing critical extinction rates (IUCN, 2021; WWF, 2018). Large mammals play important ecological roles and require vast areas and when their habitats are adequately protected, many other species that live in these areas are also protected (Caro 2003; Kideghesho 2016). Some species (e.g. elephant) plays a crucial role in shaping the structure and functioning of savannah and forest ecosystems that support other species; (Babweteera et al., 2007; Campos-Arceiz and Blake, 2011; CITES, 2010). Butterflies play an important role in pollinating plants and respond quickly to changes in the environment and land use (Ekroos et al., 2013; Kremen, 1992; Nelson, 2007) and have been identified as ecological indicators in a variety of ecosystems worldwide (Bhardwaj et al., 2012; Stuhldreher and Fartmann, 2018; Thomas, 2005).

Overarching goal

This dissertation was part of the interdisciplinary research project "Wildlife, values, justice: reconciling sustainability in African protected areas", which aims to assess protected area effectiveness and its contribution to sustainability by combining ecological and social processes and outputs in response to governance arrangements. The overarching goal of my PhD dissertation was to assess ecological effectiveness of different protection levels (from strict to less strictly protected: national park, game reserve, forest reserve, game-controlled area, and unprotected areas) in protecting invertebrate and vertebrate biodiversity, maintaining connectivity, and reducing anthropogenic threats at the wider landscape in southwestern Tanzania. Specifically, I aimed at:

- Analyzing butterfly diversity and community composition patterns across protection levels in the Katavi-Rukwa Ecosystem, western Tanzania (Chapter 2).
- Modelling the spatial distribution of six large mammal target species in response to environmental variables and protection level in the Katavi-Rukwa Ecosystem, western Tanzania (Chapter 3).
- Investigating temporal changes in land-use, population densities and distribution of six large mammal target species across protection levels in the Katavi-Rukwa Ecosystem, western Tanzania (Chapter 4).
- Modelling habitat suitability and connectivity of wide-ranging large mammal species over time across a large protected area network in southwestern Tanzania (Chapter 5).

Brief overview of methods

This dissertation builds on a combination of sampling and methods used in spatial sciences, ecology and in the social sciences. These included for example, (i) spatial and temporal analysis of land-use and land-use changes using remote sensing and geographical information system techniques, (ii) temporal analysis of wildlife population densities using wildlife aerial surveys data, (iii) modelling habitat suitability over time using ensemble distribution models, (iv) modelling functional connectivity using least cost and circuit theory approach, (v) validating the connectivity models using local ecological knowledge (i.e., key informant interviews), and (vi) carrying out ground surveys. The ground surveys of large mammals and butterflies were based on line distance sampling framework (Thomas et al., 2010) and standardized line-transect counts (Pollard and Yates, 1994), respectively.

Data analysis for butterflies involved a range of methods that included: (i) detrended correspondence analysis, and indicator analysis for the analysis of community composition patterns; (ii) generalized linear mixed models used for analysis of species richness and functional group responses; (iii) Additive partitioning of diversity for the analysis of diversity patterns at different scales. Data analysis for large mammals from indirect wildlife detection survey was based on a density surface modelling framework, a two-stage method which first accounts for uncertain detectability (primarily as a function of distance between transect and observations; Thomas et al., 2010) and a spatial model of the density of the target populations (Miller et al., 2013).

Thesis outlook

This thesis presents five chapters, four grounded on empirical research and one framework chapter. The first four empirical studies (Chapter 2-5) aim to understand ecological effectiveness of a protected area network by analyzing biodiversity patterns and habitat connectivity at the wider landscape. Chapter 2 and 3 present the current state of biodiversity patterns for one snapshot in time, whereas chapter 4 and 5 present the temporal changes in biodiversity patterns and functional connectivity for multiple snapshots in time, respectively. Next, I provide a brief summary of each chapter.

Chapter 2 provides an account of ecological effectiveness by analyzing butterfly diversity patterns across protection levels (from strict to less strictly protected: national park, game reserve, forest reserve, game-controlled area, and unprotected areas) at the wider landscape. Based on butterfly data collected along foot transects across protection levels: (i) I analyzed total species richness and abundance, and richness and abundance of functional traits across protection levels, (ii) assessed species composition along a protection and land cover gradients, (iii) analyzed the influence of environmental variables on community composition, species richness, and richness of functional traits and; iv) investigated hierarchical patterns of butterfly diversity at different spatial scales; and (v) identified appropriate indicator species for each protection level. I found that species richness and abundance were highest in the game reserves followed by game-controlled areas and forest reserves; national park and unprotected areas had intermediate butterfly species richness and abundance. I found that species composition differed significantly among protection levels. Moreover, I found that landscape heterogeneity, forest cover, and primary productivity influenced species composition, while burned areas, forest cover, and primary productivity explained the richness of species and functional traits. In addition, I found that game reserves hosted most indicator species. My findings revealed the high conservation value of areas with different protection levels in the Katavi-Rukwa Ecosystem. My findings suggest that conserving butterfly diversity across areas differing in protection levels requires consideration of the entire landscape and execution of appropriate measures at different spatial scales.

In **Chapter 3** I modelled the spatial distribution of six large mammal species in response to environmental variables and protection level. Using a density surface modelling framework, I estimated relative densities as proxy for conservation effectiveness within areas differing in protection levels (from strict to less strictly protected: national park, game reserve, forest reserve, game-controlled area, and unprotected areas). I found that relative densities were highest in the national park and game reserves, intermediate in forest reserves and game-controlled areas, and lowest in unprotected areas. I found that protection level and land-use play crucial role in moderating the spatial distribution of target species within the Katavi-Rukwa Ecosystem. While findings show relative high wildlife densities in strictly protected areas, this study also shows a worrying lack of wildlife outside of these protected areas. In sum, my findings suggest that a better integration of conservation efforts outside of protected areas is needed in the Katavi-Rukwa Ecosystem.

Chapter 4 investigated the ecological effectiveness of protected areas by assessing temporal changes in land-use, population densities and distributions of six large mammal target species (buffalo *Syncerus caffer*, elephant *Loxodonta africana*, giraffe Giraffa *camelopardalis*, hartebeest *Alcelaphus buselaphus*, topi *Damaliscus korrigum*, and zebra *Equus burchellii*) across protection levels (from strict to less strictly protected: national park, game reserve, forest reserve, game-controlled area, and unprotected areas) in the Katavi-Rukwa Ecosystem. During six survey periods between 1991 and 2018, I analyzed data from remote sensing and aerial wildlife surveys to derive (i) spatiotemporal patterns of cropland cover in relation to protection gradient; (ii) population densities of the six-target species; and (iii) distribution of these species across protection level, land-use and environmental variables. I found that between 1991 and 2018, cropland increased from 3.4 % to 9.6 % in unprotected areas and from ≤0.05 % to <1 % in protected areas. Among the protected areas, forest reserves recorded the highest amounts of cropland expansion over time followed by game reserves, national park and game-controlled areas. I found that wildlife densities of most, but not all target species declined across the entire landscape. Among protected areas, populations of large mammals occurred at much greater densities in the national park and game reserves, and lowest in the forest reserves, game-controlled area, and unprotected areas. Further, I found that the main wildlife declines occurred during the 1990s before the onset of massive cropland expansion that took place between 2001 and 2018. Thus, the major wildlife declines largely preceded habitat loss. Further, I found consistent effects of protection level and land-use change on the distribution of all investigated target species. Target species preferred areas distant to cropland and preferred strictly protected area national park over other less strictly protection levels (game reserve, forest reserve, game-controlled area, unprotected areas) with fewer restrictions on resource utilization and perhaps also less protection from legal and illegal hunting. In sum, my findings do not support a direct link between land-use change and wildlife densities, additional factors may explain the apparent ecosystem-wide decline in wildlife. Together my findings suggest that proactive strategies are needed to reduce direct threats to wildlife and cropland expansion toward wildlife dispersal areas and migratory corridors.

In **Chapter 5** I modelled habitat suitability and connectivity for the African elephant (*Loxodonta africana*) in a protected area network of southwestern Tanzania. During three survey periods between 2000 and 2019, I quantified land-use changes through remote sensing data; estimated habitat suitability through wildlife aerial survey data, remotely sensed variables and ensemble species distribution models; modelled least-cost corridors; identified the relative importance of each corridor for the connectivity of the protected area network and potential bottlenecks over time through circuit theory; and validated corridors through local ecological knowledge and ground wildlife surveys. I found that from 2000 to 2019, cropland increased from 7% to 13% in the region, with an average expansion of 634 km^2 per year. Despite cropland expansion, the locations of the modelled elephant corridors (n=10) remained similar throughout the survey period. Based on local ecological knowledge, I found nine of the modelled corridors were active, whereas one modelled corridor had been inactive since the 1970s. Based on circuit theory, I prioritize three corridors for protected area connectivity. In addition, I found that key indicators of corridor quality varied over time, whereas elephant movement through some corridors appears to have become costlier over time. In sum, my findings indicated that for over the past two decades, functional connectivity across the surveyed protected area network has largely persisted. Restoring and enhancing ecological connectivity in the study region requires enforcing land use plans and having alternative and sustainable forms for generating income (e.g., income from selling carbon credits, beekeeping, and ecotourism) from the modelled corridors without impairing wildlife habitat.

Synthesis

This dissertation is one of the few empirical studies aimed to investigate ecological outcomes of different protection levels (from strict to less strictly protected: national park, game reserve, forest reserve, game-controlled area, and unprotected areas), and model functional connectivity of a protected area network at the wider landscape over time. The key findings show that: (i) less strictly protection levels hold the highest species richness and abundance of butterflies (Chapter 2) compared to strictly protection areas (ii) strictly protected areas generally hold the highest population densities (Chapter 3 and 4) of most large mammal target species compared to less strictly protection levels; (iii) over the past six decades cropland largely increased on unprotected land compared to protected land (Chapter 4); (iv) over the past six decades wildlife densities of most target species declined across the entire landscape, yet the onset of the observed wildlife declines occurred several years before the onset of cropland expansion (Chapter 4); (v) protection level, land-use, and land-use changes play vital in moderating the spatial distribution of large mammals and butterflies (Chapter 2, 3 and 4); (vi) nine of the modelled corridors were active, whereas one modelled corridor had been inactive since the 1970s, and key indicators of corridor quality varied over time over (Chapter 5). Based on these findings I discuss three interlinked themes that span the different studies. First, I discuss response of biodiversity patterns to protection levels. Second, I discuss response of biodiversity patterns to land-use and land-use changes, and finally, I discuss connectivity conservation.

Responses of biodiversity patterns to protection levels

The empirical studies which form part of this dissertation revealed that biodiversity patterns varied widely across protection levels. First, I found that strictly protected level embraced higher population densities (Chapter 3 and 4) of most large mammal target species than areas with less strictly protection levels or unprotected areas. My findings support conclusions from previous studies in the same (Giliba et al., 2022) and other Tanzanian ecosystems (Kiffner et al., 2020; Oberosler et al., 2020) that unprotected areas may no longer support viable population densities of large mammal species. Second, I found that less strictly protection levels embraced higher butterfly species richness and abundance (Chapter 2) than strictly protection level. Compared to unprotected areas, butterfly species richness and abundance in the strictly protected national park were not significantly greater than those in the unprotected areas. In contrast, population densities and relative densities of all six large mammal target species where generally highest in the national park and lowest in unprotected areas. A possible explanation for this pattern may be due to the fact that larger mammal species are often more prone to illegal hunting (Caro, 1999; Caro, 2008; Martin et al., 2013; Martin & Caro, 2012; Mgawe et al., 2012) or suffer from habitat loss (Giliba et al., 2022; Lobora et al., 2017) as a result of their higher energy demands and subsequent need for larger home ranges (McNab, 1963; Ofstad et al., 2016), which predominate in unprotected areas of Katavi-Rukwa Ecosystem. Moreover, my density surface models (Chapter 3) and logistic regression models (Chapter 4) demonstrated a consistent influence of protection level on the spatial distribution of all six large mammal target species. All target species preferred the national park over less strictly protection levels (Chapter 4) and they were generally widely distributed in the national park compared to less strictly protection levels (Chapter 3). This suggest that the protection level largely explains the spatial distribution of large mammals in the Katavi-Rukwa Ecosystem. These findings confirm the strong influence of the protection level in regulating distributions and densities of large mammals in East Africa (Bhola et al., 2012; Kiffner et al., 2020). Preference of strictly protected national park possibly is due to better protection from legal and illegal hunting (Waltert et al., 2009), and from habitat degradation (Schwartz et al., 2002) compared to less strictly protection levels. In sum my findings underpin differences in relative ecological effectiveness of protected areas within one ecosystem. My main conclusion from these findings is that while less strictly protection levels (especially unprotected areas but also game-controlled areas and forest reserves) were relatively effective in supporting butterfly communities, they were largely ineffective in conserving populations of large mammal species. These findings suggest landscape approach to incorporate the entire protection gradient into land-use plans that integrate the needs of both biodiversity and people.

Responses of biodiversity patterns to land-use and land-use change

Analyses of nearly three decades of land cover and wildlife aerial surveys (Chapter 4) indicated that cropland increased massively in the unprotected areas and marginally in the protected areas, and wildlife densities of most target species declined across the entire landscape. However, the major wildlife declines occurred during the 1990s, whereas the massive land-use changes occurred during the 2000s and 2010s. Thus, because wildlife declines largely preceded habitat loss in the Katavi-Rukwa Ecosystem, it is probable that the initial wildlife declines were caused by other factors. Several previous studies in the Katavi-Rukwa Ecosystem have pointed to illegal hunting (prompted by extensive bushmeat consumption and the selling of animal parts) as the main reason for the decline of large mammal populations. Moreover, my density surface models (Chapter 3) and logistic regression models (Chapter 4) demonstrated a consistent influence of land-use and land-use changes (especially distance to cropland) on the spatial distribution of all six large mammal target species respectively.

Generally, target species avoided areas near to cropland and partially also avoided areas in immediate proximity to houses, suggesting that land-use thrusts large mammal species further into the core areas of protected areas. This observation backs up what other case studies in East Africa (e.g., Msoffe et al., 2011; Ogutu et al., 2012; Veldhuis et al., 2019) have found, which is that expanding cropland towards the edges of protected areas not only largely confines large mammals to protected areas but also makes edge areas within protected areas less suitable for large mammal populations. Similarly, my generalized linear mixed-effects models from the butterfly study (Chapter 2) further support the influence of land-use on the spatial distribution of butterfly species richness. I found that species richness was positively associated to distance to cropland and houses, signifying that species richness increased distant to these anthropogenic structures. This tendency may be attributable to the enormous distances between habitat patches in farmland (Loos et al., 2022, 2015) as well as the use of pesticides, which I noticed during butterfly surveys within farmland, and the corresponding reduction in flowering plants (Tambara et al., 2013). My main conclusion from these findings is that expanding cropland and human settlements not only diminishes the actual amount of available habitat but also lessens the amount of habitat that is effectively used by butterflies and large mammals. These findings suggest proactive strategies (implementing and enforcing site-specific land-use planning) to reduce direct threats to biodiversity and cropland expansion towards dispersal areas and migratory corridors in the Katavi-Rukwa Ecosystem.

Connectivity conservation

Connecting established protected areas through corridors is an effective way to ensure that protected areas can meet their core conservation goals (Gilbert-Norton et al., 2010; Sekhran et al., 2010; Simberloff et al., 1999), but as shown here elephant corridors are vulnerable to the effects of land-use changes (Chapter 5). Findings from this dissertation indicated that among the 10 key corridors identified, one was inactive and had reportedly been blocked before the start of this study. The remaining nine active corridors were characterized by increasing movement costs over time and contraction caused by expansion of human settlements and cropland. For instance, between 2000 and 2019, cropland cover rose by 634 km^2 per year, primarily at the cost of natural vegetation (habitat for wildlife) around protected areas. This land-use change in the study region is likely related to a rise in the number of rural human population (World Bank, 2019), which is partially boosted by immigration from other regions (NBS, 2012). Tobacco and cotton being the dominant cash crops in the study region (NBS, 2012), unsustainable agriculture or shifting cultivation particularly for tobacco production likely contributed to land-use change near elephant corridors and near core protected areas in the study region. The key factors for shifting cultivation in the region include the low soil fertility of the region (Chidumayo, 1999), the high nutrient requirements of tobacco (Baris et al., 2000), as well as the need for biomass energy to dry the tobacco leaves (Jew et al., 2017).

Moreover, the expansion of the Ruaha National Park in 2006 resulted in further displacement of Usangu farmers and Sukuma pastoralists from Mbarali District to frontier areas around the western part of the park (Sirima, 2016). Possibly, such migration to frontier areas around the western part of Ruaha National Park contributed to the observed encroachment within elephant corridors. My main conclusion from these findings is that if the observed trend in land-use change continues, elephant movements within the study region will most likely be hampered further in the near future. This calls for timely conservation action to protect and partly restore the functional connectivity in study region. Based on my findings, I recommend the following conservation actions. First, delineating the corridors would be a key first step in protecting wildlife corridors in locations where they are becoming more constrained and encroached. This also requires enforcing land use plans and having alternative and sustainable forms for generating income from the land without impairing wildlife habitat. One possible strategy would be producing a forest and wildlife-based economy from the modelled corridors (e.g., income from selling carbon credits, beekeeping, and ecotourism) in seeking to generate benefits from nature to outweigh the costs associated with wildlife conservation. Second, in highly degraded areas within some modelled corridors due to human encroachment from arable farming, restoration may be an option through natural regeneration of miombo. In sum, a long-term approach would be to include protected area networks in land-use plans that consider the requirements of both people and wildlife.

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Chapter 2

Chapter 2

Butterfly diversity patterns along a protection gradient in western Tanzania

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Abstract

Although vital for regional conservation planning, little is known about invertebrate diversity patterns across areas with different protection levels from sub-Saharan Africa. For their sensitivity to interventions, we studied butterfly diversity patterns in five protection levels in the Katavi-Rukwa Ecosystem (KRE), western Tanzania. We surveyed 105 randomly selected sites for butterfly species richness and abundance in the national park, game reserve, game-controlled area, forest reserve, and unprotected areas during the dry season of 2021. We compared the total species richness, abundance, and community composition of butterflies in the five protection levels using univariate and multivariate statistics. We used generalized linear mixed-effects models on total species richness and species richness within functional groups in response to landscape heterogeneity, forest cover, primary productivity, elevation, climate, burned areas, and proximity to anthropogenic structures. We analyzed butterfly diversity at different scales using additive partitioning and detected indicator species related to each protection level using multi-level pattern analysis. Species richness and abundance did not decline systematically along a protection gradient. Species richness and abundances were significantly higher in less strictly compared to strictly protected areas. Based on permutational multivariate analysis of variance test species composition differed significantly among protection levels and land cover. Based on detrended correspondence analysis landscape heterogeneity, forest cover, and primary productivity influenced species composition. Based on generalized linear mixed effects model burned areas, forest cover, and primary productivity explained the total richness of species and species richness within functional groups. β-diversity contributed with 89 % of the diversity within the community, whereas α-diversity represented 11 % of the sampled community. Game reserves hosted most indicator species. Our study revealed the high conservation value of areas with different protection levels in the KRE. Conserving invertebrate diversity in the KRE requires consideration of the entire landscape and implementation of appropriate measures to maintain woodland and heterogeneity at different spatial scales.

1. Introduction

The biodiversity crisis is no longer debatable (Butchart et al., 2010; Ripple et al., 2019). Across the globe, biodiversity is rapidly declining mostly due to manifold anthropogenic pressures (Ferrier et al., 2019; IPBES, 2019; Mammides, 2020). The main direct causes are overexploitation and habitat loss associated with an increasing human population, per capita resource use and changes in land-use (IPBES, 2019; Maxwell et al., 2016; Ripple et al., 2017). In sub-Saharan Africa, land grabbing by big multinational corporations from wealthy countries for large-scale agriculture (Balehegn, 2015; Williams et al., 2021), and widespread poverty, human population growth, and heavy dependence on natural resources pose serious threats to biodiversity (Coad et al., 2008; Fisher et al., 2005; Redford and Fearn, 2007).

One of the most widespread strategies to slow or halt biodiversity loss and ecosystem degradation is the establishment of protected areas (PAs). In implementation of this, signatory parties globally agreed to a target to protect at least 17% of all lands and 10% of seascapes by 2020 through ecologically effective systems of PAs, with an increase towards 30% until 2030 (CBD, 2022). Although the amount and coverage of protected areas worldwide has almost arrived at the areal goal, with 16.6% of global land area protected under national authority dominion (UNEP-WCMC and IUCN, 2020), the effectiveness to actually conserve biodiversity remains disputed (Adams et al., 2019; Wauchope et al., 2022). Donating to this total, Tanzania, a CBD signatory, has designated 38% (363,541 km^2) of its land area into a PA system (UNEP-WCMC and IUCN, 2020; URT, 2015). However, to develop effective landscape-scale conservation strategies, it is indispensable to assess the contribution of areas with different conservation categories, ranging from unprotected to strictly protected areas towards regional diversity (IPBES, 2019; Loos, 2021; Webb et al., 2020).

Protected areas in Tanzania (and in our study region) vary greatly in their characteristics, from strictly protected (IUCN Categories I to V) to less strictly protected, permitting human activities and resource extraction to some extent (IUCN Category VI). Despite having large coverage of PAs with different designation in managing biodiversity (IUCN, 2020; Riggio et al., 2019), multiple anthropogenic pressures challenge their effectiveness

(Giliba et al., 2022; Martin and Caro, 2012; WCMC-UNEP, 2016). One region with documented biodiversity declines in large mammals is the Katavi-Rukwa Ecosystem (KRE) in western Tanzania (Caro et al., 2009; Giliba et al., 2022; Mtui et al., 2017). Overexploitations, and expansion of human settlements and agriculture elevated by increasing human population and demand for natural resources being the reasons for the declines (Caro et al., 2013; Giliba et al., 2022; Masanja, 2014). Several studies already investigated the ecological outcomes of PAs with different management forms in protecting biodiversity within the KRE (Caro et al., 2009; Giliba et al., 2022; Mtui et al., 2017; Stoner et al., 2007). However, these studies focused on vertebrate taxa, while studies on invertebrates from this area are rare, and concentrated on the strictly protected national park (Fitzherbert et al., 2006). Assessing spatial diversity patterns of invertebrate taxa across areas with different conservation categories may offer data on variety of taxa and deliver meaningful insights for effective planning and management of biodiversity at the landscape scale (CBD, 2010).

To safeguard biodiversity in these remaining anthropogenically modified ecosystem, and integrating megadiverse invertebrate taxa into conservation planning, it is necessary to understand their current diversity patterns and obtain large-scale baseline data for future monitoring (Hanspach et al., 2015; Jew et al., 2015). To this end, we analyzed butterfly diversity patterns in areas with different conservation categories, ranging from unprotected to strictly protected areas within KRE, where no large-scale numerical data on butterflies have been collected to the best of our knowledge. We chose butterflies as a target group, because they respond quickly to changes in the environment and land use (Ekroos et al., 2013; Kremen, 1992; Nelson, 2007) and have been identified as ecological indicators in a variety of ecosystems worldwide (Bhardwaj et al., 2012; Stuhldreher and Fartmann, 2018; Thomas, 2005).

To address our overarching goal of providing relevant information for understanding butterfly diversity patterns in areas with different levels of protection, ranging from unprotected to strictly protected areas, we sought to answer the following research questions:

i. Does the total species richness and abundance as well as the species richness and abundance within functional groups differ systematically along a protection gradient?
ii. Does the community composition vary significantly across protection levels and land cover?
iii. Which environmental and anthropogenic variables influence total species richness and species richness within functional groups, and community composition?
iv. What is the hierarchical pattern of butterfly diversity at different spatial scales, including the contribution of α-diversity (i.e., within transect) and β1-diversity (i.e., among transects), β2-diversity (i.e., among protection levels) to total γ-diversity (i.e., the entire study area)?
v. Which indicator species represent typical butterflies of a specific protection level?

2. Methods

2.1 Study area

Our study focused on the RKE in western Tanzania, which covers about 15,110 km^2 and contains PAs with different designation in the area. The study area lies between 6° to 7° S and 30° to 31° E, (Fig. 1) and is characterized by a mosaic of unprotected areas (UA, i.e. land that does not have a formal conservation category), and formally protected areas. Here, unprotected areas and formally protected areas together represent the protection gradient underlying our study design. Protection categories range from areas with little enforcement of human land-use restrictions (Game Controlled Areas, GCA: here, settlement, agriculture, livestock keeping are not allowed, but hunting on permit in specific hunting blocks is allowed), areas that allow regulated resource extractions such as Forest Reserves (FR, here, limited timber and non-timber products extraction is permitted) and Game Reserves (GR, here, tourist game hunting on permit is allowed) to strictly protected national parks (NP) where human activities are restricted to photographic tourism and research (Caro and Davenport, 2016; Caro, 1999). Distinguished PAs in the study area include: Katavi National Park (KNP) and Rukwa Game Reserve (RGR), and Lwafi Game Reserve (LGR), Mlele Game Controlled Area (GCA), Mpanda Line Forest Reserve, Msaginia Forest reserve (MFR), and Nkamba Forest reserve (NKF) (Fig. 1). KRE receives an annual rainfall between 800 - 1200 mm, while the temperature ranged between 17 - 26 °C. Elevation ranges from 600-

1800 m asl. The soil types range from alluvial soils (black cotton soils) in grassland/flood plains to loamy soils in woody vegetation. The vegetation consists of miombo woodlands and flood plains (Banda et al. 2006). Miombo forms a single story, with open canopy of deciduous woodland dominated by trees of the genera *Brachystegia, Julbernadia,* and *Isoberlinia* (Banda et al. 2008). The human population in the KRE has rapidly grown due to increasing migration of pastoralist from other regions over the past 40 years (Salerno 2016; Izumi 2017). Agriculture and livestock keeping are the main land-use activities in the KRE (Caro 1999). Rice farming is restricted to river terraces and flood plains while shifting cultivation for other crops, i.e. maize, cotton and tobacco, is practiced at the expense of clearing natural vegetation around the PAs (Giliba et al., 2022, Jew et al. 2015).

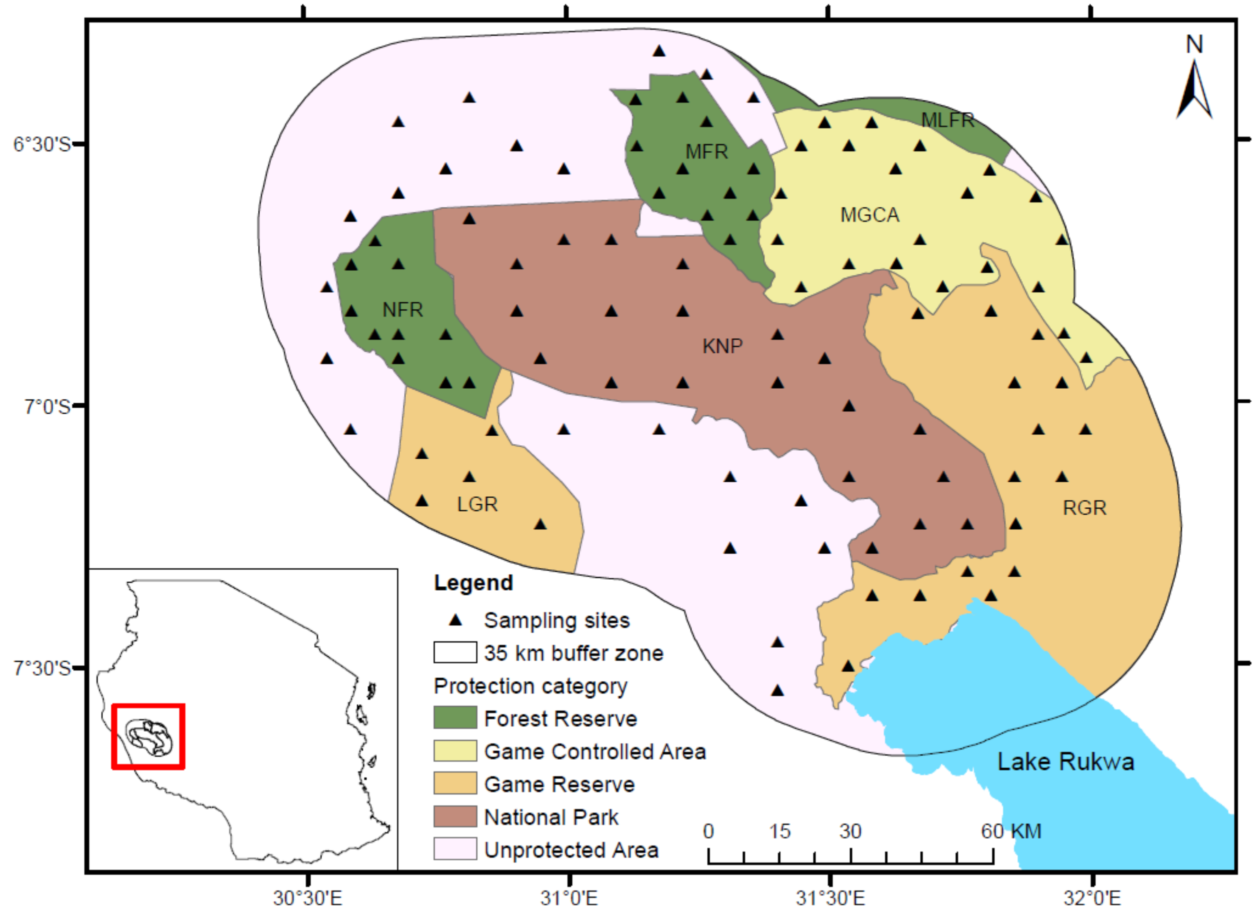

Fig. 1. Map of the study area, highlighting the spatial distribution of butterfly sampling sites (triangular transects with three sections of 1 km length each) across protection levels (KNP = Katavi National Park, RGR = Rukwa Game Reserve, LGR = Lwafi Game Reserve, MGCA= Mlele Game Controlled Area, NFR= Nkamba Forest Reserve, MFR= Msaginia Forest Reserve, MLFR= Mpanda Line Forest Reserve). The inset in the lower left shows the location of the study area within Tanzania.

2.2 Butterfly surveys

We established a 35 km buffer around the boundary of KNP to include areas with different protection levels, ranging from unprotected to strictly protected (UA, GCA, FR, GR, NP). To capture even coverage of butterfly transects across different protection levels, we divided our study area into 5 km by 5 km grids, so that transects had a minimum distance of 5 km to minimize spatial autocorrelation of the data. We randomly selected 105 grids (21 grids within each protection level) for placement of triangularly fixed transects of 3 km length (divided into three sections of 1 km length, Fig. 1). We recorded butterfly species and their abundances per section of 1000 m by walking transects of 5 m width (2.5 m to each side, 5 m above and in front of the observer). We recorded species names and counted the number of individual butterflies captured butterflies with a sweep net and released them after identification. All butterfly species were identified to the species level in the field and verified using national and regional field guides (Kielland, 1990; Larse, 1991; Martins and Collins, 2016; Woodhall, 2020), except for six species that were identified to genus level (*Tuxentius sp, Chilades sp, Mylothris sp, Pseudacraea sp, Acleros sp, Lepidochrysops sp*) in the field. All surveys were conducted by the same observers under suitable weather conditions and without strong wind between 9 am and 5 pm, during the dry season between July and September 2021.

2.3 Butterfly richness within functional groups

To understand how species richness and abundance within functional groups (i.e., habitat specialization, host plant specialization, and wingspan) varies across different protection levels, we classified species into six functional traits from the literature on East and Southern Africa butterflies (Kielland, 1990; Larse, 1991; Martins and Collins, 2016; Woodhall, 2020): 1. generalists (using more than one habitat); 2. specialists (only using one habitat); 3. polyphagous (using host plants in multiple genera); 4. monophagous (only using one host plant species); 5. large (>50 mm); and 6. small (<50 mm) wingspan for both male and female, which is often used as an indicator for mobility (Kuussaari et al., 2014; Öckinger et al., 2010). Mobility is a crucial factor governing butterfly species responses to different environmental and anthropogenic variables (Loos et al., 2014c; Topp et al., 2022).

2.4 Environmental variables

To understand the influence of environmental and anthropogenic variables on species richness and abundance, and community composition, we used the 5 km by 5 km grids for each of the 105 transects; first, to quantify mean annual temperature, mean annual precipitation , and solar radiation from WorldClim database (www.worldclim.org; (Fick and Hijmans, 2017) using ArcMap 10.6 (ESRI, 2018). Second, to quantify mean elevation from SRTM digital elevation model from the U.S. Geological Survey (https://earthexplorer.usgs.gov), and slope, terrain ruggedness index from DEM using QGIS (QGIS, 2020). Third, to quantify primary productivity calculated as mean enhanced vegetation index (EVI) values for the period (i.e. between July and September) that overlap with our butterfly surveys from Google Earth Engine - Landsat 8 Collection 1 Tier 1 8-Day EVI Composite (Gorelick et al., 2017). Fourth, to quantify proximity to anthropogenic structures calculated as mean distances to houses (spatial features were obtained from OpenStreetMap (http://download.geofabrik.de/africa/tanzania.html), and mean distances to cropland (obtained from our land cover) using the Euclidian distance tool in ArcMap 10.6 (ESRI, 2018). Fifth, to quantify compositional heterogeneity calculated as Simpson index of diversity and configurational heterogeneity calculated as edge density, forest cover, burned area cover, and cropland cover from our land cover map (Fig. S1) using FRAGSTATS v4.2 (McGarigal et al., 2012).

To produce the land cover map, we used Google Earth Engine (GEE) to build stacks of Landsat 8 Surface Reflectance Tier 1 atmospherically corrected surface reflectance images (Gorelick et al., 2017). Image collections were constrained to the dates from July to September that overlapped with our butterfly surveys. Image composite was created using median a default metric for GEE that balanced oversaturated and low pixel values (Würsch et al., 2017). A total of 600 training samples were used for land classification through composite imagery, high-resolution Google Earth images, field knowledge (Giliba et al., 2022; John et al., 2021), and ground truthing using ArcMap 10.6 (ESRI, 2018). We used the scatterplot tool to evaluate our training samples to find out if there was enough distinction between land cover classes. We employed a supervised classification approach using a support vector machine algorithm to classify satellite images (Giliba et al., 2022; Heydari and Mountrakis, 2019; Maulik and Chakraborty, 2017). We classified five major land cover categories (dense woodland, open woodland, burnt area, cropland, and water bodies, Supplementary Information, Fig. S1). We generated 500 points using stratified random sampling in ArcMap to assess the accuracy of our classified map. We used high-resolution images from Google Earth and base-map layers from Google Satellite, ESRI Satellite, and Bing Satellite available in ArcMap and QGIS to validate the land cover map (Connette et al., 2016; Hu et al., 2013; Yu and Gong, 2012). Our land cover classification obtained an overall accuracy of 98 % and a kappa coefficient of 0.97 (Supplementary Information, Table S1).

2.5 Statistical analyses

2.5.1 Species richness and abundance

We pooled all observed butterfly species and individuals from the three transect sections for each survey site. First, we aggregated total species richness and abundance, and species richness and abundance within functional groups (i.e., generalist, specialist, polyphagous, monophagous, large and small wingspan) across protection levels (Table 1). Afterwards, we tested for differences in total species richness and abundance, and species richness and abundance within functional groups among protection levels by using Analysis of Variance (ANOVA), followed by multiple comparisons Tukey's HSD test (at the $\alpha=0.05$ level) to determine whether differences occurred (Fig. 2 & 3).

2.5.2 Community composition across protection levels and land cover

We tested for differences in butterfly species composition among protection levels and land cover using permutational multivariate analysis of variance (PERMANOVA) with Bray–Curtis dissimilarity and 999 permutations. The PERMANOVA was conducted using the adonis function in the vegan R package (Oksanen, 2022). We performed pairwise comparisons to determine where differences in species composition occurred using the pairwise.adonis function in the PairwiseAdonis R package (Arbizu, 2020). Beforehand, we confirmed the homogeneity of multivariate dispersion by using betadisper function in the vegan R package (Oksanen, 2022).

2.5.3 Responses of community composition and species richness to environmental variables

To investigate the influence of environmental variables on butterfly species composition, we conducted a detrended correspondence analysis (DCA) for all levels of protection. Prior to the DCA, all numerical explanatory variables were scaled to mean zero and unit variance. To understand the responses of total species richness and species richness within functional groups to environmental variables, we used a generalised linear mixed effects model with Poisson error distribution in the lme4 R package (Bates et al., 2022). Richness of generalist, polyphagous species and species with a small wingspan were over-dispersed, and consequently a negative binominal generalised linear model was fitted using the MASS R package (Ripley et al., 2022). In our all models, “sites” was included as a random effect, as the transects were nested within the sites. Beforehand, we tested the explanatory variables for collinearity and retained only variables with $r < 0.7$ (Dormann et al., 2013) in the model (Table 2). For total species richness and species richness within functional groups, we fitted a global model with all potential variables. Best fitting models were selected using the dredge function of the MuMiN R package (Barton and Barton, 2020), which returned models with the lowest delta AIC values < 4 (Burnham and Anderson, 2002).

2.5.4 Additive partitioning of diversity

To investigate hierarchical patterns of diversity at multiple spatial scales, we performed additive partitioning of diversity (Crist et al., 2003) to determine which scale (alpha, beta and gamma) contributes more to the total butterfly diversity (γ). We used species richness to perform an additive partitioning of diversity, in which γ-diversity is the sum of the α- and β-diversity values ($\gamma = \alpha + \beta$). We calculated the spatial hierarchy of the butterfly species’ β-diversity as follows: i) α-diversity: average richness within transect; ii) β1-diversity: the mean difference of assemblages between transects within protection level; and iii) β2-diversity: the mean difference of the assemblages between protection levels. To compare the observed and expected α- and β-diversity, we randomized 999 times to generate the expected values to which observed values can be compared (Crist et al., 2003; Layou, 2007). We used adipart function in the vegan R package (Oksanen, 2022) to perform additive partitioning of diversity.

2.5.5 Indicator species

To determine indicator species for each protection level, we performed a species indicator value (IndVal) analysis to detect associations of butterfly species to protection levels using the multipatt function in the indicspecies R package (De Caceres et al., 2022).

3. Results

3.1 Species richness and abundance across protection levels and land cover types

We recorded a total of 10578 individuals of 172 butterfly species (Table S2) belonging to five Lepidopotera families (83 Nymphalidae, 43 Pieridae, 21 Lycaenidae, 21 Hesperiidae, 8 Papilionidae) and 72 genera. Sixty-two percent of all individuals belonged to 10 species: *Bicyclus safitza, Hamanumida daedalus, Eurema hecabe, Precis archesia, Catopsilia florella, Belenois aurota, Hyalites eponina, Ypthima asterope, Neptis saclava,* and *Junonia natalica.* Overall, species richness (ANOVA, df= 4, F = 5.61, $P < 0.001$) and abundance (ANOVA, df=4, F=5.13, $P < 0.001$) varied significantly between all five protection levels. Butterfly species richness and abundance were consistently higher in the order of GR>GCA>FR>NP>UA (Table 1, Fig. 2a & b). However, values from UA were not significantly different to those in NP (Fig. 2a & b). Similarly, across functional groups, species richness and abundance for generalist, specialist, polyphagous, large wingspan, and small wingspan varied significantly between all five protection levels. Butterfly species richness and abundances across all six groups were consistently higher in the GR and GCA than for FR, NP, and UA (Table 1). However, values from UA were not significantly different to those in NP across all six functional groups. (Fig. 3a-l). We detected four species that were unique to farmland, 113 species that occurred exclusively in woodland and 55 species that occurred in both land cover types. Among those species occurring on farmland were *Actizera lucida, Coeliades forestan* and *Colotis aurigeneus;* the most abundant species in woodland were *Junonia artaxia, Eurema brigitta,* and *Bicyclus anynana;* and the most abundant species sharing those land cover types were *Bicyclus safitza, Hamanumida daedalus,* and *Eurema hecabe.* The completion of our butterfly sampling seemed adequate at the time and season of our survey as sized-based rarefaction extrapolation curves almost reached asymptote in all protection levels (Fig. S2a), and coverage-based rarefaction and extrapolation curves suggested that diversity in our study region was well represented with a sample coverage percentage above 95 % (Fig. S2b).

Table 1: Total butterfly species richness and abundance as well as species richness and abundance within functional groups in the different protection levels in the Katavi-Rukwa Ecosystem (UA: Unprotected Area; GCA: Game-Controlled Area; FR: Forest Reserves; GR: Game Reserves; NP: National Park). Total species richness displays the observed (obs.) species richness during butterfly transects, Chao1 is mean ± standard deviation of the expected species richness. Obs: Chao1 is the ratio of observed and expected number of species. Human land-use restrictions are consistently lower in the order of UA<GCA<FR<GR<NP.

Protection levels						**Total**
Species richness	**UA**	**GCA**	**FR**	**GR**	**NP**	
Total species richness	76	109	80	115	81	172
Chao1	86.42 ± 4.09	128.30 ± 6.78	93. 37 ± 5.65	132.79 ± 8.00	93.53 ± 6.15	192.93 ± 6.08
Obs: Chao1	87.94%	84.95%	85.68%	86.60%	86.60%	89.15%
Habitat specialization						
Generalists	56	73	54	72	55	103
Specialists	20	36	26	43	26	69
Host plant specialization						
Polyphagous	63	80	63	86	66	122
Monophagous	13	29	17	29	15	50
Wingspan						
Large	28	41	33	42	36	59
Small	48	68	47	73	45	113
Species abundance						
Total species abundance	1360	2315	2137	3119	1647	10578
Habitat specialization						
Generalists	1216	2070	1954	2661	1405	9306
Specialists	144	245	183	458	242	1272
Host plant specialization						
Polyphagous	1251	2100	2023	2716	1439	9529
Monophagous	109	215	114	403	208	1049
Wingspan						
Large	565	1003	1031	1382	643	4624
Small	795	1312	1106	1737	1004	5954

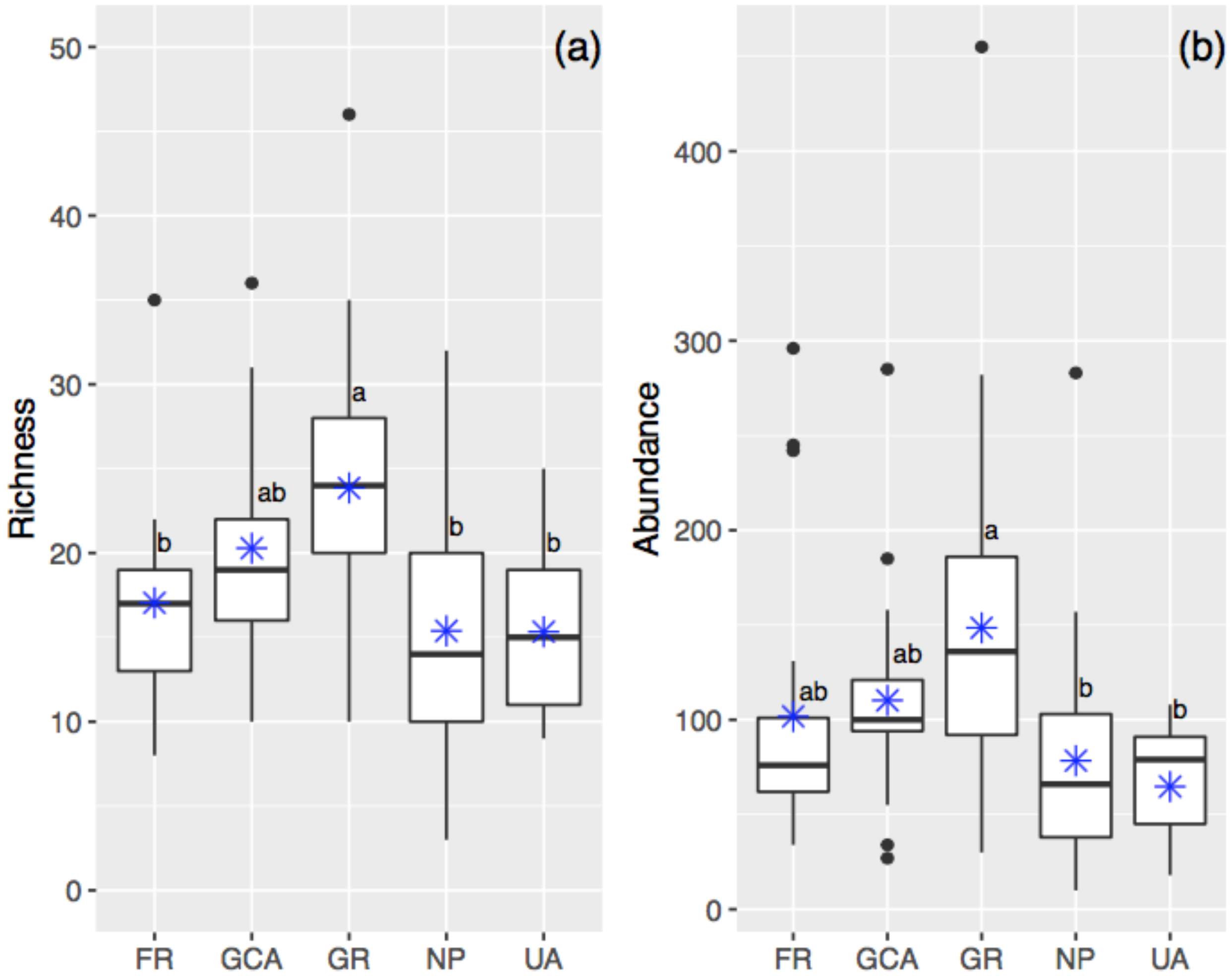

Fig. 2. Boxplots of species richness and abundance across protection levels in the Katavi-Rukwa Ecosystem (FR, Forest Reserve; GCA, Game Controlled Area; GR, Game Reserve; NP, National Park; UA, Unprotected Areas), western Tanzania. Different letters above the boxplots indicate significant differences between protection levels at $P < 0.05$ (Post-Hoc Tukey test).

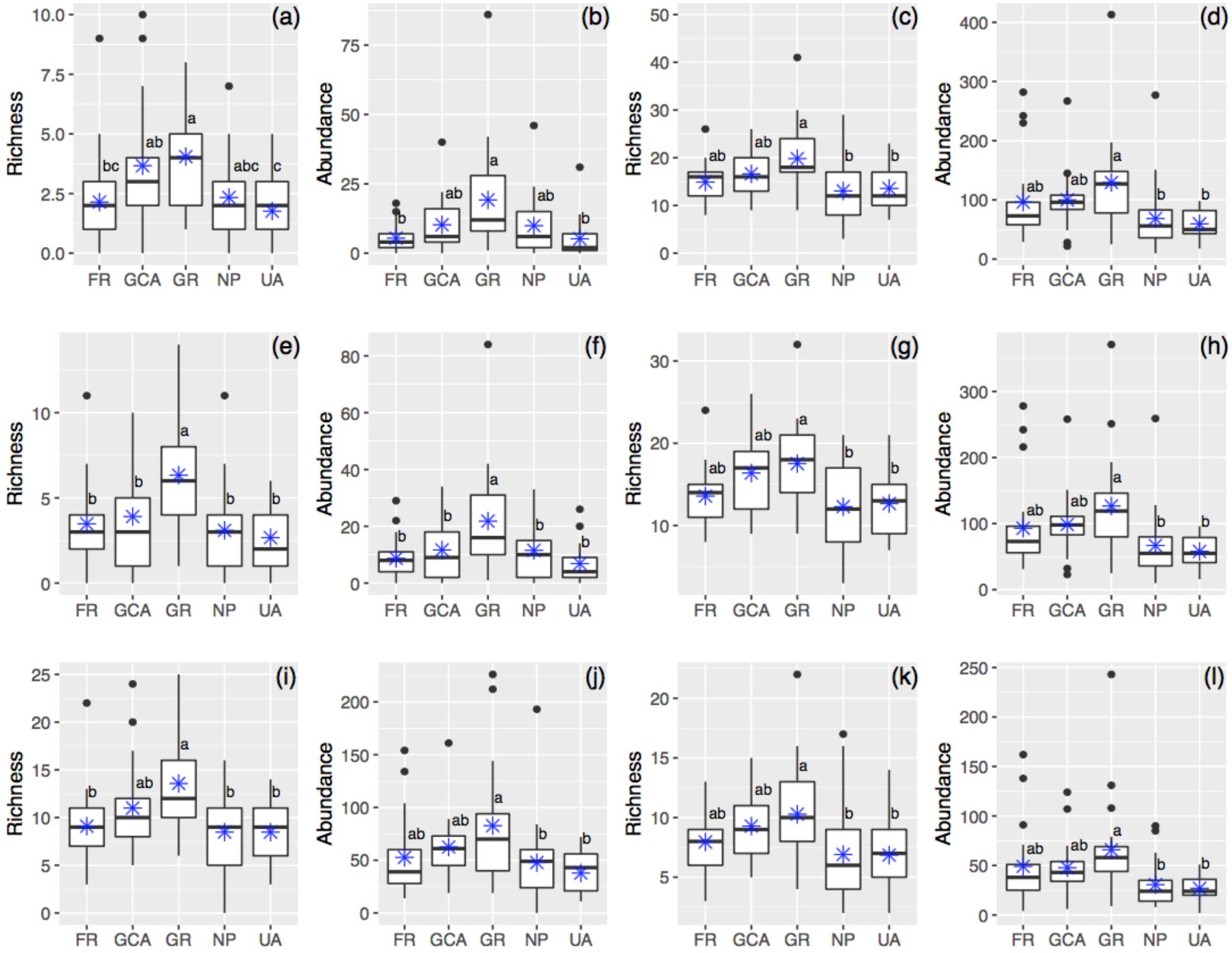

Fig. 3. Boxplots of species richness and abundance within functional groups [(a) and (b) Monophagous, (c) and (d) Polyphagous, (e) and (f) Habitat specialists, (g) and (h) Habitat generalists, (i) and (j) Small wingspan, (k) and (l) Large wingspan] in response to protection levels within the Katavi-Rukwa Ecosystem (FR, Forest Reserve; GCA, Game Controlled Area; GR, Game Reserve; NP, National Park; UA, Unprotected areas), western Tanzania. Different letters above the boxplots indicate significant differences between protection levels at $P < 0.05$ (Post-Hoc Tukey test).

3.2 Community composition across protection levels and land cover

Despite no complete species turnover (length of first axis = 2.89) in the DCA, species composition still varied significantly across all protection levels ($P < 0.001$, Df = 4): Species composition differed between NP and GR, between NP and GCA, between FR and GCA, between GR and UA, between FR and UA, and between GCA and UA (Table S3. However, species composition did not differ significantly between NP and FR, GCA, and

UA ($P > 0.05$; Table S3). Also, species composition in GR, and FR and GCA did not differ significantly ($P > 0.05$; Table S3). Thus, we find some differentiation between species composition across protection levels, but overall a large similarity. Likewise, we detected a significant variation in species composition across all land cover types ($P < 0.001$, Df = 2), with differing species composition between dense and open woodlands; and between dense woodland and farmland (Table S3). Some farmland transects seemed to differentiate most visibly from other transects (Fig. 4). However, species composition was similar between open woodland and farmland ($P > 0.05$; Table S3).

3.3 Responses of community composition and species richness to environmental variables

The variability on transect species composition extracted by DCA (Fig. 4) showed that a correlation of the first axis (Eigenvalue = 0.28) with composition heterogeneity, configurational heterogeneity and temperature to one side and to the enhanced vegetation index, forest cover, distances to houses and cropland, and elevation to the other side. Forest cover emerged as the most important variable driving the species composition. The second axis (Eigenvalue = 0.23) positively correlated to composition heterogeneity, configurational heterogeneity, and distance to houses; and negatively correlated to the enhanced vegetation index, forest cover, temperature, distance to cropland, and elevation. Total species richness and species richness within some functional groups were related to enhanced vegetation index, forest cover, and configurational heterogeneity (Table 3). Total species richness and species richness within most functional groups were related to burned areas (Table 3). Total species richness was related to distance to houses and distance to cropland (Table 3). Species richness within some functional groups were associated to temperature, rainfall and elevation (Table 3).

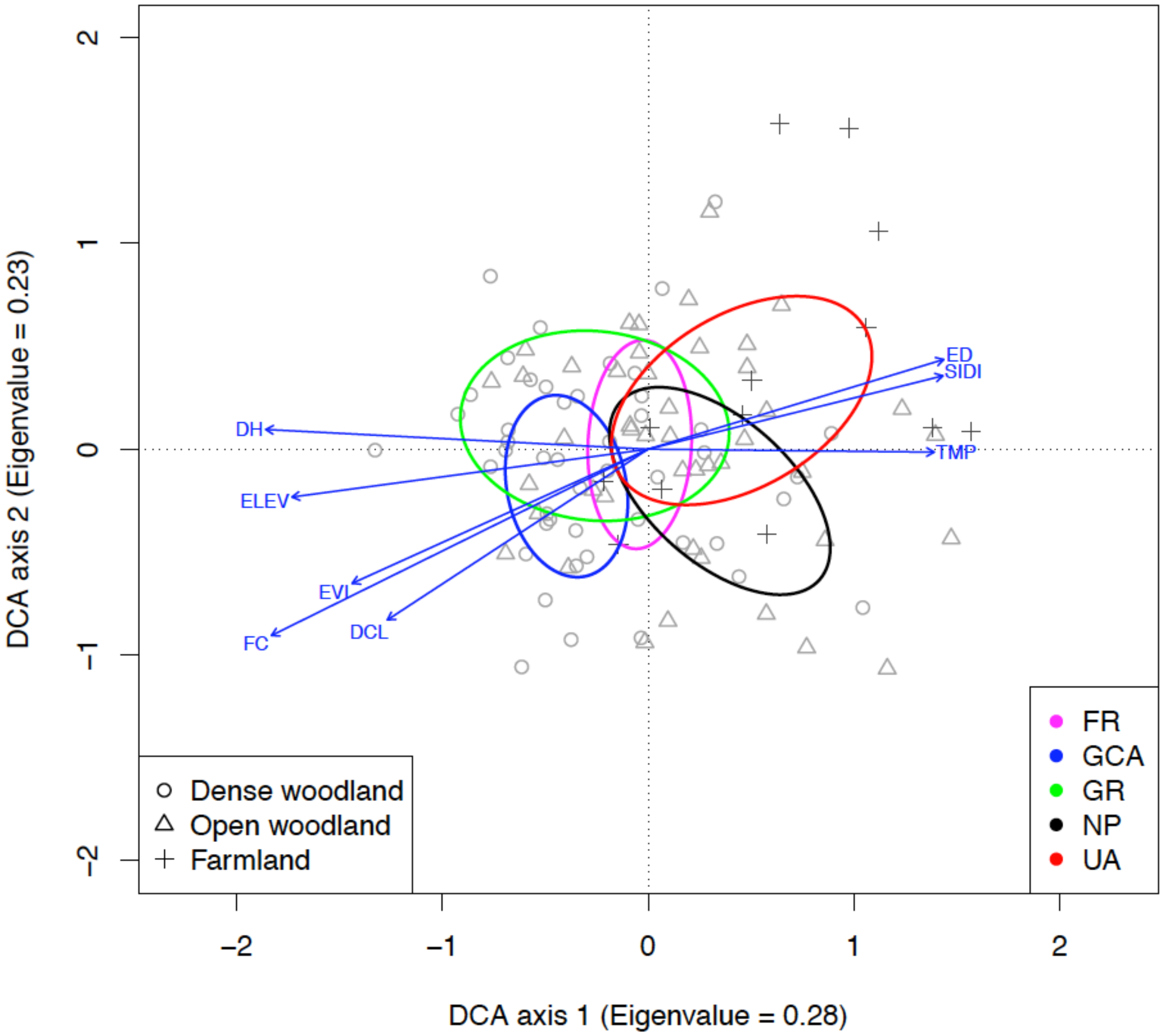

Fig. 4. DCA ordination plot of butterfly species, with significant environmental variables superimposed ($P < 0.05$) (Abbreviations: EVI, Enhance Vegetation Index; FC, Forest cover; DH, Distance to houses; ED, landscape configurational heterogeneity; TMP, Temperature; DCL, Distance to cropland; ELEV, Elevation; SIDI, landscape compositional heterogeneity).

Table 2: Summary statistics of generalized linear mixed-effects models describing associations between explanatory variables and the species richness with significance levels indicated by: ***$P < 0 .001$; **$P < 0.01$; *$P < 0.05$.

	Species richness	**Monophagous species**	**Polyphagous species**	**Specialists species**	**Generalists species**	**Large wingspan species**	**Small wingspan species**
Intercept	2.882	1.046	2.723	1.329	2.651	2.079	3.955
BA	-0.128***	ns	-0.123**	-0.377***	-0.135**	-0.121*	-0.377***
EVI	0.155***	0.271**	ns	0.234**	0.119***	ns	0.186**
FC	ns	ns	0.113**	ns	ns	0.155***	ns
AR	ns	-0.153*	ns	ns	ns	ns	ns
DH	0.075**	ns	ns	ns	ns	0.098**	ns
ED	0.056*	ns	ns	ns	ns	ns	ns
TMP	ns	ns	-0.084*	-0.289*	ns	ns	ns
DCL	0.066*	ns	ns	ns	0.069*	ns	0.251***
ELEV	ns	ns	ns	-0.222*	ns	ns	-0.119*

Abbreviations: BA, Burned areas; EVI, Enhance Vegetation Index; FC, Forest cover; AR, Annual rainfall; DH, Distance to houses; ED, Edge density; TMP, Temperature; DCL, Distance to cropland; ELEV, Elevation; ns, not significant.

3.4 Additive partitioning of diversity

Spatially hierarchical partitioning of butterfly species richness showed that β-diversity contributed with 89 % of the diversity within the community, whereas α-diversity (average richness within transect – α1) represented 11 % of the sampled community (Table 2). The β-diversity among transects within protection level (β1) accounted for 44 %, while the β-diversity among protection levels (β2) accounted for 45 % of the total diversity (γ, Table 2). When comparing the observed and the expected species richness results, we observed that only β2-diversity is higher than expected at random (OBS = 77.60, EXPS = 46.88, $P < 0.001$), while β1-diversity is significantly lower than the expected at random (OBS = 76.01, EXPS = 90.54, $P < 0.001$). Similarly, the α-diversity is lower than expected at random (OBS = 18.39, EXPS = 34.62, $P < 0.001$; Table 2).

Table 3: Spatial partitioning of the assemblage of butterflies at different scales (α- within transects, β1- among transects, β2- between protection levels in RKE. The expected value is the mean of the null distribution by 999 randomizations to which observed values can be compared with significance levels indicated by: ***$P < 0$ .001; **$P < 0.01$; *$P < 0.05$.

Index	Scales		Observed	%	Expected	P-value
Richness						
	α	Within transect	18.39	10.69	34.62	0.001***
	β1	Among transects	76.01	44.19	90.50	0.001***
	β2	Among protection levels	77.60	45.12	46.88	0.001***
	γ	Total	172.00	100.00	172.00	

3.5 Indicator species

We identified 11 indicator butterfly species across all five protection levels (Table 4), out of which seven species were both generalist and polyphagous with small wingspan (*Bicyclus dentatus, Eurema desjardinsii, Heteropsis simonsii, Lampides boeticus*) and big wingspan (*Phalanta phalantha, Papilio demodocus, Vanessa cardui*), three species were both specialist and monophagous with small wingspan (*Euryphura concordia, Colotis danae, Neptis jordani*), and one species was a generalist but monophagous with small wingspan (*Dixeia pigea*). Six species were associated with GR, two species with UA, one with NP, one with FR, and one with GCA (Table 4).

Table 4: Indicator species across levels of protection (IV = Indicator Value, significance levels indicated by: ***$P < 0$ .001; **$P < 0.01$; *$P < 0.05$.

FR			GCA			GR			NP			UA		
Species	**IV**	**P-value**	**Species**	**IV**	**P-value**	**Species**	**IV**	**P-value**	**Species**	**IV**	**P-value**	**Species**	**IV**	**P-value**
Phalanta phalantha	0.324	0.0061**	*Dixeia pigea*	0.43	0.0007***	*Euryphura concordia*	0.403	0.0006***	*Colotis danae annae*	0.35	0.0042**	*Vanessa cardui*	0.359	0.0019**
						Lampides boeticus	0.38	0.0011**				*Papilio demodocus*	0.282	0.044*
						Eurema desjardinsii marshalli	0.344	0.0009***						
						Heteropsis simonsii	0.343	0.0006***						
						Bicyclus dentatus	0.32	0.01670*						
						Neptis jordani	0.293	0.0016**						

4. Discussion

Our butterfly diversity patterns analyses covering areas with different protection level, ranging from unprotected to strictly protected in western Tanzania suggest that less strictly protected areas can be species-rich, and species richness and composition are mediated by multiple anthropogenic and environmental variables at the landscape level.

4.1 Species richness and community composition

Our analyses revealed that butterfly species richness and abundance did not decline systematically along a gradient of decreasing conservation protection (i.e., in this order NP>GR>FR>GCA>UA), and species numbers and in contrast to our expectation, butterfly abundances were not systematically higher in the NP. We even found that areas that allow regulated resource extraction (i.e., GR, FR, GCA) are more species-rich and abundant than strictly protected areas (i.e., NP, Table 2 & Fig 2). Less species richness and abundance in the NP is likely linked to the influence of late burning observed during butterfly surveys though it is used as a management tool in the NP. This observation stands in contrast to other studies that have detected differing patterns of butterfly species richness and abundance according to their mobility across a gradient of time since fires (Mason et al., 2021; Topp et al., 2022). It would thus be interesting to study the effect of fire on patterns in butterfly diversity over time in the KRE. Our findings indicated that species richness and abundance was similarly high in NP and UA (Fig 2). This highlights that human dominated landscapes on UA may host substantial numbers of butterfly species richness and abundances, which might be enabled by the mosaic of fallow land and remnants of natural vegetation (i.e., miombo woodland). This mosaic of low-intensity agricultural landscapes may contain habitat patches for butterflies (Bennett et al., 2006; Loos et al., 2022; Wurz et al., 2022). However, those four species exclusively occurring on farmland are widely distributed, generalist species (Martins and Collins, 2016; Woodhall, 2020), which questions whether farmland within the miombo ecoregion might be considered highly valuable habitat for specific butterfly species. Notwithstanding, those 55 species that used both woodland and farmland express a suitability of farmland for occurrences of many different species, which calls for the maintenance of the rather small-scale agricultural structures, which became visible by the heterogeneity variables driving species richness and species community patterns (Loos et al., 2014a; Wurz et al., 2022). Previous studies have demonstrated that small-scale farming profits biodiversity by supporting diverse resources for butterflies (Loos et al., 2014b; Wurz et al., 2022). We found differences in species composition between less strictly protected areas (e.g., GR, GCA) and strictly protected areas (e.g., NP), likely due to differences in vegetation composition in these areas. Unlike NP, GR and GCA were largely covered by dense woodland dominated by miombo. Considering land cover, we found higher species richness and abundances in dense woodland than in open woodland and farmland. A possible explanation for this pattern may be the high availability flowering plants, litter, debris and microhabitat conditions observed during dry season butterfly survey and many host plants occur in denser forest cover (Curtis et al., 2015; Jew et al., 2015; Loos et al., 2014b; Nkwabi et al., 2021; Schmitt et al., 2020).

4.2 Response of species richness to environmental variables

We found that butterfly species richness was associated with enhanced vegetation index and forest cover. High enhanced vegetation index and forest cover indicate dense woodland that could offer diverse resources for butterflies (Curtis et al., 2015; Jew et al., 2015; Munyuli, 2013; Nkwabi et al., 2021). This was evidenced by the high richness and abundance of butterfly within dense woodland areas compared to open woodland and farmland. Furthermore, butterfly species richness was associated to distance to cropland and houses, suggesting that species richness increases with increasing distance to anthropogenic structures (i.e., human settlements). This pattern might be likely due to large distances between habitat patches in farmland (Loos et al., 2014c, 2022) as well as the use of pesticides, which we observed during butterfly surveys within farmland, and the related limitation in flowering plants (Tambara et al., 2013). We found that butterfly species richness was significantly negatively associated with annual rainfall, annual temperature, and elevation, suggesting that species richness was lower in areas with higher elevation, rainfall and temperature. A possible explanation for this is that areas with high elevation and rainfall are associated with elevated hilly rocky areas whereas areas with high temperature associated with cultivated areas, which recorded low enhanced vegetation index and forest cover. Temperature and precipitation, which in turn moderated by elevation are well known to influence butterfly abundance and species richness (Acharya and Vijayan, 2015; Kucherov et al., 2021; Pires et al., 2020; Rija, 2022). We found that butterfly species richness significantly positively associated with landscape configurational heterogeneity represented by edge density, suggesting that species richness increases with increasing edge density. Likely, this pattern might be explained by the increased availability of herbaceous vegetation along habitat edges, which resulted from a certain level of habitat fragmentation (Fahrig et al., 2011; Loos et al., 2014b; Rossi and Van Halder, 2010).

4.3 Additive partitioning of diversity

Contributions of α-diversity and β-diversity to γ-diversity form the root for understanding the biodiversity components at different spatial scales (Crist et al., 2003; Meynard et al., 2011; Zhang et al., 2014). We found significantly higher contribution of β2-diversity (i.e., among protection levels) than α-diversity (i.e., within transect) to γ-diversity (i.e., region) (Table 2). This suggests that butterfly diversity in the region may benefit most from managing several areas with different conservation category including unprotected areas. Increasing our understanding of how α and β-diversity vary across spatial scales could help in choosing the appropriate spatial scale for species conservation (Crist et al., 2003; Gering et al., 2003).

4.4 Indicator species

Determining a set of indicator species is vital in long-term environmental monitoring for conservation and biodiversity management (De Caceres et al., 2012; Rossi and Van Halder, 2010; Sharma et al., 2020). We found 11 indicator butterfly species associating with different protection levels in the region that can be useful for future monitoring and assessment of biodiversity in the ecologically sensitive region of KRE. These indicator species were mostly habitat generalist and polyphagous. However, a few indicator species were habitat specialists, monophagous and had a small wingspan (*Euryphula concordia, Colotis danae, Neptis jordani*), which suggests limited dispersal ability and high dependence on specific habitat that may occur only under specific environmental conditions (Tiple et al., 2011). Previous studies have shown that the plant-abundance relationship is mediated by butterfly traits and it is strongest for species that are habitat specialist, monophagous, and less mobile (Curtis et al., 2015; Dainese et al., 2017).

Conclusions

Conserving biodiversity across areas with different conservation category, ranging from unprotected to strictly protected is vital for the long-term persistence of invertebrate taxa, such as butterflies. Our investigations on butterfly diversity patterns suggest that less strictly protected areas in the KRE are more species rich than strictly protected areas. Our findings on additive partitioning of diversity could help in the conservation of butterfly diversity at multiple spatial scales in the region. To reinforce butterfly conservation in the KRE, as proactive strategies, we recommend the implementation and enforcement of site-specific land-use planning to reduce direct threats to butterfly diversity, maintain both woodland and heterogeneity, and avoid homogenization through monocultures and deforestation in the KRE.

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Supplementary Information

Table S1: Cross-tabulation error matrix for 2021 land cover classification in Katavi-Rukwa Ecosystem (KRE) western Tanzania.

Land cover 2021	Dense woodland	Open woodland	Burned area	Cropland	Water bodies	Total	User accuracy
Dense woodland	98	2	0	0	0	100	0.980
Open woodland	1	98	1	0	0	100	0.980
Burned area	0	1	98	1	0	100	0.980
Cropland	0	1	2	97	0	100	0.970
Water bodies	0	0	0	0	100	100	1.000
Total	99	102	101	98	100	500	
Producer accuracy	0.990	0.961	0.970	0.990	1.000		
Overall accuracy							0.982
Kappa							0.977

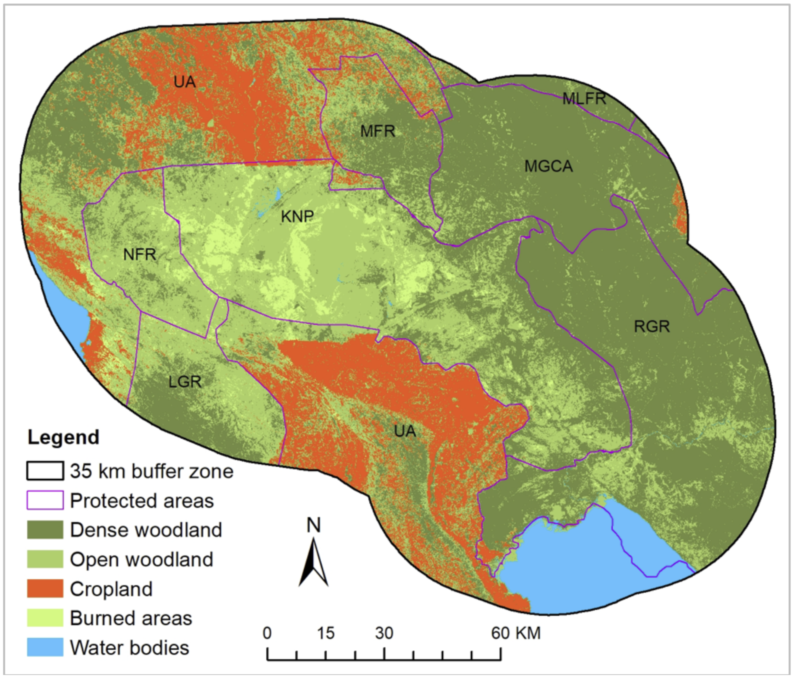

Fig. S1: Map of the study region, showing land cover distribution in protected and unprotected areas in 2021. Abbreviations: KNP = Katavi National Park, RGR = Rukwa Game Reserve, LGR = Lwafi Game Reserve, MGCA= Mlele Game Controlled Area, NFR= Nkamba Forest Reserve, MFR= Msaginia Forest Reserve, MLFR= Mpanda Line Forest Reserve, and UA= unprotected areas.

Table S2: Permutational multivariate analysis of variance (PERMANOVA) with Bray–Curtis dissimilarity and 999 permutations of species composition among protection levels (NP, National park; GR, Game reserve; FR, Forest reserve, GCA, game-controlled area; Unprotected areas, UA) and land cover (DW, Dense woodland; OW, open woodland; FL, Farmland) with pairwise comparisons with significance levels indicated by ***P < 0 .001; **P < 0.01; *P < 0.05.

Variable	***F*** **model**	***P*** **value**	**Multiple comparisons**	***P*** **value**
Protection levels	$F_{4,100} = 3.23$	< 0.001***	NP vs GR	0.020*
			NP vs FR	0.103
			NP vs GCA	0.032*
			NP vs UA	0.172
			GR vs FR	0.099
			GR vs GCA	0.273
			GR vs UA	< 0.001***
			FR vs GCA	0.025*
			FR vs UA	0.004**
			GCA vs UA	< 0.001***
Land cover	$F_{2,102} = 3.61$	< 0.001***	DW vs OW	0.006**
			DW vs FL	0.013*
			OW vs FL	0.099

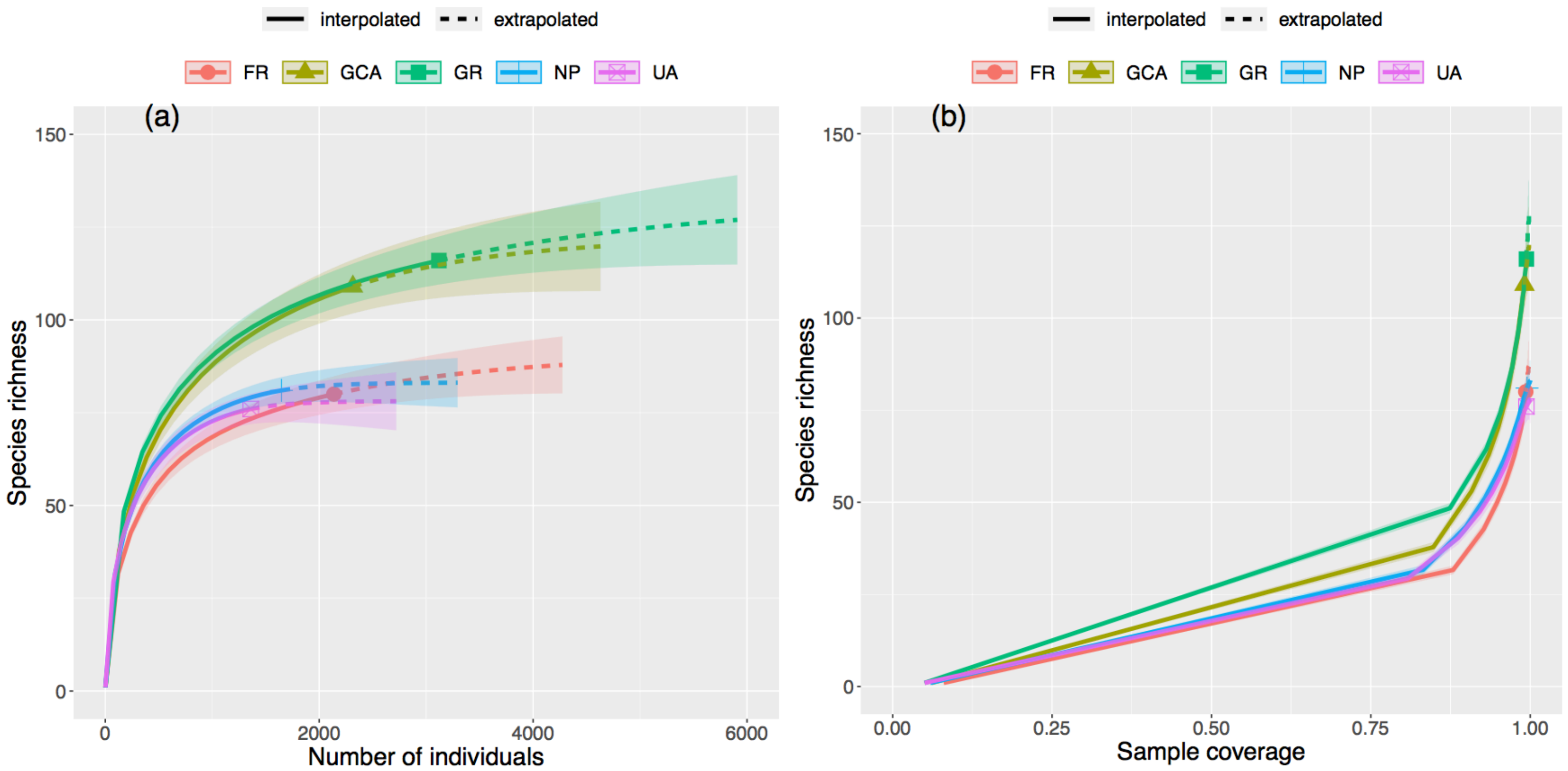

Fig. S2: Species richness at regional level across protection levels (Hill number q = 0), shown by the sized-based rarefaction and extrapolation curves (a) and sample coverage-based rarefaction and extrapolation curves (b). The solid line represents the interpolation, whereas the dashed line represents the extrapolation. The shaded region in (a) represents the 95% confidence intervals.

Chapter 3

Chapter 3

Using density surface models to assess the ecological effectiveness of a protected area network in Tanzania

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Abstract

Understanding the responses of wildlife populations across different area-based protection levels is crucial to estimating conservation effectiveness at the wider landscape. As wildlife populations are also influenced by environmental variables, such comparisons require accounting for environmental heterogeneity. To this end, we modelled the spatial distribution of six target mammal species across environmental and protection gradients in the Katavi-Rukwa Ecosystem, western Tanzania. We conducted line distance sampling surveys and counted dung of six target mammal species along foot transects within areas differing in protection levels (from strict to less strictly protected: national park, game reserve, forest reserve, game-controlled area, and unprotected areas). We modelled the spatial distribution of six mammal species (elephant, giraffe, buffalo, zebra, topi, hartebeest) in response to environmental variables and protection level using a density surface modelling framework. Based on species-specific density surface models, we found relatively consistent effects of protection level and land-use variables on the spatial distribution of the target mammal species: relative densities were highest in the national park and game reserves, intermediate in forest reserves and game-controlled areas, and lowest in unprotected areas. Beyond species-specific environmental predictors for relative densities, our results highlight consistent negative associations between relative densities of the target species and distance to cropland and avoidance of areas in proximity to houses. Our findings underpin differences in relative ecological effectiveness of protected areas within one ecosystem. Protection level and land-use play crucial roles in moderating the spatial distribution of all considered mammal species in the Katavi-Rukwa Ecosystem. Our findings suggest that a landscape approach needs to guide effective conservation across the entire protection gradient of the Katavi-Rukwa Ecosystem.

1. Introduction

Globally, and despite their ecological and economic values, large mammals are rapidly declining due to anthropogenic pressures (Geldmann et al., 2019, 2014; Ripple et al., 2015). Large mammal populations on the African continent (Craigie et al., 2010; WCMC-UNEP, 2016) and in Tanzania (Stoner et al., 2007) are no exceptions to this worrying global trend. To respond to increasing human pressures, protected and conserved areas (PCAs) are the main approach for safeguarding biodiversity including large mammals (CBD, 2022; IPBES, 2019). PCAs in Tanzania vary greatly in their protection levels, ranging from strictly protected (IUCN Categories I to V) to less strictly protected, permitting human activities and resource extraction to some extent (IUCN Category V; Caro & Davenport, 2016). However, their ecological effectiveness in protecting large mammals and natural habitat is challenged, mostly because of i) direct exploitation and habitat degradation inside protected areas, and ii) increasing isolation through habitat loss and other anthropogenic pressures in the wider landscape in which the PCAs are embedded (Caro, 2008; Giliba et al., 2022; Lobora et al., 2018; Martin et al., 2013). Thus, it is important to better understand the effectiveness of these different area-based protection levels not only by monitoring the distribution and abundance of wildlife inside PCAs, but also by quantifying wildlife populations in the wider landscape. Through spatially explicit information on wildlife densities, it may be possible to determine the effectiveness of the PCA network from a landscape perspective. However, assessing ecological effectiveness of PCAs based on average wildlife densities across space for one snapshot in time without controlling for environmental variables is challenging because environmental conditions [which may primarily determine the carrying capacity of a given species (e.g. Pettorelli et al., 2009)] vary between PCAs (Rosenblatt et al., 2019, 2016). Thus, it is necessary to disentangle whether differences in wildlife densities are due to inherent differences in environmental conditions or due to specific area-based conservation efforts (Waltert et al., 2009).

While a suite of wildlife detection methods are available, wildlife surveys are typically labor- and cost-intensive, or are difficult to implement over large spatial scales (Jachmann, 2002, 1991; Schwarz and Seber, 1999; Williams et al., 2002). Over the past 30 years, aerial counts have been widely used in wildlife monitoring within the

Katavi-Rukwa Ecosystem (Caro, 2016; Giliba et al., 2022; Stoner et al., 2007); however, the estimates derived from aerial counts are typically lower than estimates from ground counts due to sighting and visibility bias (Greene et al., 2017; Jachmann, 2002, 1991). To overcome potential bias associated with aerial surveys, terrestrial line surveys have been suggested for wildlife monitoring and applied within the study region to estimate wildlife densities across different protected areas (Caro, 1999a, 1999b). However, these surveys were conducted along the existing road network and this non-random placement of sample units may yield biased density estimates (Kiffner et al., 2022b; Waltert et al., 2008). To address the shortcomings of systematic aerial surveys and of road counts, foot counts along systematically distributed transects have been used to estimate wildlife in Katavi National Park and Rukwa Game Reserve (Waltert et al., 2008). However, walking transects carried out in the ecosystem yielded sufficient number of detections for few species only: despite more than 1000 km of walking transect effort, only four species were detected > 60 times (Waltert et al., 2008), which is the recommended threshold for estimating robust detection functions in a line distance sampling framework (Buckland et al., 2001; Thomas et al., 2010).

The low detection rates from direct counts could be partially due to animal behavior, which itself can be mediated by protection level. For instance, animals may be relatively indifferent towards human observers inside strictly PCAs but very skittish (and thus less likely to be detected) in less strictly in PCAs where legal or illegal hunting takes place (Caro, 2005). In addition, species may adjust their diel use of certain areas and use human-dominated areas primarily during nighttime (de Jonge et al., 2022). Thus, relying on direct sightings during daytime to estimate wildlife density along a protection gradient could be biased due to variation in animal behavior. A solution for this is the use indirect survey methods such as dung surveys (Jachmann, 1991; Kiffner et al., 2019).

To address our overarching goal of providing robust information on the ecological effectiveness of different PCAs across western Tanzania, we combined data from a systematic dung survey and remotely sensed data to quantify relative wildlife densities using a spatially explicit density surface modelling framework (Miller et al., 2013). We focused our analyses on six numerically dominant terrestrial mammal species in the ecosystem (Caro, 2008; Caro, 1999a), which can reliably be monitored through indirect ground surveys: buffalo *Syncerus caffer*, elephant *Loxodonta africana*, giraffe *Giraffa camelopardalis*, hartebeest *Alcelaphus buselaphus*, topi *Damaliscus korrigum*, and zebra *Equus burchellii*;. We hypothesized that, while accounting for environmental conditions which could influence species-specific relative densities, the relative densities of target species would consistently be higher in strictly protected areas. We designed our study to deliver spatially explicit information on the distribution of selected mammal species that are of interest to conservation and that allow an evidence base for comparing the ecological effectiveness of a PCA network across a Miombo ecosystem.

2. Methods

2.1 Study area

Our study focused on the Katavi-Rukwa Ecosystem in western Tanzania, which covers 20,961 km^2 and contains PCAs with different designation. The study area lies between 6° to 7° S and 30° to 31° E (Fig. 1), and is characterized by a mosaic of unprotected areas (UA, i.e. land that does not have a formal conservation category), and formally protected areas. Protection categories range from areas with little enforcement of human land-use restrictions (Game Controlled Areas, GCA: here, settlement, agriculture, livestock keeping are not allowed, but hunting on permit in specific hunting blocks is allowed), areas that allow regulated resource extractions such as Forest Reserves (FR, here, limited timber and non-timber products extraction is permitted) and Game Reserves (GR, here, tourist game hunting on permit is allowed) to strictly protected national parks (NP) where human activities are restricted to photographic tourism and research (Caro & Davenport, 2016; Caro, 1999a). The study area includes multiple PCAs, and we centred this study around Katavi National Park (KNP), the adjacent Rukwa Game Reserve (RGR), Lwafi Game Reserve (LGR), Mlele Game Controlled Area (GCA), Mpanda Line Forest Reserve, Msaginia Forest Reserve (MFR), and Nkamba Forest Reserve (NKF) (Fig. 1).

The Katavi-Rukwa Ecosystem receives an annual rainfall between 800 - 1200 mm, while the temperature ranges between 17 - 26 °C. Elevation ranges from 600-1800 m asl. The soil types range from alluvial soils (black cotton soils) in flood plains to loamy soils in areas that are not seasonally inundated. The vegetation consists of miombo woodlands in non-inundated areas and grasslands in the flood plains (Banda et al., 2006). Miombo forms a single story, with open canopy of deciduous woodland dominated by trees of the genera *Brachystegia, Julbernadia,* and *Isoberlinia* (Campbell, 1996). The human population in the Katavi-Rukwa Ecosystem has rapidly grown due to increasing migration of pastoralist from other regions over the past 40 years (Izumi, 2017; Salerno, 2016). Agriculture and livestock keeping are the main land-use activities (Caro, 1999a). Rice farming is restricted to river terraces and flood plains while shifting cultivation for other crops such as maize, cotton and tobacco, is practiced in areas were natural vegetation had previously been cleared (Giliba et al., 2022; Jew et al., 2015).

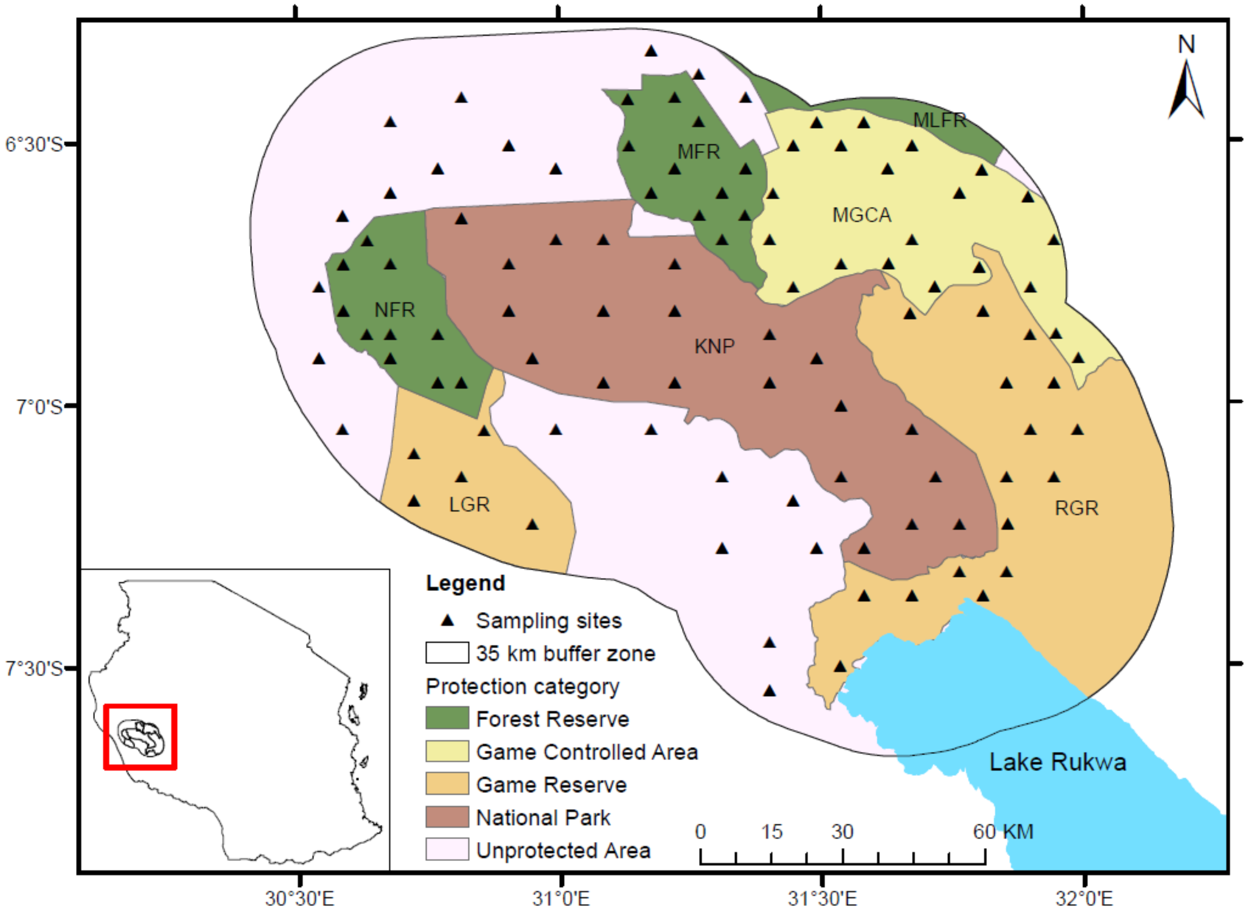
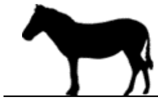


Fig. 1. Map of the study area, highlighting the spatial distribution of wildlife dung sampling sites (triangular transects with three sections of 1 km length each) across protection levels (KNP = Katavi National Park, RGR = Rukwa Game Reserve, LGR = Lwafi Game Reserve, MGCA= Mlele Game Controlled Area, NFR= Nkamba Forest Reserve, MFR= Msaginia Forest Reserve, MLFR= Mpanda Line Forest Reserve). The inset in the lower left shows the location of the study area within Tanzania, whereas the insert middle left shows the transect walks navigation.

2.2 Field survey

We established a 35 km buffer around the boundary of KNP to include areas with different protection levels, ranging from unprotected to strictly protected. To capture an even coverage of transects across different protection levels, we divided our study area into 5 km by 5 km grids, so that transects were separated by 5 km to minimize spatial autocorrelation of the data. We randomly selected 105 grids (21 grids within each protection level) and placed triangular-shaped transects of 3 km total length in the centre of each selected grid. To ease logistics in the field (see Waltert et al., 2008), we opted for 1 km segment length (Fig. 1). We surveyed each transect once during the dry season between July and September 2021. Three people (one each primarily responsible for navigating, observing, and recording) walked along the transect. We used a handheld GPS and compass to navigate between segments (i.e. we moved towards 90° E in the first segment, 330° NW in the second segment, and 210° SW in the third segment; Fig. 1). In each transect, we counted and recorded the number of individual dung piles. To measure perpendicular distances from the centre of a dung pile to the centre line of a transect, we used a tape measure. To define the centre line of the transect (and avoid rounding of distances near the line to zero), we used a walking stick (Marques et al., 2001). Upon detection, we identified each dung pile to species level. Before the formal survey, we conducted a literature review and a pilot survey to establish species-specific dung pile definitions based on the shape of pellets and quantity of pellets per dung pile (Table 1).

Table 1: Attributes used to define individual dung piles for each target species based on number/pile and shape of pellets in the Katavi-Rukwa Ecosystem, western Tanzania.

Species	**Sample size**	**Minimum no. of pellets/ pile**	**Maximum no. of pellets/ pile**	**Median no. of pellets/ pile**	**Mean no. of pellets/ pile**	**Standard error**	**Pellets shape**
Buffalo 	12	1	2	1	1.16	0.11	Thick pancake-like pellets, very variable size and structure (Stuart and Stuart, 2019).
Elephant 	12	3	6	4	4.42	0.28	Large barrel-shaped pellets (over 10 cm in diameter) accumulate in large dung heaps or partially broken up (Stuart and Stuart, 2019).
Giraffe 	12	109	185	145	148.83	7.68	Roughly spherical pellets usually in scattered heaps, pellets pointed at one end (Stuart and Stuart, 2019).
Hartebeest 	12	107	226	171	162.67	12.44	Roughly spherical or cylindrical commonly in heaps, pellets pointed at one end, diameter is relatively wider compared to topi (Hibert et al., 2008).
Topi 	12	103	216	153	154.25	10.28	Roughly spherical or cylindrical commonly in heaps, pellets pointed at one end, diameter is relatively smaller compared to hartebeest (Hibert et al., 2008).
Zebra 	12	10	32	22	22.67	2.12	Several separate kidney-like shape pellets with central vertical groove (Stuart and Stuart, 2019).

2.3 Estimating relative animal densities

We analysed the data in a density surface modelling framework, a two-stage method which first accounts for uncertain detectability (primarily as a function of distance between transect and observations; Thomas et al., 2010) and a spatial model of the density of the target population (Miller et al., 2013). We used the function `ds´ in the R package `distance´ (Miller and Lawrence, 2022) to fit species-specific global detection functions. Due to low sample sizes per PCA category, we pooled species-specific sightings of dung piles across all protection levels to fit global detection functions (Thomas et al., 2010). We truncated the farthest 10% of observations (Buckland et al., 2001), and fitted three models for each species: 1. half-normal with no adjustment terms, 2. uniform with cosine adjustment, and 3. hazard-rate with cosine adjustment (Table 2). For all six species, we selected the half-normal function due to formal fit criteria (high chi-squared goodness-of-fit value), low AIC values (Table 2), adequate visual fit (Fig. 2), and evidence that half-normal detection functions typically yield unbiased estimates (Prieto Gonzalez et al., 2017).

Table 2: Parameters for the different models fitted to estimates relative densities of six target species surveyed on foot in the Katavi-Rukwa Ecosystem, western Tanzania. GOF stands for chi-squared goodness of fit, SE for standard error, and AIC for Akaike information criterion.

Species	Model	Truncation distance (%)	GOF p-value	Average detectability	SE (Average detectability)	Delta AIC
(a) Buffalo						
	Half-normal	10	0.058	0.632	0.030	0.000
	Uniform	10	0.064	0.619	0.025	0.001
	Hazard-rate	10	0.073	0.590	0.050	2.985
(b) Elephant						
	Half-normal	10	0.063	0.758	0.036	0.000
	Uniform	10	0.060	0.729	0.036	0.278
	Hazard-rate	10	0.071	0.723	0.061	2.891
(c) Giraffe						
	Half-normal	10	0.064	0.580	0.030	0.000
	Hazard-rate	10	0.092	0.517	0.042	0.806
	Uniform	10	0.064	0.578	0.023	2.405
(d) Hartebeest						
	Uniform	10	0.049	0.737	0.041	0.000
	Half-normal	10	0.052	0.773	0.041	1.414
	Hazard-rate	10	0.050	0.798	0.056	3.235
(e) Topi						
	Hazard-rate	10	0.001	0.026	0.006	0.000
	Uniform	10	0.067	0.648	0.065	13.825
	Half-normal	10	0.059	0.679	0.071	15.497
(f) Zebra						
	Uniform	10	0.070	0.602	0.027	0.000
	Half-normal	10	0.064	0.610	0.033	0.707
	Hazard-rate	10	0.078	0.602	0.054	1.892

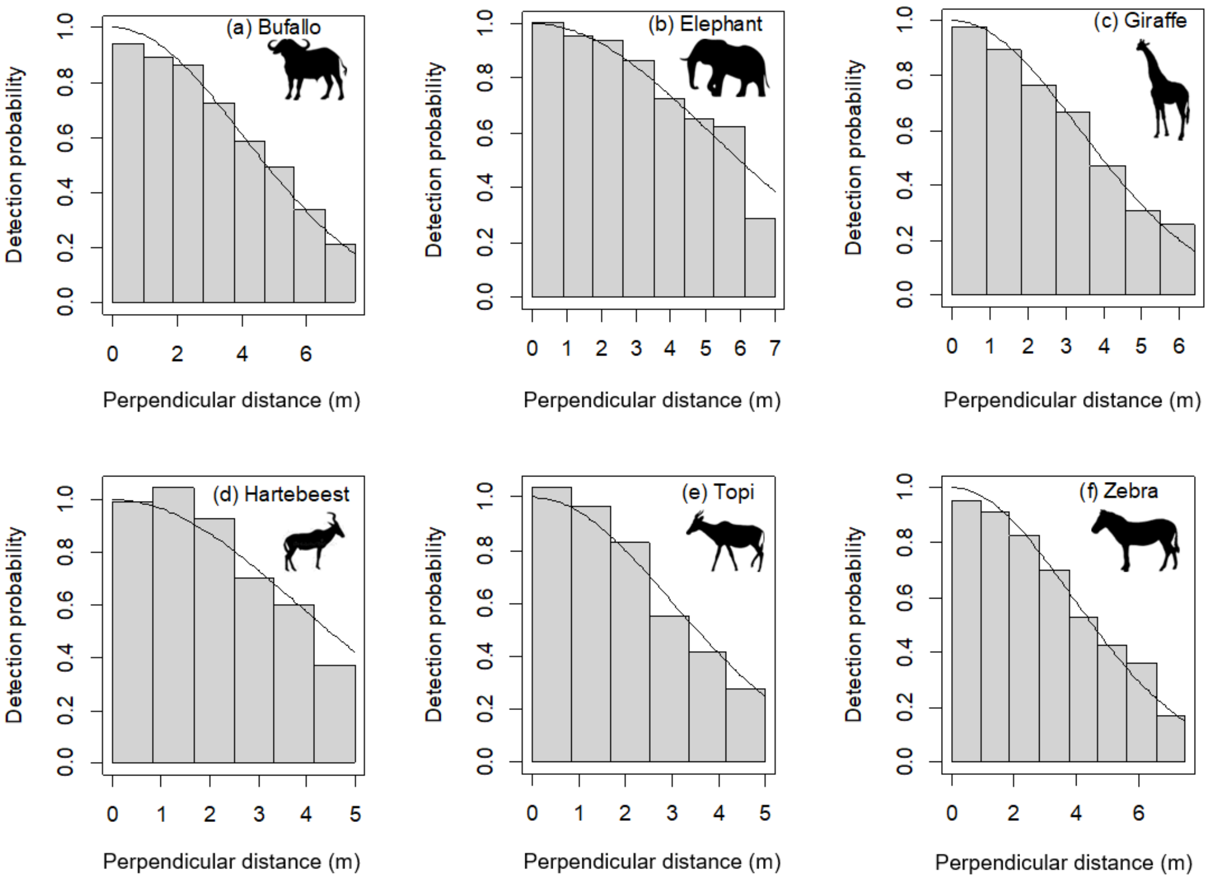


Fig. 2. Detection functions (black line) of conventional distance sampling models for (a) buffalo, (b) elephant, (c) giraffe, (d) hartebeest, (e) topi, and (f) zebra sighted along foot transects in the Katavi-Rukwa Ecosystem in western Tanzania. The histograms (grey bars) show the observed frequency of dung sightings against perpendicular distance; detection functions were modelled using half-normal key functions.

2.3 Density surface modelling

To model the spatial distribution of the relative densities of the six target species, we used the function `dsm´ in the R package ´density surface modelling (DSM)´ (Miller et al., 2022). In a first step, based on hypothesized relationships between the distribution of large savanna mammals in Tanzanian ecosystems and landscape features (Bond et al., 2017; Giliba et al., 2022; Van de Perre et al., 2014), we selected the following landscape variables for our spatially explicit models: the five-level categorical variable protection level (as an indicator of ecological effectiveness), and the following numerical variables to account for environmental heterogeneity: elevation, slope, rainfall, distance to cropland, houses, rivers and Enhanced Vegetation Index (EVI). We choose

EVI as a proxy for primary productivity due to its advantages of reducing the background noise, atmospheric noise, and saturation in most cases compared to NDVI (Huete et al., 2002). We extracted elevation and slope data from SRTM digital elevation model from the U.S. Geological Survey (https://earthexplorer.usgs.gov), and annual rainfall data from CHIRPS (https://data.chc.ucsb.edu/products/CHIRPS-2.0/, using ArcMap 10.6 (ESRI, 2018). We quantified proximity to rivers and houses from spatial features obtained from OpenStreetMap (http://download.geofabrik.de/africa/tanzania.html), and proximity to cropland from 2021 land cover map generated by Giliba et al. (2022) in ArcMap 10.6 (ESRI, 2018), and EVI from Google Earth Engine - Landsat 8 Collection 1 Tier 1 8-Day EVI Composite (Gorelick et al., 2017). In a first step prior to the DSM, all spatial layers were resampled to a 1 km resolution to overlap with our transects of 1 km segment length in ArcMap 10.6 (ESRI, 2018). Moreover, all numerical explanatory variables were scaled to mean zero and unit variance and tested for collinearity. For model fitting, we retained all variables because none of the variable dyads exceeded the (r) ≥ 0.7 (Pearson's correlation coefficient) threshold (Dormann et al., 2013). In a second step, we prepared the segment data (table with sample label identifier for the segments, effort/length of segment, and the landscape variables, observation data (table with unique object identifier, sample label identifier for the segment where observation occurred, dung counts and distance to observations), and prediction data (a table/grid holds all the potential landscape variables for prediction). In a third step, we modelled species-specific density and spatial distribution as a sum of spline smooth functions for the selected landscape variables using a generalized additive models with Tweedie family (Miller et al., 2013; Wood, 2017). This probability distribution is able to deal with zero-inflated data (Peel et al., 2013; Strindberg et al., 2018), a prerequisite for our data that contained many transects without any sightings, particularly in unprotected areas. We used the stepwise backward selection procedure for variable selection ($P > 0.05$ as criteria for removing non-significant variables) within generalized additive models (Marra and Wood, 2011).

3. Results

After controlling for associations with fine-scaled (1 km resolution) environmental and anthropogenic variables, our density surface models generally revealed that protection level was positively correlated with species-specific relative densities: among all target species, relative densities were highest in either the national park (buffalo, giraffe, topi, zebra) or game reserves (elephant, hartebeest) and lowest in the unprotected areas (Table 3).

The density surface model for buffalo suggested that relative buffalo densities increased with increasing distance from cropland and rivers, and was positively associated with EVI, and slope; elevation and distance to houses showed hump-shaped relationships with relative buffalo densities (Fig. S1a). Controlling for these associations, relative buffalo densities were highest in the national park, followed by the game reserves, forest reserves, game-controlled areas, and unprotected areas had by far the lowest relative densities (Table 3a). Similarly, relative elephant densities increased with distance to cropland and rivers, and were negatively associated with slope and showed a hump-shaped relationship with distance to houses (Fig. S1b). Beyond these associations, their relative densities were greatest in game reserves, closely followed by the national park; game-controlled areas and forest reserves had intermediate relative elephant densities (Table 3b). Unprotected areas had the lowest relative densities (Table 3b).

The density surface model for giraffe suggested that their relative densities increased with distance from cropland and rivers; relative densities were negatively associated with the amount of precipitation and followed a hump-shaped curve with EVI (Fig. S1c). Controlling for these associations, relative giraffe densities were highest in the national park, followed by the forest reserves, game reserves, game-controlled areas, and unprotected areas had by far the lowest relative densities (Table 3c). Relative hartebeest densities increased with distance to houses and rivers, and decreased with EVI (Fig. S1d). Beyond these associations, their relative densities were greatest in game reserves, closely followed by the national park, forest reserves, game-controlled areas. Unprotected areas had lowest relative densities (Table 3d).

Relative densities of topi decreased with EVI and showed a hump-shaped association with distance to houses (Fig. S1e). Controlling for these associations, relative topi densities were highest in the national park, followed by the game-controlled areas, forest reserves, game reserves; unprotected areas had the lowest relative densities (Table 3e). The density surface model for zebra suggested that their relative densities increased with increasing distance to cropland, was positively associated with slope, and decreased with increasing distance from rivers (Fig. S1f). Beyond these associations, their relative densities of zebra were greatest in the national park followed by the game reserves, forest reserves, game-controlled areas; unprotected areas had the lowest relative densities (Table 3f).

Table 3. Parameter estimates of density surface models (parameterized as general additive models) to describe relative densities of target species across protection levels while accounting for environmental variables in the Katavi-Rukwa Ecosystem, western Tanzania. Protection level was defined as factor whereas the baseline variables is national park (NP).

(a) Buffalo

Parametric variable	Estimate	SE	t-value	p-value
Intercept	-3.472	0.1815	-19.127	<0.001***
Protection level FR	-1.153	0.2758	-4.180	<0.001***
Protection level GCA	-2.149	0.504	-4.263	<0.001***
Protection level GR	-1.136	0.3584	-3.170	0.002**
Protection level UA	-87.92	6980000	0.000	0.999
Smooth term	**Estimated df**	**F-value**	**p-value**	
Distance to cropland	4.158	3.004	<0.001***	
Distance to houses	4.927	3.476	<0.001***	
Elevation	4.007	2.303	<0.001***	
EVI	1.506	0.584	0.019*	
Slope	2.104	1.18	0.001**	
Distance to rivers	2.156	0.805	0.011*	

(b) Elephant

Parametric variable	Estimate	SE	t-value	p-value
Intercept	-3.724	0.089	-41.892	<0.001***
Protection level FR	-0.534	0.184	-2.907	0.004**
Protection level GCA	-0.218	0.242	-0.899	0.369
Protection level GR	0.174	0.115	1.522	0.129
Protection level UA	-1.013	0.279	-3.632	<0.001***
Smooth term	**Estimated df**	**F-value**	**p-value**	
Distance to cropland	0.800	0.439	0.023*	
Distance to houses	4.929	4.109	<0.001***	
Distance to rivers	0.861	0.435	0.024*	
Slope	0.775	0.366	0.034*	

(c) Giraffe

Parametric variable	Estimate	SE	t-value	p-value
Intercept	-3.433	0.101	-34.159	<0.001***
Protection level FR	-0.271	0.252	-1.077	0.282
Protection level GCA	-0.827	0.307	-2.696	0.007**
Protection level GR	-0.432	0.173	-2.495	0.013*
Protection level UA	-86.140	6992000	0.000	0.999
Smooth term	**Estimated df**	**F-value**	**p-value**	
Distance to cropland	1.882	1.144	0.002**	
Rainfall	2.388	0.703	0.040*	
EVI	1.887	0.742	0.018*	
Distance to rivers	0.931	1.470	<0.001**	

(d) Hartebeest

Parametric variable	Estimate	SE	t-value	p-value
Intercept	-3.205	0.114	-28.003	<0.001***
Protection level FR	-0.051	0.178	-0.287	0.774
Protection level GCA	-0.406	0.190	-2.136	0.033*
Protection level GR	0.026	0.150	0.173	0.863
Protection level UA	-2.791	0.588	-4.748	<0.001***
Smooth term	**Estimated df**	**F-value**	**p-value**	
Distance to houses	2.524	1.620	<0.001***	
EVI	1.037	0.350	0.047*	
Distance to rivers	1.893	1.199	0.001**	

(e) Topi

Parametric variable	Estimate	SE	t-value	p-value
Intercept	-4.475	0.250	-17.894	<0.001***
Protection level FR	-0.758	0.364	-2.084	0.038*
Protection level GCA	-0.653	0.425	-1.538	0.125
Protection level GR	-0.827	0.406	-2.034	0.043*
Protection level UA	-68.460	7136000	0.000	0.999
Smooth term	**Estimated df**	**F-value**	**p-value**	
Distance to houses	3.197	1.709	0.020*	
EVI	1.200	0.528	<0.001***	

(f) Zebra

Parametric variable	Estimate	SE	t-value	p-value
Intercept	-3.712	0.111	-33.401	<0.001***
Protection level FR	-0.624	0.280	-2.225	0.027*
Protection level GCA	-1.150	0.304	-3.789	<0.001***
Protection level GR	-0.268	0.184	-1.460	0.145
Protection level UA	-81.770	6997000	0.000	0.990
Smooth term	**Estimated df**	**F-value**	**p-value**	
Distance to cropland	0.750	0.324	0.044*	
Distance rivers	1.984	0.983	0.006**	
Slope	2.176	1.164	0.004**	

Significance codes: '***' <0.001 '**' 0.01 '*' 0.05; GR, Game Reserve; GCA, Game-controlled Area; FR, Forest Reserve; UA, Unprotected Area; EVI, Enhanced Vegetation Index; df, degree of freedom; SE, Standard Error

4. Discussion

Our study is one of few recent empirical attempts to model (relative) densities of terrestrial wildlife species across different protection levels and across a large spatial extent (but see Maisels et al., 2013; Strindberg et al., 2018). While accounting for environmental variables, our model provides evidence on the effectiveness of area-based conservation measures for large mammal populations in a Sub-Saharan African context. Specifically, we show for western Tanzania that areas with a stricter protection level embraced higher relative densities of large mammals than areas with less strict protection levels or unprotected areas. Our findings support conclusions from previous studies in the same (Giliba et al., 2022) and other Tanzanian ecosystems (Kiffner et al., 2020; Oberosler et al., 2020) that unprotected areas may no longer support viable population densities of large mammal species (Giliba et al., 2022; Kiffner et al., 2020; Oberosler et al., 2020).

Generally, all considered species were widely distributed in strictly protected areas (especially Katavi National Park but also Game Reserves) compared to less strictly protected areas (Fig. S2a-f), suggesting that the protection level largely explains the spatial distribution of large mammals in the Katavi-Rukwa Ecosystem. These findings confirm the strong influence of the protection level in regulating distributions and densities of large mammals in East Africa (Bhola et al., 2012; Kiffner et al., 2020). As our study is of correlative nature, we can merely hypothesize on the underlying, mutually non-exclusive, mechanisms for the positive impact of strict, area-based conservation management on wildlife populations in this ecosystem: stricter protection could (1) result in lower human-caused mortality either due to legal (in game reserves and game-controlled areas) and/or illegal hunting (all PCAs) (Waltert et al., 2009); (2) lead to better habitat quality due to better protection from habitat degradation compared to less strictly protected areas (Schwartz et al., 2002). In addition, (3) stricter PCAs could have an inherently greater carrying capacity for the target species that could not be explained by the selected environmental variables.

While these findings indicate ecological effectiveness of core protected areas, we also observed a lack of integration of these areas into the wider landscape and a possible failure to ensure functional connectivity.

Although the target species appear relatively widely distributed across the core PCAs in the ecosystem (NP, GR, FR, GCA), they were mostly absent from the UA (Fig. S2a-f). Since large-scale connectivity is pivotal especially for large and wide-ranging mammals (Cisneros-Araujo et al., 2021b; Riggio et al., 2022), we recommend targeted efforts in areas outside of protected areas to ensure functional connectivity to adjacent ecosystems in order to support the persistence of wildlife populations over the long term.

Similarly, our density surface models demonstrated a consistent influence of land-use (especially distance to cropland) on the spatial distribution of all considered species (Table 3a-f). Generally, target species avoided areas near to cropland and partially also avoided areas in immediate proximity to houses, suggesting that land-use thrusts large mammal species further into the core areas of protected areas. This observation underpins findings from other case studies across East Africa (e.g., Msoffe et al., 2011; Ogutu et al., 2012; Veldhuis et al., 2019), highlighting that expansion of cropland towards protected areas boundaries negatively impairs the distribution of large mammal species. We did not detect signs of most considered species beyond protected area boundaries (Fig. 3a-f), possibly indicating the unsuitability of unprotected land for wildlife to disperse, use and survive. This unsuitability of unprotected land has likely been increasing over the last decades due to destruction of natural habitats around protected areas of the Katavi-Rukwa Ecosystem (Giliba et al., 2022) and high levels of bushmeat poaching (Martin et al 2013). Notwithstanding, we detected relatively high relative densities of elephant and hartebeest even in less strictly protected areas (Fig. S2b and S2d). Possibly, this is due to their preferences for woodland habitats (De Knegt et al., 2011; Rodgers, 1979), which are found inside Katavi National Park to some extent but predominate in game and forest reserves of the Katavi-Rukwa Ecosystem (Waltert et al., 2009). Notably, these two species occurred at relatively high relative densities in areas designated for trophy hunting (i.e. Game Reserves), providing further support that well-managed hunting areas with relatively low hunting offtake can sustain substantial wildlife populations and contribute to landscape-wide conservation goals (Di Minin et al., 2016; Pinheiro et al., 2019).

Compared to data from aerial surveys carried out in this ecosystem (Giliba et al. 2022), our dung survey also provides evidence that several species are much more widely distributed across the PCA network. For example, aerial surveys suggested that several of our target species were rarely or not detected during aerial surveys carried out in GCAs and FRs during the 2010s (see e.g. Table 3 in Giliba et al. 2022), yet we frequently detected their dung in GCAs and FRs during our 2021 survey (Fig. S2a-f). We hypothesize that this discrepancy is mostly due to visibility bias associated with aerial surveys (Greene et al., 2017; Jachmann, 2002, 1991) and due to behavioral adjustments of wildlife species. Several target species (e.g. elephants, buffalo, zebra) are cathemeral [i.e. active during both day and night; (Clauss et al., 2021)], thus exhibiting the behavioral flexibility to potentially use human-dominated or less strictly protected areas primarily during nighttime to avoid direct interference with humans (de Jonge et al., 2022). While we cannot disentangle the exact causes for the method-related density differences, these comparisons provide circumstantial evidence that indirect survey methods (such as dung, camera trap, or acoustic surveys) are well suited for monitoring wildlife populations along anthropogenic gradients.

Conclusions

Based on our density surface models, protection level and land-use play crucial roles in moderating the spatial distribution of large mammals within the Katavi-Rukwa Ecosystem. While our findings show relative high wildlife densities in strictly protected areas, our study also shows a worrying lack of wildlife outside of these designated areas. Considering that effective and hands-off (i.e. not requiring intensive management such as translocations or supplementary feeding) conservation of wildlife populations ultimately depends on the connectivity of a network of habitats and ecosystems, a better integration of conservation efforts outside of protected areas is needed in the Katavi-Rukwa Ecosystem. The long-term survival of mammals here and possibly also in other places on Earth can only be achieved not only through establishing protected areas, but to conserve a gradient of protection arrangements across entire landscapes.

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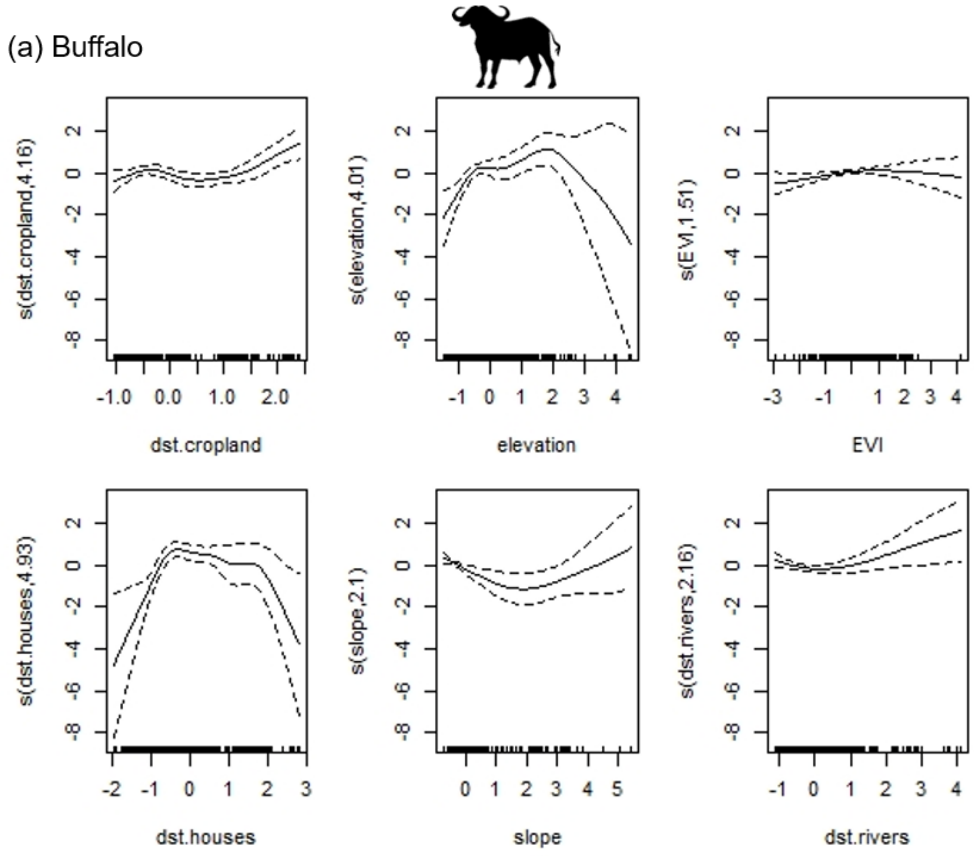
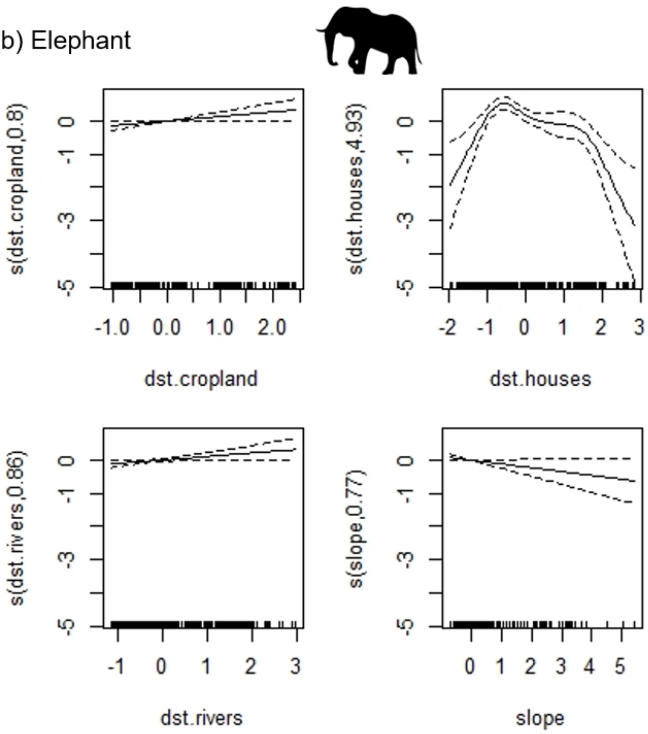
Supplementary Information

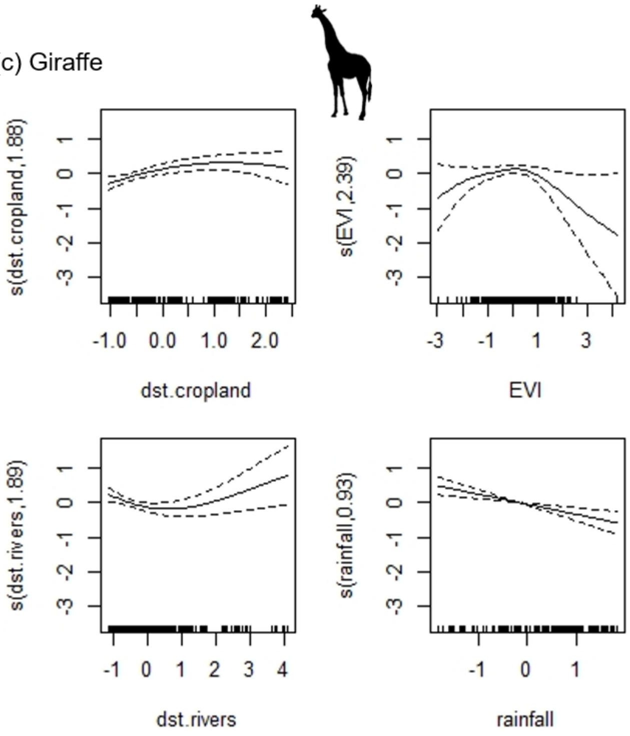
Figure S1. Predicted effects of significant explanatory continuous variables (derived from generalized additive models) on the relative densities of target mammal species [(a) buffalo *Syncerus caffer*, (b) elephant *Loxodonta africana*, (c) giraffe *Giraffa camelopardalis*, (d) hartebeest *Alcelaphus buselaphus*, (e) topi *Damaliscus korrigum*, and (f) zebra *Equus quagga*] in the Katavi-Rukwa Ecosystem southwestern Tanzania. The tick marks on the x-axis are surveyed data points. The x-axis represents scaled values to mean zero and unit variance. The y-axis represents the predicted effect of each variable at a certain effective degree of freedom. The dashed lines indicate the 95% confidence intervals. The explanatory variables are: EVI = Enhanced Vegetation Index; dst.cropland = distance to cropland; dst.houses = distance to houses; dst.rivers = distance to rivers.


(a) Buffalo

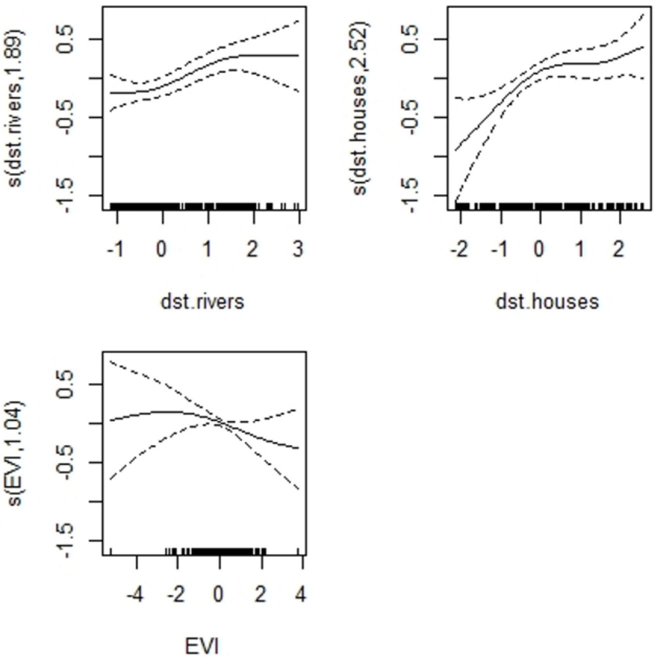
(b) Elephant



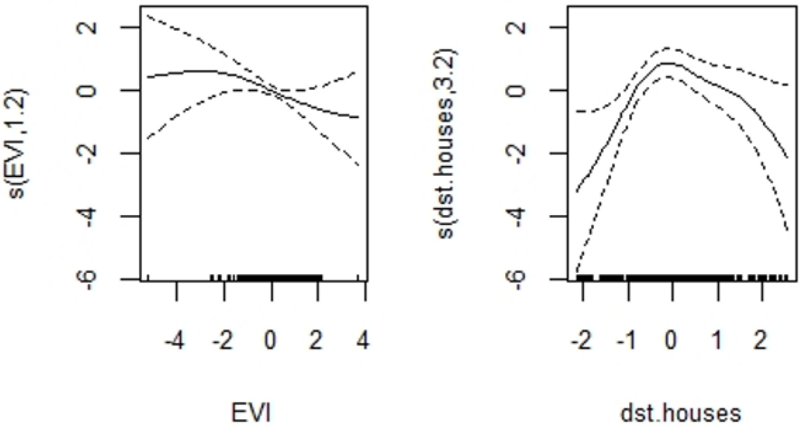
(c) Giraffe



(d) Hartebeest



(e) Topi



(f) Zebra

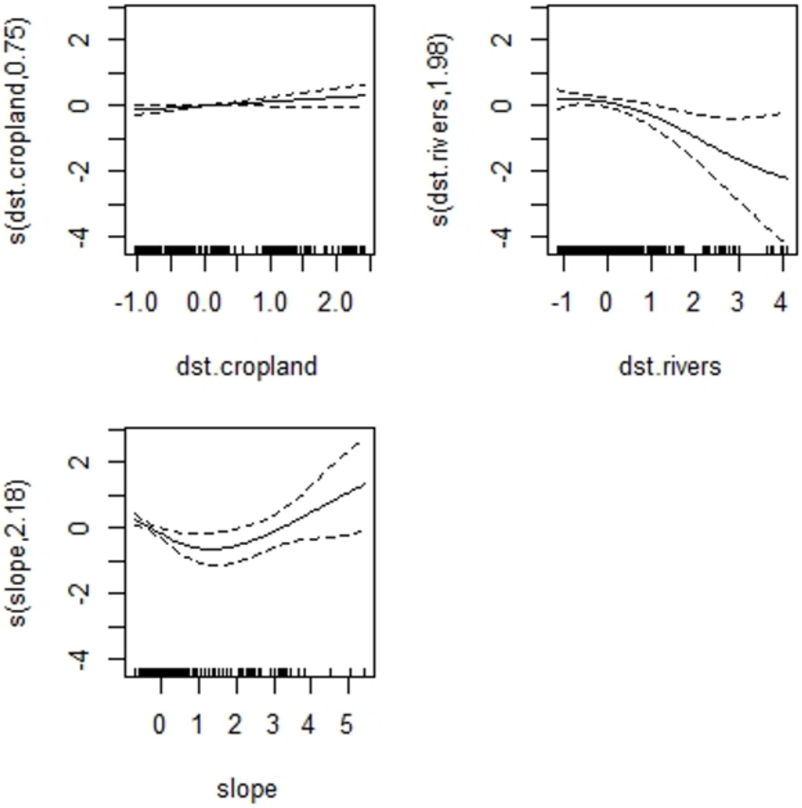
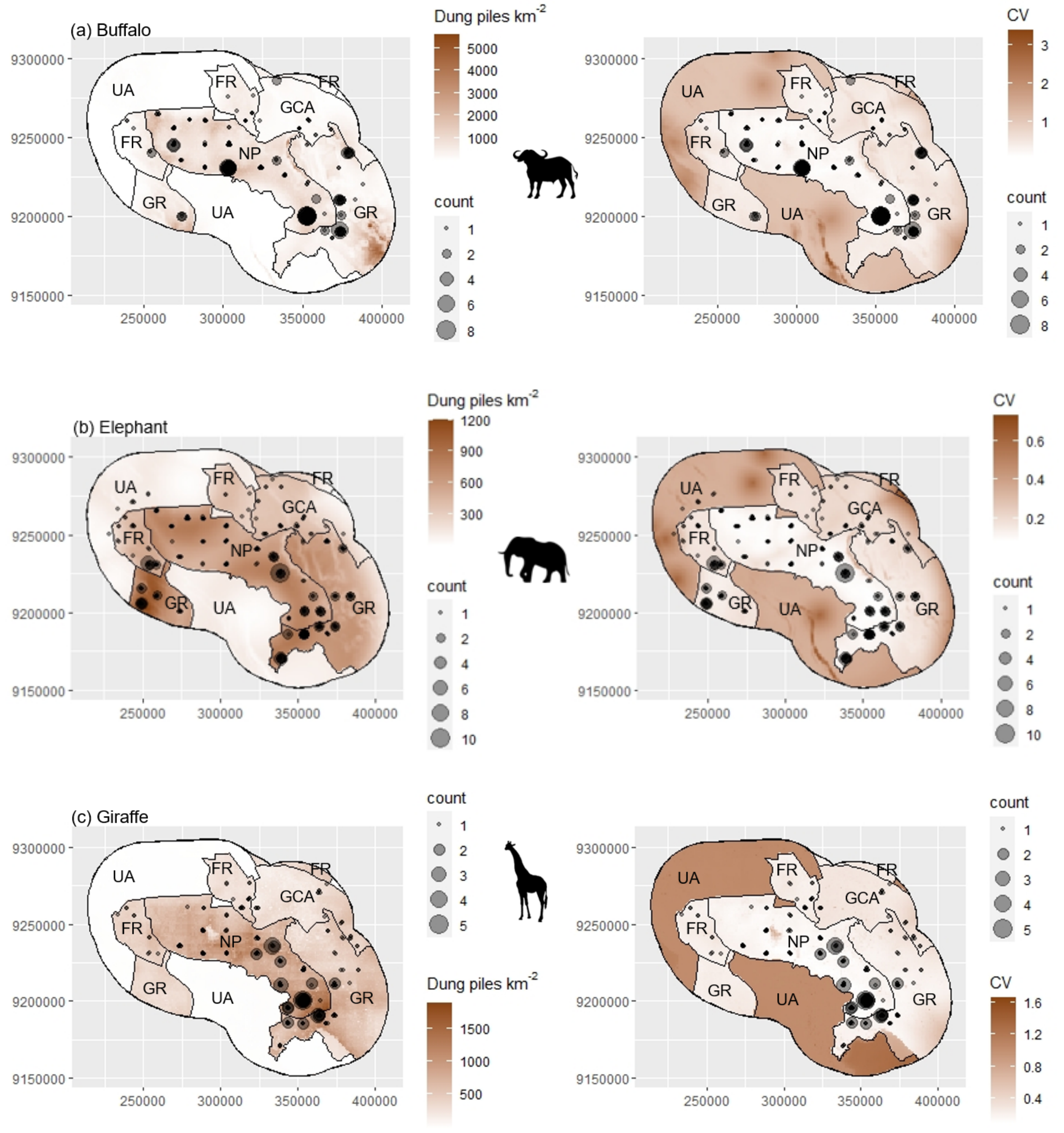
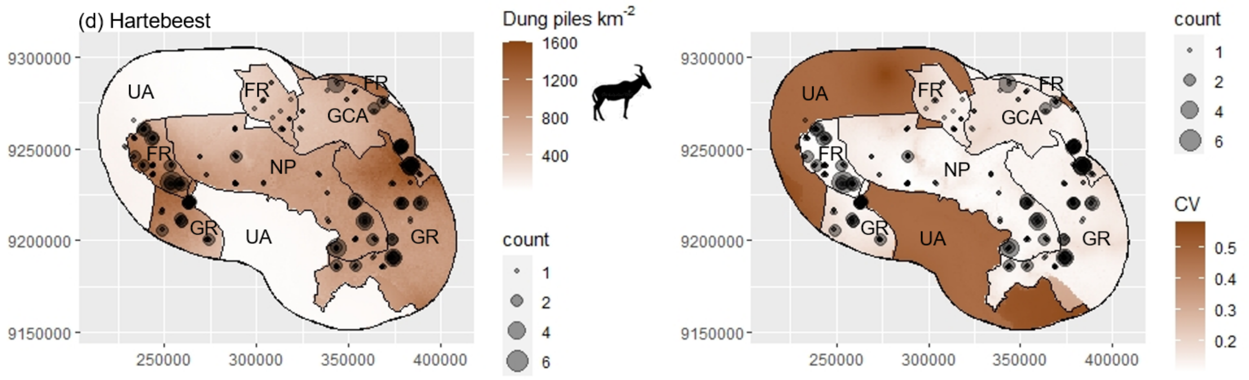

s(dst.cropland,0.75)
2
0
-2
-4
-1.0
0.0
1.0
2.0
dst.cropland
s(dst.rivers,1.98)
2
0
-2
-4
-1
0
1
2
3
4
dst.rivers
s(slope,2.18)
2
0
-2
-4
0
1
2
3
4
5
slope

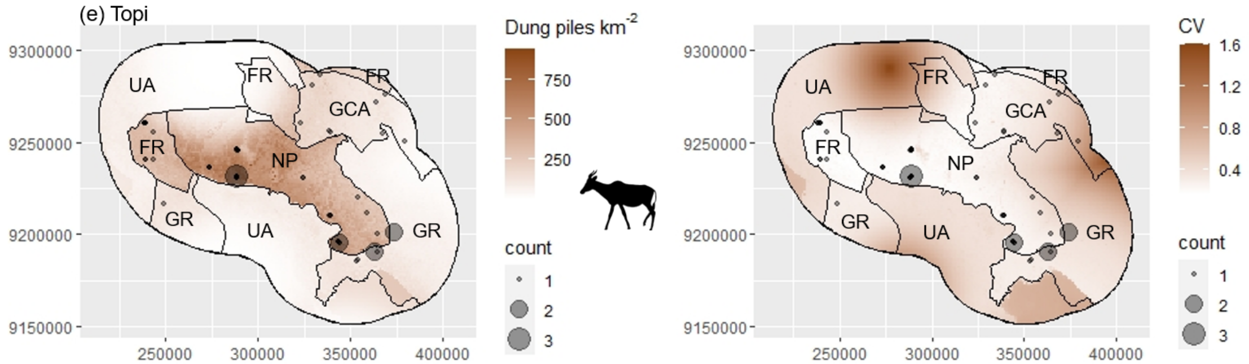
Figure S2. Map of dung density (dung piles km^{-2}) and of associated coefficient of variation for (a) buffalo, (b) elephant, (c) giraffe, (d) hartebeest, (e) topi, and (f) zebra. across protection levels (FR: Forest Reserve; GCA: Game Controlled Area; GR: Game Reserve; NP: National Park; UA: Unprotected Area) of the Katavi-Rukwa Ecosystem in western Tanzania. Black and grey dots represent the distribution and magnitude dung sighted.



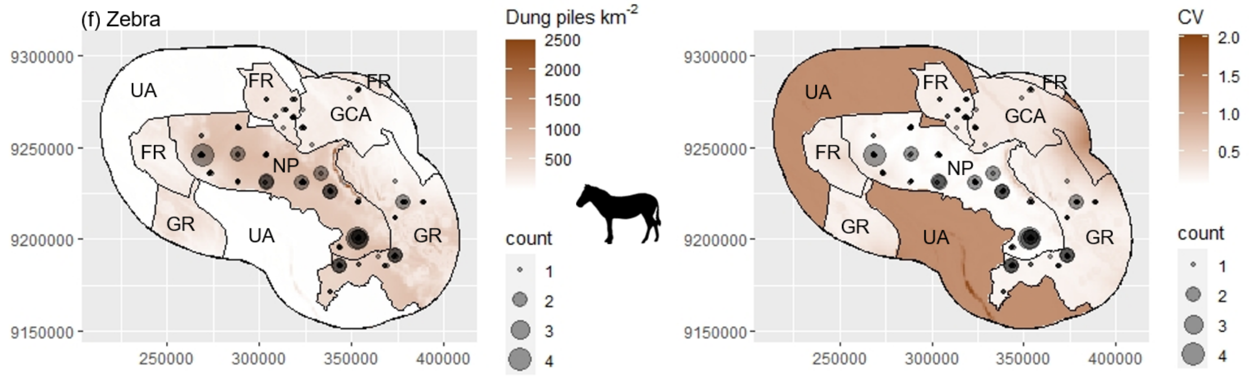
(d) Hartebeest



(e) Topi



(f) Zebra



Chapter 4

Chapter 4

Multiple anthropogenic pressures challenge the effectiveness of protected areas in western Tanzania

Richard A. Giliba, Pascal Fust, Christian Kiffner, Jacqueline Loos

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Abstract

Despite being key conservation instruments, the ecological effectiveness of protected areas is contested. To assess the ecological effectiveness of protected areas in the Katavi-Rukwa Ecosystem in western Tanzania, we investigated temporal changes in land-use and population densities of six large mammal target species (elephant, buffalo, giraffe, zebra, topi and hartebeest) across areas with different conservation category, ranging from unprotected to strictly protected. During six survey periods between 1991 and 2018, we analysed data from remote sensing and aerial wildlife surveys to derive i) spatio-temporal patterns of cropland cover in relation to protection category; ii) population densities of the six-target species; and iii) distribution of these species across protection category, land-use and environmental variables. During the surveyed period, cropland increased from 3.4 % to 9.6 % on unprotected land and from ≤0.05 % to <1 % on protected land. Wildlife densities of most, but not all target species declined across the entire landscape, yet the onset of the observed wildlife declines occurred several years before the onset of cropland expansion. Logistic regression models indicated that target species preferred the national park over less strictly protected areas and areas distant to cropland. As our data do not support a direct link between land-use change and wildlife densities, additional factors may explain the apparent ecosystem-wide decline in wildlife. To bolster wildlife conservation in the Katavi-Rukwa Ecosystem, we recommended proactive strategies to reduce direct threats to wildlife and cropland expansion towards wildlife dispersal areas and migratory corridors.

1. Introduction

Across the globe, biodiversity is rapidly declining mostly due to human-induced pressures (IPBES, 2019; Mammides, 2020; WWF, 2020). Direct exploitation of organisms, climate change, pollution, invasive species, and changes in land-use are presumably the most influencing direct drivers for biodiversity loss (IPBES, 2019). As a response to these multiple human pressures on ecosystems, protected area (PA) establishment is one key approach to safeguard biodiversity and human wellbeing (Gaston et al., 2008). However, the effectiveness of PAs is contested, and their ability to withstand anthropogenic pressures varies (Geldmann et al. 2019). To increase PA effectiveness, knowledge on the drivers and responses determining their ability to safeguard biodiversity is pivotal (Burkmar and Bell, 2015; Mazor et al., 2018).

Despite an impressive PA network in Africa (Riggio et al., 2019; WCMC-UNEP, 2016), some of the most severe declines in large mammal populations have occurred here over the past decades (Craigie et al., 2010; Ogutu et al., 2011; Ripple et al., 2015; WCMC-UNEP, 2016), with habitat loss and direct exploitation considered to be the main direct drivers. Available evidence strongly suggests that the underlying reasons for these developments to be rooted in human population growth, reduced functional connectivity (Fynn and Bonyongo, 2011; Riggio and Caro, 2017; Roever et al., 2013), insufficient staff and capacities to manage PAs adequately (Lindsey et al., 2014), and subsequent failure to implement and enforce effective conservation measures (Henson et al., 2016; Lindsey et al., 2014; Muhumuza and Balkwill, 2013). In particular, many PAs lack enforcement on the ground (Di Minin and Toivonen, 2015), suffer from underfunding (Coad et al., 2019) and data deficiency may hinder evaluation of their effectiveness (Craigie et al., 2010; Geldmann et al., 2019; Loos, 2021b).

One region with documented mammal wildlife declines is the Katavi-Rukwa Ecosystem in western Tanzania (Caro, 2008; Mtui et al., 2017). Despite its relative high coverage with designated PAs (IUCN, 2020; Riggio et al., 2019), a growing human population (Masanja, 2014) and an increasing demand for natural resources stimulates land-use changes and overexploitation of species (Caro et al., 2013; Martin and Caro, 2012). The expansion of land for cultivation and unsustainable (and often illegal) harvesting of species pose a dual and increasing pressure on PAs in the area (Martin and Caro, 2012; WCMC-UNEP, 2016). However, insights on the extent of land-use change on wildlife populations remain scarce (Kiffner et al., 2013).

Besides unprotected land, different categories of PAs exist in Tanzania (and in our specific study area), ranging from strictly protected (International Union for Conservation for Nature, IUCN categories I to V) to less strictly protected, permitting human activities and resource extraction to some extent (IUCN categories VI). Previously, the effectiveness of PAs in protecting wildlife populations has been studied across Tanzania (Stoner et al., 2007), but this nationwide assessment considered only two protection categories (i.e., National Parks and Game Reserves) and did not consider other PA categories which may also support wildlife populations (Caro, 1999a). To date, however, wildlife population trends have neither been linked to land-use changes nor to different protection categories across an entire ecosystem. To this end, we integrate both wildlife population densities and land-use change analyses over time to assess the effectiveness of four protection categories (i.e., National Park, Game Reserve, Forest Reserve, Game Controlled Areas), as well as unprotected areas (UA) in safeguarding wildlife populations and reducing anthropogenic threats. Understanding how conservation category mediates wildlife populations and anthropogenic threats over time is crucial in ensuring the delivery of positive ecological outcomes (Caro et al., 1998; Gardner et al., 2007; Stoner et al., 2007; WWF, 2020).

In the context of East Africa, scholars have mostly focused on two indicators for assessing the ecological effectiveness of protected areas: land-use change in previously natural habitats (Riggio et al., 2019), and wildlife densities and their trends over time (Kiffner et al., 2020). Both indicators of PA effectiveness are important metrics for conservation management, but analyzing each in isolation provides only limited insights (Ghoddousi et al., 2021) because land-use change is not only an indicator of PA effectiveness, but could also be the main driver of wildlife declines (Pereira et al., 2012). Here, we looked into this relationship to understand whether and to what extent land-use change relates to wildlife population densities in western Tanzania. Since land-use change is a driver responsible for the destruction of natural habitats and could affect habitat and resource availability for wildlife species (Dirzo et al., 2014; Tucker et al., 2021; Young et al., 2016), we hypothesized that a decline of available habitat for wildlife, would be followed by a time-lagged decline in wildlife populations. This scenario is often referred to as ‘extinction debt’ (Halley et al., 2016; Kuussaari et al., 2009). Such a scenario is particular plausible for the Katavi-Rukwa Ecosystem, where, similar to the Serengeti ecosystem in northern Tanzania (Veldhuis et al. 2019), rapid conversion of natural habitats reached the border of Katavi National Park within a few decades. However, it is unclear to what extent this land-use change, in particular cropland expansion, is related to the distribution of wildlife species. Although the distribution of wildlife and population dynamics are not identical, understanding how wildlife species are distributed across landscapes and how wildlife responds to land-use changes could provide important insights for targeted spatial planning that caters both for human and wildlife needs (Kremen and Merenlender, 2018).

To address our research goal of assessing and understanding the ecological effectiveness of PAs in western Tanzania, we aimed at: (i) analyzing the patterns of cropland expansion across different protection categories over time; (ii) analyzing population trends of six large ungulate populations (buffalo *Syncerus caffer*, elephant *Loxodonta africana*, giraffe *Giraffa camelopardalis*, hartebeest *Alcelaphus buselaphus*, topi *Damaliscus korrigum*, and zebra *Equus burchellii*) across areas with different protection categories over time; and (iii) generating species-specific models to identify key ecological and anthropogenic spatial variables associated with the presence of the target species. We hypothesized that: (i) the extent of cropland within all areas would show an increasing trend over time and that the increase in cropland would be particularly pronounced on unprotected land; (ii) population trajectories of target species would be particularly negative in unprotected or less strictly protected areas and be constant or only slightly negative in strictly protected areas; (iii) target species would prefer the national park and areas distant to cropland; and (iv) the distribution of target species would be mediated by environmental variables, such as preferences for areas near rivers and areas with intermediate primary productivity (Esmaeili et al., 2021). Our findings can be used in implementing conservation plans beyond PA boundaries and can provide information on how different conservation categories affect conservation outcomes.

2. Methods

2.1 Study area

Our study focused on the Katavi-Rukwa Ecosystem (KRE) which is located between 6° to 7° S and 30° to 31° E, situated in Mpanda and Katavi Districts, western Tanzania (Fig. 1). The KRE covers c. 15,110 km^2 (this is the extent of area that was consistently covered by aerial surveys carried out from 1991 to 2018), and comprises eight different administrative units (Caro, 2011; TAWIRI, 2014, 2018): Katavi National Park, managed by Tanzania National Park (TANAPA); Rukwa and Lwafi Game Reserves, Mlele and Rungwa-River Game Controlled Areas, managed by the Tanzania Wildlife Management Authority (TAWA); Nkamba and Msaginia Forest Reserves, managed by the Tanganyika District Council and Tanzania Forest Service Agency (TFS), respectively; as well as Usevia, and Sitalike Unprotected Areas, managed by the district council. These administrative units fall under four protection categories ranging from areas with little enforcement of human land-use restrictions [Game Controlled Areas (GCA): here, settlement, agriculture, livestock keeping are not allowed, but hunting on permit in specific hunting blocks are allowed], areas that allow regulated resource extractions such as Forest Reserves (FR: here, limited timber extraction is permitted) and Game Reserves (GR: here, touristic game hunting with permits is allowed) to a strictly protected National Park (NP) where human activities are restricted to photographic tourism and research (Caro and Davenport, 2016; Caro, 1999a). Beyond, we investigated Unprotected Areas (UA) i.e. land that does not have a formal conservation category. Hence, our approach entails land under different conservation categories across the KRE, spanning the entire gradient of formal conservation approaches in this landscape. Large mammals found within KRE include buffalo, elephant, giraffe, hartebeest, topi, and zebra (Caro, 2008, 1999b; TAWIRI, 2018, 2014). We focused on these six species for two reasons; they are the numerically dominant terrestrial species in the ecosystem (TAWIRI, 2018, 2014), and they can reliably be monitored through aerial surveys as their relatively large body sizes facilitate detection during aerial surveys (Jachmann, 2002).

From 1991 to 2018 (the period of our data collection), the KRE received an annual rainfall between 800 - 1200 mm, while the temperature ranged between 15 - 25 °C. Elevation ranges from 600-1800 m asl. The soil types range from alluvial soils (black cotton soils) in grassland/flood plains to loamy soils in woody vegetation. The vegetation consists of miombo woodlands and flood plains (Banda et al., 2006). Miombo forms a single story, with open and closed canopy of deciduous woodland dominated by trees of the genera *Brachystegia, Julbernadia*, and *Isoberlinia* (Banda et al., 2008). The flood plains predominantly occur on the flat terrains of the Katavi, Chada, and Katisunga plains that are drained by the Katuma River (Mtui et al., 2017). The human population in the KRE has rapidly grown due to increasing migration of pastoralist from Simiyu, Shinyanga, Mwanza, and Geita regions over the past 40 years (Izumi, 2017; Salerno, 2016). The main land-use activities in the KRE include agriculture and livestock keeping (Caro, 1999a). Rice farming is restricted to river terraces and flood plains while shifting cultivation for other crops, i.e. maize, cotton and tobacco, is practiced in deforested areas (Jew et al., 2017). In 1991, Katavi National Park was enlarged by annexing parts of Rukwa Game Reserve. Its area increased from 2,253 km^2 in 1991 to 4,471 km^2 in 1998, while Rukwa Game Reserve area decreased from 6,412 km^2 in 1991 to 4,194 km^2 in 1998, and 1,294 km^2 from Game Controlled Area become part of Rukwa Game Reserve in 1998. To be consistent, we used the PA category at the time of the survey for cropland cover analyses, and to capture species-specific aerial survey strip segments for wildlife density analyses.

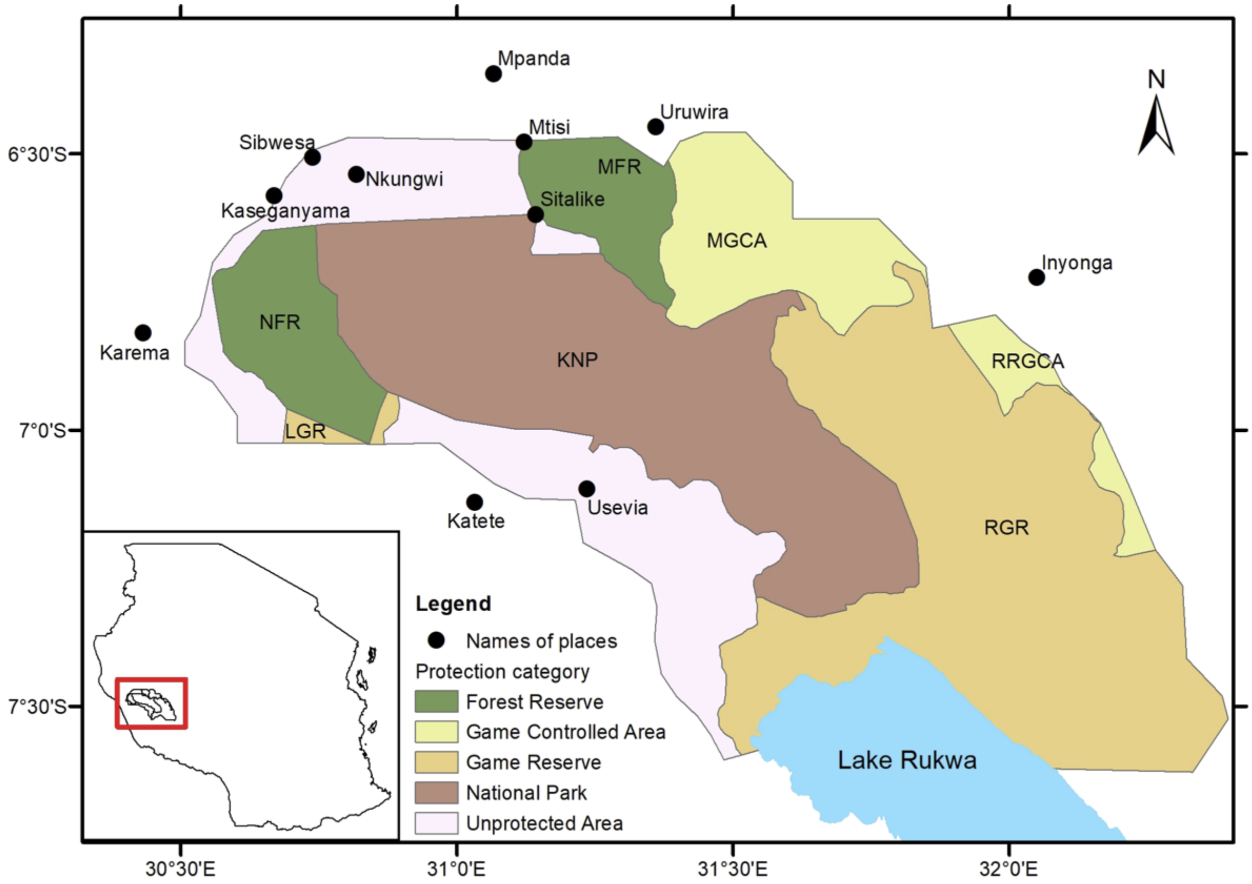


Fig. 1. Map of the Katavi-Rukwa ecosystem (KRE), highlighting the spatial distribution of different conservation areas [Katavi National Park (KNP); Rukwa Game Reserve (RGR); Lwafi Game Reserve (LGR); Mlele Game Controlled Areas (MGCA); Rungwa-River Game Controlled Areas (RRGCA); Nkamba Forest Reserve (NFR); Msaginia Forest Reserve (MFR)] and Unprotected Areas (UA), as well as major towns and villages. The inset in the lower left shows the location of the study area within Tanzania.

2.2 Large mammal population data

We obtained a total of 892 target species sightings for the years 1991, 1998, 2001, 2006, 2014, and 2018, for KRE from the Tanzania Wildlife Research Institute (TAWIRI) following our formal requests. Aerial counts were conducted during the dry season following the systematic reconnaissance flight technique as described by Norton-Griffiths (1978). Transects were flown in east-west directions at predefined 5 km spacing for 1991, 1998, 2001 and 2006 surveys. For 2014 and 2018 surveys some transects were flown in southwest directions and others in north-east directions. (TAWIRI, 2018, 2014).

2.3 Land cover and environmental variables

Based on published relationships between the distribution of large savanna mammals in Tanzanian ecosystems and landscape features (Bond et al., 2017; Van de Perre et al., 2014), we selected the following environmental variables in our species-specific binomial regression models (see below): land cover (as a proxy for habitat structure and land-use), Enhanced Vegetation Index (EVI; as a proxy for primary productivity due to its advantages of reducing the background noise, atmospheric noise, and saturation in most cases compared to NDVI (Huete et al., 2002)), elevation, slope, terrain ruggedness and proximity to rivers, lakes, roads, houses, and the amount of rainfall in the year of the survey.

To produce land cover maps for the KRE, we acquired readily available 30 m resolution Landsat 5 and Landsat 8 imagery from U.S. Geological Survey's Earth Explorer (https://earthexplorer.usgs.gov/). Our choice of date for satellite imagery was based on availability of aerial surveys data for the dry seasons between 1991 and 2018, and imagery free from cloud cover. We used the atmospheric correction algorithm ATCOR to remove haze and calculate top of atmosphere reflectance for Landsat 5 and Landsat 8 imagery using PCI Geomatica version 2018 (PCI Geomatics 2018). We generated 1,106 training polygons for each year for our land classification through composite imagery, high-resolution Google Earth images and field knowledge. We used the scatterplot tool to evaluate our training samples to find out if there was enough separation between landcover classes using ArcMap (ESRI, 2018). We employed a supervised classification approach using a support vector machine algorithm to classify satellite imagery (Heydari and Mountrakis, 2019; Maulik and Chakraborty, 2017). We mapped five major land cover categories (dense woodland, open woodland, burnt area, cropland, and swamp areas) and linked these land cover categories with wildlife species presence. We generated 475 points using stratified random sampling in ArcMap to assess the accuracy of our classified maps. We used high-resolution images from Google Earth and base-map layers from Google Satellite, ESRI Satellite, and Bing Satellite available in ArcMap and QGIS to validate our land cover maps (Connette et al., 2016; Hu et al., 2013; Yu and Gong, 2012). Our overall land cover classification accuracy for the six dates ranged from 96 % to 98 % with kappa coefficients between 0.95 and 0.98 (Supplementary Table 4). We used the overall accuracy and kappa coefficient to validate our classified maps. We calculated the mean EVI values for the dry season (i.e. between July and September) of each year from Google Earth Engine - Landsat 5/8 Collection 1 Tier 1 8-Day EVI Composite (Gorelick et al., 2017). To extract information on elevation, we obtained the global 30 m SRTM digital elevation model (DEM) for the KRE from the U.S. Geological Survey (https://earthexplorer.usgs.gov). We used DEM to derive slope and terrain ruggedness raster surface using QGIS 3.16 (QGIS, 2020). We obtained spatial layers for major roads and rivers from OpenStreetMap (http://download.geofabrik.de/africa/tanzania.html), and for seasonal lakes and houses from TAWIRI (TAWIRI, 2018). We generated distance raster surfaces for rivers, lakes, roads, and houses at resolution of 30 m using the Euclidian distance tool in ArcMap 10.6 (ESRI, 2018). Finally, we obtained the annual rainfall at a resolution of 5 km for each year for the KRE from CHIRPS (https://data.chc.ucsb.edu/products/CHIRPS-2.0/).

2.4 Temporal trends of cropland cover and large mammal populations

We used time-matched administrative boundaries of the PAs at the extent of KRE and aerial surveys to extract cropland cover across different protection categories for each year using the Tabulated Tool in ArcMap (ESRI, 2018). We plotted cropland cover against the year to explore cropland cover across different protection categories over time. To estimate species- and PA-specific wildlife densities for each dry season count, we used Jolly's method 2 for unequal-sized sample units (Jolly, 1969). We plotted estimated densities of the six target species against the year to explore annual densities of target species within the different protection categories over time. We used Kendall's correlation tests to investigate the strength and direction of temporal trends of cropland and wildlife densities. We approximated mean annual rates of change of wildlife populations by subtracting wildlife density estimates of the last (2018) survey from the density estimates of the first (1991) survey, divided by the time period in years. Because our data were not normally distributed (based on visual inspection of histograms and Shapiro-Wilk tests), we used non-parametric Kruskal-Wallis test to assess if overall wildlife densities in both 1991 and 2018 differed between protection categories. We used the species-specific densities as replicates for these analyses of variance (ANOVAs). We used the same non-parametric test to assess whether the extent of cropland differed between protection categories. Because we had no replicates for a given time step, we used the year-specific estimates as replicates. Finally, we used Dunn's post hoc test to assess which protection categories differed from each other in terms of wildlife densities and extent of cropland cover. Statistical significance was set at $P < 0.05$. We analysed all data in R 4.0.4 (R Core Team 2020).

2.5 Identifying correlates for the distribution of large mammals

To model habitat associations for the six-target species, we first overlaid TAWIRI survey block polygons with the time-matched PAs administrative boundaries to obtain the overall extent of the landscape (i.e., 15,110 km^2) that has consistently been surveyed throughout the six aerial surveys from 1991 to 2018. As a next step, we intersected the overlay from step one with aerial survey strips to obtain presence/absence strips in each protection category. For each of these species-specific aerial survey strip segments (median width = 310 m, range 80 to 2,000 m, median length = 5 km, range 1.5 to 5 km), we extracted ecological and anthropogenic spatial variables using the Tabulated Tool in ArcMap 10.6 (ESRI, 2018). All variables, except for protection category (categorical variable with five levels: NP, GR, FR, GCA, and UA) and land cover (categorical variable with five levels: closed woodland, open woodland, cropland, burnt area, and swampy area), were continuous variables. For continuous variables we computed mean values for each segment while for categorical variables we extracted majority values of the most frequently occurring category in each segment. To avoid potential problems arising from collinearity, we tested explanatory continuous variables for cross correlations using the corrplot package (Wei and Simko, 2017). Due to high levels of autocorrelation [(r) > 0.7 (Zhu and Peterson, 2017)], we removed the variables 'terrain ruggedness index', and 'distance to seasonal lakes' and used eight uncorrelated continuous variables to fit the models along with two categorical variables based on ecologically relevant hypotheses (Table 1). To test for a unimodal relationship in response to vegetation productivity, we included a quadratic term of EVI. We used generalized linear mixed models (GLMMs) with binomial error distribution and survey period (year) as a random factor to assess the strength and direction of associations between environmental variables and the presence of target species within the KRE. For each target species, we first fitted a global model with all potential variables. Using the dredge function of the MuMiN package

(Barton and Barton, 2020), we generated models with all combinations of variables in the global model. We ordered these candidate models according to the sample-size corrected Akaike's information criterion (AICc) score (i.e., lowest on top) and model weights (i.e., highest on top). Due to model selection uncertainty, we opted for model averaging and considered models with delta AICc < 4 (Burnham and Anderson, 2002). Because our aim was to determine which variables are most important predictors of target species presence, we estimated model averaged coefficients using the full average method (Anderson and Burnham, 2002; Nakagawa and Freckleton, 2011).

Table 1: Predictor variables for modelling of large mammal distributions and associated hypotheses. Protection category and land cover are categorical data; other variables are continuous data.

Predictor	**Hypotheses: Large mammal presence**
Protection category	Level of protection varies between protected area and affecting large mammal presence. Large mammals are expected to prefer strictly protected areas and avoid unprotected areas.
Land cover	Habitat type which may be avoided or preferred by large mammals. Due to species-specific differences in feeding ecology, we expected specific responses to natural land cover types.
Enhanced vegetation index	Large mammals prefer areas with medium or high primary productivity; due to species-specific food preferences, we expected that these associations would differ by species.
Rainfall	Influences vegetation growth and surface water availability which in turn drives large mammal distribution.
Elevation	Determines habitat type which in turn drive large mammal presence.
Slope	Steeper slopes constrain movement for some species.
Distance to river	During the dry season, large mammals prefer sites closer to rivers as they provide water. As water dependency differs by species, we expected species-specific responses.
Distance to cropland	Large mammals avoid sites closer to cropland, as these areas potentially represent elevated risks exerted by humans.
Distance to houses	Large mammals avoid sites closer to houses as these areas potentially represent elevated risks exerted by humans.
Distance to roads	Large mammals avoid sites closer to roads as these areas potentially represent elevated risks exerted by humans.

3. Results

3.1 Patterns of cropland cover across different protection categories

In 1991, cropland covered 3.4 % of the entire study area; in 2018, the area under cropland covered 9.6 % of the entire surveyed area. In 1991, the extent of cropland in all PAs was marginal (≤1 %) (Fig. 2a) and cropland cover was mainly restricted to UA (9.6 %) (Fig. 2b). From 1991 to 2018, cropland cover increased within all considered protection categories (Fig. 2a & 2b). The temporal trend of this expansion differed between protection categories, evidenced by different average annual rates of cropland expansion: NP = 0.02 % increase year^{-1}; GCA = 0.02 % increase year^{-1}; GR = 0.03 % increase year^{-1}; FR = 0.10 % increase year^{-1}; and UA = 1.29 % increase year^{-1}. The temporal trend of cropland expansion appeared non-linear and the timing of cropland expansion differed between protection categories. For example, inside the NP, cropland showed a sharp increase between 2006 and 2018 (Fig. 2a) while cropland expansion inside the GR started earlier in 2001 (Fig. 2a). In the GCA, we observed a sharp increase in cropland expansion between 2006 and 2018 (Fig. 2a), while cropland in FR and UA increased almost linearly throughout the observation period (1991-2018) (Fig 2a, b). A Kruskal-Wallis test showed that there was a significant difference in cropland expansion across protection categories from 1991 to 2018 ($H = 19.85$, $df = 4$, $p < 0.001$). Dunn's post-hoc test showed that the extent of cropland cover within UA was greatest and differed significantly from other protection categories (NP, GR, FR, GCA). Among the other protection categories, cropland cover did not differ significantly over time. In 2018, cropland cover approached the northern and southern borders of NP, in areas previously covered by dense and open woodlands (Fig. 3a-d).

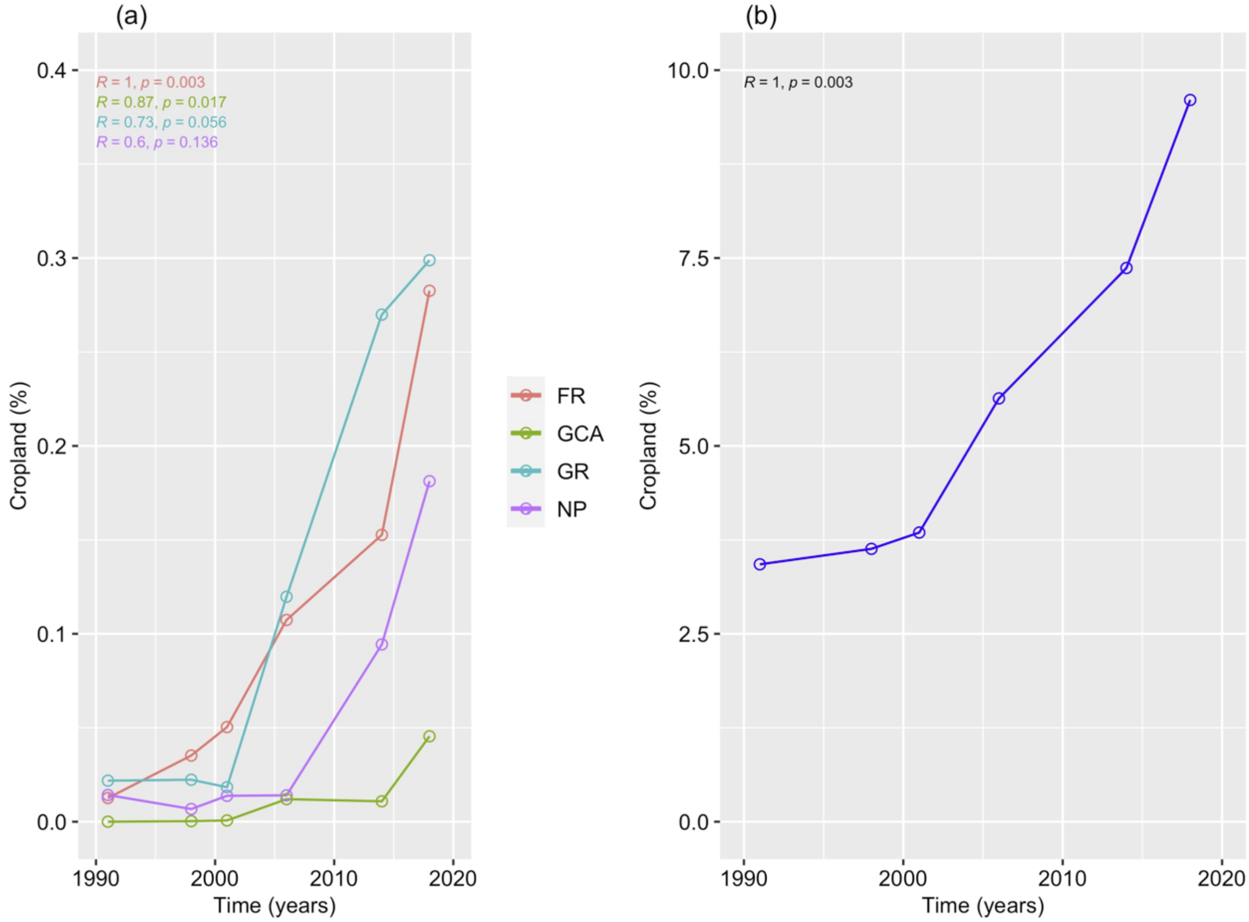


Fig.2 Percent of cropland cover from 1991 to 2018 within different PAs (a) and within UA (b) of the Katavi-Rukwa ecosystem and associated results of non-parametric correlation analyses to describe the temporal trends.

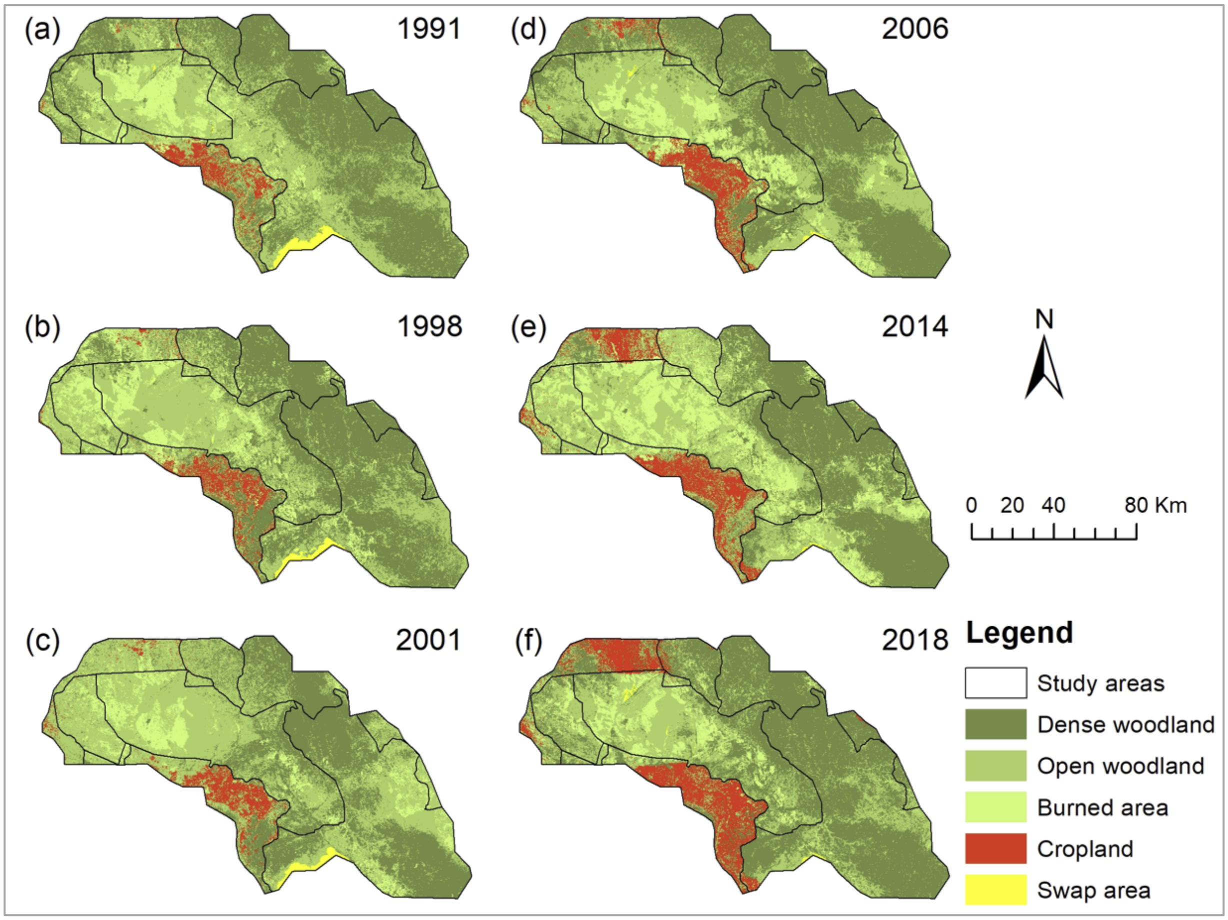


Fig. 3. Extent of cropland around Katavi National Park between 1991 (a) and 2018 (f).

3.2 Population trends of large mammals across different protection categories

In 1991, high densities of buffalo occurred in the NP, GR, FR and OA, and zebra also occurred at high densities in the UA. For the 1991 survey data, a Kruskal-Wallis test showed that there was no significant difference in overall wildlife densities (i.e. species-specific densities as replicates) across protection categories ($H = 7.63$, $df = 4$, $p = 0.11$), however, a follow up Dunn's post-hoc test for pairwise comparisons showed that wildlife densities in the NP were significantly greater than those in the FR and GCA. However, in 2018, wildlife densities differed significantly between protection categories ($H = 10.19$, $df = 4$, $p = 0.03$). A follow up Dunn's post hoc test showed that wildlife densities in the NP were significantly greater than those in the FR, GCA, UA, but not different to densities in the GR. The population trends of all target species combined differed between protection categories, evidenced by different average annual rates of change in densities: NP = 0.58 % decline year^{-1}; GCA = 0.69 % decline year^{-1}; GR = 0.17 % decline year^{-1}; FR = 2.7 % decline year^{-1}; and UA= 3.3 % decline year^{-1}. Specifically, we observed steep declines of previously high population density of zebra and buffalo in FR and UA (Fig. 4). These species also declined in NP and GR (Fig. 4). However, in the NP and GR their densities seem to have stabilized at a lower level, whereas in the less strictly protection categories (i.e., FR, GCA, UA), the density of these species seems to have declined precipitously, or these species are no longer using these areas (Table 3). Population densities of elephant, giraffe, topi, and hartebeest remained relatively stable at low levels or seem to have disappeared in the less strictly protection categories (Fig. 4, Table 3). Although not significant (likely due to low test power), the combined densities (i.e. the summed densities of all six target species) seemed negatively associated with the extent of cropland in a given area (R = -0.60, p = 0.13, n = 6).

Table 3: Survey-specific densities of wildlife (ind. km^{-2}) across different protection categories [National Park (NP), Game Reserve (GR), Forest Reserve (FR), Game Controlled Area (GCA), Unprotected Area (UA)].

	1991	**1998**	**2001**	**2006**	**2014**	**2018**
NP	**18.73**	**14.12**	**10.61**	**7.93**	**12.80**	**3.00**
Buffalo	14.26	7.84	4.24	3.74	10.89	1.78
Elephant	1.79	0.95	1.53	1.10	0.88	0.38
Giraffe	0.23	0.35	1.53	0.03	0.25	0.13
Hartebeest	0.42	0.22	0.29	0.07	0.04	0.16
Topi	0.66	1.29	1.83	0.20	0.24	0.15
Zebra	1.36	3.48	1.19	2.78	0.51	0.39
GR	**7.94**	**2.05**	**1.50**	**1.62**	**1.93**	**3.28**
Buffalo	5.58	1.49	0.50	1.27	1.39	2.90
Elephant	0.11	0.11	0.28	0.05	0.09	0.04
Giraffe	0.35	0.10	0.28	0.07	0.04	0.02
Hartebeest	0.45	0.05	0.11	0.11	0.19	0.02
Topi	0.19	0.01	0.00	0.08	0.01	0.00
Zebra	1.26	0.30	0.33	0.03	0.22	0.31
FR	**6.70**	**0.27**	**0.35**	**0.61**	**0.27**	**0.48**
Buffalo	6.11	0.00	0.01	0.00	0.00	0.04
Elephant	0.00	0.05	0.16	0.56	0.20	0.30
Giraffe	0.22	0.10	0.16	0.01	0.07	0.00
Hartebeest	0.37	0.11	0.00	0.04	0.00	0.06
Topi	0.00	0.00	0.03	0.00	0.00	0.00
Zebra	0.00	0.02	0.00	0.00	0.00	0.09
GCA	**1.18**	**0.76**	**1.74**	**0.84**	**0.17**	**0.25**
Buffalo	0.55	0.57	0.61	0.00	0.00	0.09
Elephant	0.00	0.00	0.32	0.67	0.00	0.00
Giraffe	0.19	0.00	0.32	0.17	0.03	0.00
Hartebeest	0.43	0.00	0.49	0.00	0.01	0.16
Topi	0.00	0.03	0.00	0.00	0.00	0.00
Zebra	0.00	0.17	0.00	0.00	0.13	0.00
UA	**20.71**	**0.83**	**0.44**	**0.16**	**0.19**	**0.41**
Buffalo	13.89	0.07	0.22	0.05	0.00	0.00
Elephant	0.00	0.49	0.00	0.02	0.03	0.00
Giraffe	0.60	0.17	0.00	0.09	0.00	0.00
Hartebeest	0.14	0.10	0.15	0.00	0.00	0.27
Topi	0.57	0.00	0.00	0.00	0.00	0.00
Zebra	5.52	0.01	0.08	0.00	0.16	0.15

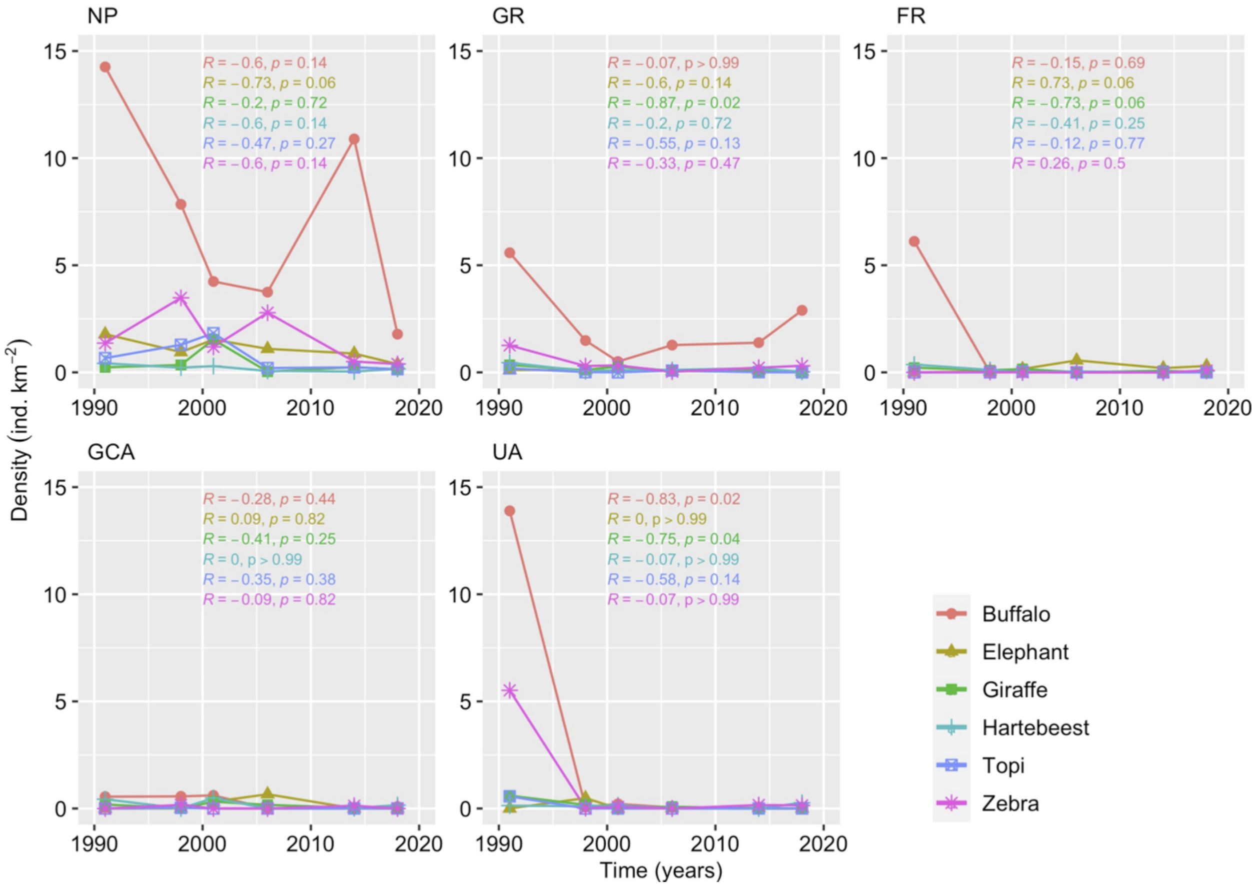


Fig. 4. Densities of large ungulate species within NP (a), GR (b), FR (c), GCA (d), UA (e) based on aerial counts conducted during dry seasons between 1991 and 2018 and associated results of non-parametric correlation analyses to describe the temporal trends.

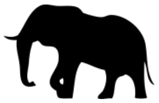
3.3 Anthropogenic and environmental variables associated with the distribution of target species

Model averaged estimates of generalized linear mixed models indicated that six environmental variables, namely EVI, land cover, elevation, slope, distance to rivers, distance to roads; and three anthropogenic variables, distance to cropland, distance to houses and protection category, were strongly associated to the distribution of the target species (Table 2a-f). The distributions of all target species were positively associated with distance to cropland. All target species except for hartebeest had lower likelihoods to occur in GR, GCA, FR, and UA compared to the reference category, NP (Table 2a-f). The presence of buffalo, elephant, and zebra was negatively associated with distance to rivers (Table 2a, b, e & f). Buffalo, and elephant presence was negatively associated with EVI (Table 2a & b). Giraffe, and hartebeest presence was negatively associated with the quadratic term of EVI, while the distribution of buffalo was positively associated with the quadratic term of EVI (Table 2a, c & d). The distributions of giraffe and zebra were negatively correlated with elevation (Table 2c & f), while buffalo and hartebeest were negatively correlated with slope (Table 2a & d). Topi and elephant preferred open woodland and hartebeest preferred burnt areas (Table 2b & e). Zebra distribution was positively correlated with distance to houses while the distribution of topi was negatively correlated with distance to houses (Table e & f). Distributions of buffalo, giraffe and topi were negatively associated with distance to roads (Table 2a, c & e).

Table 2: Summary statistics of generalized linear mixed models describing associations between explanatory variables and the presence of target species [(a) buffalo, (b) elephant, (c) giraffe, (d) hartebeest, (e) topi, and (f) zebra] in the Katavi-Rukwa ecosystem. Protection category and land cover were defined as factors, whereas the baseline variables are national park (NP) and closed woodland (CW), respectively. Estimates are log odds.

(a)

	β	SE (β)	*z*-value	*P*-value
(Intercept)	-1.341	0.333	-4.033	<0.001***
Distance to cropland	0.025	0.008	3.284	0.001**
Distance to rivers	-0.020	0.007	-2.674	0.007**
Distance to roads	-0.024	0.011	-2.184	0.029*
Slope	-0.075	0.036	-2.098	0.036*
EVI	-7.388	2.472	-2.989	0.003**
I(EVI^2)	12.883	6.277	2.052	0.040*
Protection category FR	-1.437	0.532	-2.700	0.007**
Protection category GCA	-1.061	0.453	-2.341	0.019*
Protection category GR	-0.183	0.232	-0.791	0.429
Protection category UA	-1.129	0.375	-3.006	0.003**



(b)

	β	SE (β)	*z*-value	*P*-value
(Intercept)	-2.46	0.44	-5.60	<0.001***
Distance to cropland	0.03	0.01	3.53	<0.001***
Distance to rivers	-0.02	0.01	-2.29	0.02*
EVI	-3.48	1.54	-2.26	0.02*
Landcover BA	0.32	0.32	0.99	0.32
Landcover CL	-0.39	1.11	-0.35	0.73
Landcover OW	0.60	0.25	2.39	0.02*
Landcover SA	-26.04	523.00	0.00	1.00
Protection category FR	-0.12	0.32	-0.38	0.70
Protection category GCA	-1.68	0.61	-2.77	<0.006**
Protection category GR	-1.65	0.33	-5.01	<0.001***
Protection category UA	-1.57	0.51	-3.07	0.002**

(c)

	β	SE (β)	*z*-value	*P*-value
(Intercept)	2.196	1.004	2.187	0.029*
Annual rainfall	-0.003	0.001	-2.287	0.022*
Distance to cropland	0.024	0.007	3.190	0.001**
Distance to roads	-0.016	0.010	-1.659	0.097
Elevation	-0.002	0.001	-2.421	0.016*
EVI	3.964	4.652	0.852	0.394
I(EVI^2)	-11.525	4.126	-2.793	0.005**
Protection category FR	-0.951	0.393	-2.418	0.016*
Protection category GCA	-0.528	0.440	-1.200	0.230
Protection category GR	-0.349	0.229	-1.520	0.129
Protection category UA	-0.878	0.294	-2.990	0.003**

(d)

	β	SE (β)	*z*-value	*P*-value
(Intercept)	-2.337	0.457	-5.118	0.001***
Distance to cropland	0.023	0.006	3.629	0.001***
Slope	-0.191	0.064	-3.013	0.003**
EVI	-2.413	4.599	0.525	0.600
I(EVI^2)	-15.531	5.728	-2.711	0.007**
Landcover BA	-0.961	0.435	-2.211	0.027*
Landcover CL	-1.708	1.027	-1.663	0.096
Landcover OW	-0.333	0.265	-1.256	0.209
Landcover SA	-0.146	0.851	-0.171	0.864

(e)

	β	SE (β)	*z*-value	*P*-value
(Intercept)	-3.057	0.459	-6.663	0.001***
Distance to cropland	0.033	0.015	2.276	0.023*
Distance to houses	-0.030	0.013	-2.426	0.015*
Distance to roads	-0.027	0.008	-3.581	0.001***
Landcover BA	0.736	0.437	1.683	0.092
Landcover CL	1.209	0.813	1.486	0.137
Landcover OW	0.981	0.369	2.655	0.008**
Landcover SA	-11.909	66.099	-0.180	0.857
Protection category FR	-2.381	1.023	-2.328	0.020*
Protection category GCA	-2.076	1.033	-2.010	0.044*
Protection category GR	-1.103	0.452	-2.441	0.015*
Protection category UA	-1.379	0.565	-2.440	0.015*

(f)

	β	SE (β)	*z*-value	*P*-value
(Intercept)	0.554	0.798	0.695	0.487
Distance to cropland	0.016	0.007	2.115	0.034*
Distance to houses	0.022	0.008	2.774	0.006**
Distance to rivers	-0.037	0.010	-3.646	0.001***
Elevation	-0.003	0.001	-3.762	0.001***
Protection category FR	-1.832	0.725	-2.528	0.011*
Protection category GCA	-1.314	0.529	-2.484	0.013*
Protection category GR	-0.588	0.227	-2.587	0.010**
Protection category UA	-0.695	0.293	-2.374	0.018*

Significance codes: '***' <0.001 '**' 0.01 '*' 0.05; GR, Game Reserve; GCA, Game-controlled Areas; FR, Forest Reserve; UA, Unprotected Area; EVI, Enhanced Vegetation Index; OW, Open Woodland; BA, Burnt Area; CL, Cropland; SA, Swampy area.

4. Discussion

Many parts of the world, especially those experiencing land-use changes, face unprecedented losses of mammalian megafauna (Dirzo et al., 2014; Ripple et al., 2015; Sala et al., 2000). Our time series analyses covering almost three decades of remote sensing data and aerial survey data of large-bodied mammal species in western Tanzania suggest that the KRE is no exception to this worrisome global trend, but the relation to land-use changes appears less obvious.

4.1 Land-use change

Between 1991 and 2018, cropland cover increased significantly in three (UA, FR, GCA) out of five protection categories (Fig. 2a & b) of the KRE. Our results clearly show that the highest rates of encroachment occurred in areas subject to fewer restrictions to human resource utilization, particularly in UA. Yet, starting from the early 2000s, cropland expansion occurred to a small degree even inside formally protected areas such as NP, GR, FR and GCA. Interestingly, GCAs exhibited the lowest rate of encroachment despite their relatively low level of protection (Fig. 2a). This may seem surprising as land-use change in PAs of Eastern Africa typically correlates with protection category (Riggio et al., 2019). While GCAs in other parts of Tanzania such as the Tarangire-Manyara ecosystem (Msoffe et al., 2011) or the Kilombero valley (Msofe et al., 2019) are subject to substantial land-use changes, GCAs in the KRE seem to be spared of encroachment. We assume that this may be due to their remote locations in hilly terrains with relatively low adjacent human population densities.

Similarly, the GR and NP were subject to relatively small land-use changes over time. However, cropland is now directly bordering Katavi National Park in several locations (Fig. 3). Among the PAs, FR recorded the highest amounts of cropland expansion over time. Presumably, this is linked to the immigration of people from the lake zone of Tanzania. The major increase in cropland cover occurred in the unprotected areas from 2006 to 2018. This land-use change is likely associated with an increase of the human population size (119,939 people in 2002 to 179,136 people in 2012) in Mpanda district which is mostly driven by immigration of people belonging to the pastoralists Sukuma ethnicity (URT, 2016), a process that started already in the 1980s (Izumi, 2017). Sukuma usually settle in frontier areas and clear woodlands and forests for agriculture (e.g., rice, maize, cotton, tobacco) (Salerno, 2016). When population growth limits further cropland expansion and land for grazing, households typically migrate to other areas (Coppolillo, 2001). Likely, such migration to frontier areas around PAs in the KRE contributed to the observed replacement of natural vegetation cover by cropland and may accelerate the degradation of natural habitat along PA boundaries (Salerno, 2016; Veldhuis et al., 2019). Indeed, Figure 3 shows widespread edge degradation due to cropland expansion around the southern and northern boundaries of Katavi National Park over the past three decades. Our species distribution models consistently suggest that all target species spatially avoided cropland, implying that cropland expansion pushes large wildlife species further into the core areas of PAs. This pattern has previously been shown for lions (*Panthera leo*) but not for large herbivores in Katavi National Park (Kiffner et al., 2013). However, the distribution of large herbivores in the Serengeti ecosystem in northern Tanzania seems to follow the same pattern (Veldhuis et al., 2019). Our land cover analyses further indicate that cropland extended towards the northwest of Katavi National Park in 2018, towards a wildlife corridor that ensures elephant movement between Katavi and Mount Mahale National Park (Caro et al., 2009). If the observed trend in land-use change persists in the future, elephant movements between Katavi and Mahale Mountains National Park are likely impaired.

Similar loss of connectivity due to insularization of PAs have been reported in other parts of East African such as the Tarangire ecosystem (Morrison and Bolger, 2014). Acknowledging that most of the land conversion in the KRE was presumably legal (i.e. occurred in unprotected areas), we suggest that future land-use change should be planned and guided by principles that ensure meeting both the needs of a growing human population as well as those of the wildlife populations (Grass et al., 2019). To achieve this, workable trade-offs between economic land-use activities of individuals and wildlife conservation goals should be a top priority. This requires better planning for the needs and wants of different stakeholders for example by implementing participatory spatial planning tools (Rambaldi et al., 2012).

4.2 Wildlife population trends

Analyses of nearly three decades of aerial surveys confirm declines in densities of many large ungulate species across different protection categories of the KRE (Caro, 2016, 2008; Mtui et al., 2017; Stoner et al., 2007). While several of the species-specific population trends did not produce a statistically significant signal in our study (likely due to low test power inherent to six data points), the overall decline of large mammals in the KRE is apparent [indicated by 25/30 species-area (6 species x 5 protection categories) combinations exhibiting a negative population trend signal over time] and a cause for concern. Similar to earlier work by Caro et al. (1998) and Caro (1999), our results suggest that populations of large mammals in the KRE occurred at much greater densities in areas with higher protection categories (particularly NP and GR) compared to areas with fewer restrictions on land-use and that these spatial density differences appear to have grown over time. Similar to studies in other ecosystems, the differences in densities detected across different protection categories in this study may be particularly pronounced in large-bodied species (Vinks et al., 2020). Interestingly though, less strictly protection categories (particularly FR and UA and to a smaller degree also GCA) seem to have supported relatively high densities of one or two large mammal species (zebra and buffalo) at the beginning of our time series. Seemingly, these areas no longer support functional population densities of the surveyed large mammal species during the dry season (Fig. 4c, d, e). This is a worrisome finding because those species provide important ecosystem services and contribute to the functioning of important ecosystem processes such as seed dispersal, nutrient cycling, and carbon sequestration (Berzaghi et al., 2019; Brockerhoff et al., 2017; Ripple et al., 2015). In addition, the loss of large herbivorous mammals in less strictly protection categories likely has strong cascading consequences for species of other taxa who crucially depend on large herbivores such as large carnivores (Vinks et al., 2020), commensal bird species (Diplock et al., 2018), or dung beetles (Wardle and Bardgett, 2004).

While our data covered nearly three decades, the observed trends may have underestimated the full extent of anthropogenic pressures on the distribution and population densities of wildlife populations, because human activities likely exerted negative impacts on wildlife populations before the start of systematic wildlife monitoring (Mihoub et al., 2017). Notwithstanding, our study depicts an illustrative example of the defaunation process in a large network of protected areas and helps to shed more light on large mammal conservation in the KRE. Drivers of wildlife declines rarely operate in isolation; they often work in tandem and synergistically drive population declines and local extinctions. For instance, habitat fragmentation could increase accessibility to humans and facilitate further reductions in habitat availability and exploitation of wildlife (Brook et al., 2008; Di Marco et al., 2015). In tandem with variables hypothesized to drive population declines, time series of wildlife population may provide circumstantial evidence on the underlying reasons for observed population declines (Caughley, 1994), or to characterize the defaunation process which is typically characterized by three phases: (1) wildlife exploitation using traditional technologies, (2) adoption of modern technologies to exploit wildlife, and (3) habitat conversion (Dirzo et al., 2014; Young et al., 2016).

Several underlying reasons for wildlife declines in the KRE have been tested previously. Reduced water flow caused by dam construction of the Katuma river may have negatively affected large mammal populations inside Katavi National Park (Caro et al., 2013). Diseases and droughts might have caused the wildlife declines but neither disease outbreaks have been reported by Tanzania National Parks Management, nor were there indications of droughts between 1987 and 2004 (Caro, 2008). Combining time series of land cover, wildlife densities and habitat selection models suggests that cropland expansion negatively influences the distribution of wildlife species. Thus, expanding cropland not only reduces the actual amount of available habitat but also reduces the amount of habitat that is effectively used by large mammal species (Table 2).

As such, expansion of cropland can clearly contribute to the observed wildlife declines. However, wildlife declines due to habitat loss typically occur with a time lag (i.e. several years *after* habitat loss), a scenario referred to as 'extinction debt' (Halley et al., 2016; Kuussaari et al., 2009). In contrast to this often-observed sequence, it is remarkable that, in our case study, we did not find this temporal pattern. Evidently, the main wildlife declines occurred during the 1990s (Fig. 4), and thus *before* major land-use changes occurred (Fig. 3). Because large herbivore species in the KRE do not necessarily rely on resources that are outside of protected areas as they do in migratory ecosystems such as the Tarangire and Serengeti ecosystems in northern Tanzania (Bond et al., 2017; Morrison and Bolger, 2014; Veldhuis et al., 2019), and because cropland cover was mainly restricted to the UA, it is unlikely that the cropland extent prior to 1991 caused the observed wildlife declines. Thus, as wildlife declines largely preceded habitat loss in the KRE, it is plausible that the initial wildlife declines were due to other causes.

Multiple previous studies in the KRE have suggested that illegal hunting (motivated by widespread consumption of bushmeat and sale of animal parts) was the key reason for declines in large mammal populations (Caro, 1999; Caro, 2008; Martin et al., 2013; Martin & Caro, 2012; Mgawe et al., 2012). The fact that all considered species are highly valued by hunters in the KRE (Martin et al., 2013) and the spatial distribution of wildlife declines provide circumstantial support for this hypothesis. While FRs and GCAs were similarly effective in protecting against land-use change to GR and Katavi National Park, they were seemingly ineffective in conserving populations of large herbivores. Both FR and GCA in the KRE are lightly staffed and anti-poaching patrols are rarely carried out in these areas, which effectively limits their effectiveness to habitat conservation and renders them largely ineffective for conserving populations of large mammals. In Rukwa GR, signs of illegal resource utilization were encountered more frequently than in Katavi National Park, lending support to the idea that illegal activities in the KRE are inversely correlated with protection category (Waltert et al., 2009). Moreover, evidenced by declines in elephant and buffalo populations (Fig. 4) and coherent reports of illegal hunting (Jones et al., 2018; Martin et al., 2012) inside the NP, even the conservation management in areas with the highest protection status was seemingly not sufficient to effectively protect populations of large-bodied mammals. In sum, these observations suggest that increasing the management effectiveness across all existing conservation entities would be necessary to boost wildlife populations in the KRE (Lindsey et al., 2017).

4.3 Correlates for the distribution of large mammals

Generalized linear mixed models (GLMMs) revealed consistent effects of protection category and land-use on the distribution of all investigated target species. Buffalo, elephant, giraffe, hartebeest, hartebeest, topi, and zebra preferred areas distant to cropland and preferred NP over other protection categories with fewer restrictions on resource utilization and possibly also less protection from legal and illegal hunting. Our findings reinforce findings from other case studies (e.g. Msoffe et al. 2011, Ogutu et al. 2012, Veldhuis et al. 2019), demonstrating that the expansion of land-use negatively impacts the distribution of large ungulates. It is noteworthy that these results are in contrast to results of a recent meta-analysis (Tucker et al., 2021), which showed that mammal population densities were higher in human modified areas. Likely, these discrepancies emerged due to our selection of target species: large-bodied species are susceptible to species filtering (e.g. Di Marco et al. 2015) and these species may have been extinct in human modified landscapes before they could have been surveyed systematically and registered in databases used for meta-analyses. Moreover, our results suggest that even when controlling for environmental variables, large mammal species avoid areas with less protection that do not effectively limit direct exploitation, confirming the strong influence of protection category in moderating distributions and densities of large mammals in East Africa (Bhola et al., 2012; Kiffner et al., 2020).

Further, our GLMMs confirm the strong surface water dependence of buffalo, elephant and zebra (Kihwele et al., 2020) during the dry season (Anderson et al., 2010; Eby et al., 2014; Treydte et al., 2008). As bulk grazers, buffalo preferred areas with high primary productivity (Anderson et al., 2016; Kaszta et al., 2016), but also areas with low vegetation productivity; areas with low EVI may provide safety from predation due to a large field of vision. Unexpectedly, elephant preferred areas with low primary productivity. Possibly, low EVI values are indicative of open woodland. Giraffe and hartebeest preferred areas with medium vegetation productivity, broadly supporting the forage maturation hypothesis (Esmaeili et al., 2021). Giraffe and zebra preferred low elevation areas while hartebeest and buffalo favored flatter areas, as these areas may likely provide relative good visibility and low movement costs (Anderson et al., 2016). Buffalo, giraffe and topi preferred to be in areas close to roads possibly due to vegetation changes and presence of minerals along the roads, which may attract some species (Laurian et al., 2008). Furthermore, roads in the KRE and other East African ecosystem are not necessarily impermeable barriers for large mammals (Morrison and Bolger, 2014), and some species (especially carnivores) may use them to navigate between different habitats. More broadly, our species distribution models highlight that species-habitat associations differ by species, reinforcing the need to protect heterogeneous landscapes for effective conservation of intact wildlife assemblages.

Conclusions

Our spatiotemporal investigations on wildlife populations and land-use changes over three decades suggest that populations of large mammals are declining across the Katavi-Rukwa Ecosystem, possibly not only in relation to recent cropland expansion but also because of other anthropogenic factors with illegal hunting being a plausible candidate. While multiple use areas such as Game Controlled Areas and Forest Reserves in the Katavi-Ruwka Ecosystem were relatively effective in protecting against land-use change, they were largely ineffective in conserving populations of large mammal species. Thus, investing in specific conservation actions towards protecting large herbivores in and around these protected areas may be worthwhile considerations. In light of the pervasive expansion of cropland in the Katavi-Rukwa Ecosystem, holistic landscape planning approaches are required to integrate wildlife conservation needs with an expanding human population and agricultural production.

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Chapter 5

Chapter 5

Modelling elephant corridors over two decades reveals opportunities for conserving connectivity across a large protected area network

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Abstract

Protected area (PA) connectivity is pivotal for the persistence of wide-ranging wildlife species, but is challenged by habitat loss and fragmentation. We analyzed habitat suitability and connectivity for the African elephant (*Loxodonta africana*) across PAs in southwestern Tanzania in 2000, 2010, and 2019. We quantified land-use changes through remote sensing data; estimated habitat suitability through aerial survey data, remotely sensed variables and ensemble species distribution models; modelled least-cost corridors; identified the relative importance of each corridor for the connectivity of the PA network and potential bottlenecks over time through circuit theory; and validated corridors through local ecological knowledge and ground wildlife surveys. From 2000 to 2019, cropland increased from 7% to 13% in the region, with an average expansion of 634 km^2 per year. Distance from cropland influenced elephant distribution models the most. Despite cropland expansion, the locations of the modelled elephant corridors (n=10) remained similar throughout the survey period. Based on local ecological knowledge, nine of the modelled corridors were active, whereas one modelled corridor had been inactive since the 1970s. Based on circuit theory, we prioritize three corridors for PA connectivity. Key indicators of corridor quality varied over time, whereas elephant movement through some corridors appears to have become costlier over time. Our results suggest that, over the past two decades, functional connectivity across the surveyed landscape has largely persisted. Beyond providing crucial information for spatial prioritization of conservation actions, our approach highlights the importance of modeling functional connectivity over time and verifying corridor models with ground-truthed data.

1. Introduction

Habitat loss and habitat fragmentation are among the most serious threats to biodiversity conservation worldwide (Newbold et al., 2016; Sala et al., 2000). To counteract these trends, protected areas (PAs) are key conservation instruments (IPBES, 2019; Joppa et al., 2008; Pimm et al., 2018; WWF, 2020). However, accelerating human pressures in unprotected land adjacent to PAs, mainly through cropland and settlement expansion, increasingly isolate terrestrial PAs in many parts of the world (DeFries et al., 2005; Mammides, 2020; Seiferling et al., 2012), including savanna ecosystems of East Africa (Fynn and Bonyongo, 2011; Newmark, 2008, 1996).

An effective way to ensure that PAs can meet their core conservation goals is to connect established PAs through corridors (Gilbert-Norton et al., 2010; Sekhran et al., 2010; Simberloff et al., 1999). Well-designed and sufficiently protected wildlife corridors (defined here as a swath of land intended to allow passage by a focal species between two or more PAs (Beier et al., 2008)) facilitate animal movement between two PAs or across an entire PA network. From a biological perspective, such functional connectivity provides multiple benefits to wildlife populations. Corridors facilitate genetic exchange between sub-populations and thus support genetic diversity, enable species to track seasonal changes in food resources, allow for distribution shifts if the habitat of one area becomes unsuitable, for example due to climate change, enable natural recolonization in areas where a species went locally extinct, and expand the area and diversity of habitats beyond the boundaries of the PAs (Brennan et al., 2021; Caro et al., 2009; Green et al., 2018).

Functional connectivity between PAs is particularly important for large-bodied and wide-ranging terrestrial mammals, such as African savanna elephants (*Loxodonta africana,* hereafter elephants) (Cisneros-Araujo et al., 2021b; Naidoo et al., 2018; Roever et al., 2013). Elephants have large home ranges (Galanti et al., 2006; Wall et al., 2021), and they have shown remarkable site fidelity to their home ranges and movement routes even over multiple generations (Fishlock et al., 2016; Polansky et al., 2015). In Miombo ecosystems of Tanzania, elephant distribution also overlaps with the distribution of many other mammal species, suggesting that conserving corridors designed for elephants could also be beneficial for many other mammal species (Epps et al., 2011; Green et al., 2018).

For centuries, elephant populations in East Africa have experienced multiple waves of human-caused mortality, primarily driven by the demand for ivory, interspersed with periods of population recovery (Chase et al., 2016; Foley and Faust, 2010; Milner-Gulland and Beddington, 1993; Spinage, 1973). In sum, elephant populations in East Africa are nowadays much smaller compared to historic baselines (Chase et al., 2016; TAWIRI, 2015a). Southwestern Tanzania - the focus of this study - contains one of the few remaining elephant strongholds in Tanzania (Chase et al., 2016; Jones et al., 2018), yet recent surveys suggest that their populations are declining: in the Ruaha-Rungwa ecosystem, elephant numbers declined from 31,625 in 2009 to 20,090 in 2013 (TAWIRI, 2013); in the Katavi-Rukwa ecosystem the population dropped from 6,396 in 2009 to 5,738 in 2014 (TAWIRI, 2014), and in the Ugalla ecosystem, their abundance declined from 4,000 in 2006 to 1,000 in 2009 (TAWIRI, 2010). While poaching is an immediate threat to the viability of elephant populations across the African continent (CITES, 2014; IUCN, 2020; Wittemyer et al., 2014), rapid, extensive and unplanned expansion of human land-uses in many parts of East Africa reduces the functional connectivity between PAs (IUCN, 2020; Riggio and Caro, 2017; Roever et al., 2013; UNEP et al., 2013) and poses a threat for the long-term persistence of elephant populations in the region (Cisneros-Araujo et al., 2021b). Recent genetic research shows incipient signs of genetic differentiation among elephant populations in southwestern Tanzania (Lobora et al., 2018), which indicates a potential lack of exchange between populations.

Although the locations of most wildlife corridors in Tanzania are broadly known (e.g.(Caro et al., 2009; Riggio and Caro, 2017)), their exact locations and their current status are often obscured (Jones et al., 2009). Ideally, the locations of wildlife corridors are informed by the actual movement of the target species (Alavi et al., 2022; Zeller et al., 2012), yet such data are rarely available for an entire PA network and over long time periods. As an alternative to animal movement data, presence data from periodically carried out aerial surveys provide a useful proxy for space use across large spatial scales (Pittiglio et al., 2012). Based on such presence data, species distribution models can be developed for target species (Tobgay and Mahavik, 2020; Torres et al., 2010) and the inverse of the habitat suitability (i.e. landscape resistance) can be used as input for modelling movement corridors across the PA network (Cisneros-Araujo et al., 2021a; Keeley et al., 2016).

While corridor models based on available species distributions and remotely sensed data are routinely performed for large-scale conservation planning (e.g. (Cisneros-Araujo et al., 2021a)), we here aim to conduct a thorough assessment of the PA network connectivity in southwestern Tanzania by adding four key elements. First, we include connectivity analyses over time (three snapshots during two decades) to identify the role of temporal processes affecting habitat suitability and connectivity (Martin et al., 2019; Ntukey et al., 2022; Saura et al., 2019). Second, we include empirical data (i.e. elephant presence data) instead of solely relying on expert opinion (e.g. (Cisneros-Araujo et al., 2021a; Van de Perre et al., 2014)) and parameterize species distribution models with natural landscape features (land cover, vegetation quality, terrain) and anthropogenic features (distance to cropland, distance to houses, distance to roads) instead of using land cover only (e.g. (Cisneros-Araujo et al., 2021a)) as input for modelling corridors. Third, we assess the relative importance of individual corridors to provide information for prioritizing conservation efforts on the ground. Fourth, we verify our corridor models through comparison with independent data (Osipova et al., 2019). In the absence of actual animal movement data (Zeller et al., 2012), we utilize local ecological knowledge data obtained via interviews with key informants. Previous research suggests that local ecological knowledge can provide a robust validation dataset for habitat (Madsen and Broekhuis, 2020) and corridor use of large mammals (Riggio and Caro, 2017; Van de Perre et al., 2014; Zeller et al., 2011).

To address our overarching goal of providing relevant information for the conservation of functional habitat connectivity across southwestern Tanzania, we aimed at: (i) quantifying land-use changes in the region; (ii) modelling region-wide habitat suitability for elephants over time using ensemble distribution models; (iii) identifying least-cost corridors for elephant movement between PAs over time; (iv) identifying the relative importance of each modelled wildlife corridor; (v) identifying areas where elephant movement is constrained; and vi) validating the connectivity models by assessing whether identified corridors are reportedly used by elephants.

2. Methods

2.1 Study area

Our study focused on southwestern Tanzania (between 6° to 9° S and 30° to 35° E), which covers an area of about 187,308 km^2 (Fig. 1). The region is characterized by a mosaic of unprotected land (i.e. land that does not belong to a formal conservation category), and formally protected areas. Protection categories range from areas with little enforcement of human land-use restrictions (Game Controlled Areas: here, settlement, agriculture, livestock keeping are not allowed, but hunting on permit in specific hunting blocks is allowed), areas that allow regulated resource extractions such as Forest Reserves (here, limited timber and non-timber products extraction is permitted) and Game Reserves (here, touristic game hunting on permit is allowed) to strictly protected National Parks where human activities are restricted to photographic tourism and research (Caro and Davenport, 2016; Caro, 1999). Notable PAs in the study area include: Katavi National Park (KNP) and Rukwa Game Reserve (RGR), Ugalla National Park (UNP), Lukwati-Piti Game Reserve (LPGR), Rungwa-Kisigo Game Reserve (RKGR) and Ruaha National Park (RNP), Kalambo Forest Reserve (KFR), and Mount Mahale National Park (MMNP) and Lwafi Game Reserve (LGR) (Fig. 1). The dominant terrestrial mammal wildlife species include buffalo *Syncerus caffer*, elephant *Loxodonta africana*, eland *Taurotragus oryx,* giraffe *Giraffa camelopardalis*, hartebeest *Alcelaphus buselaphus*, greater kudu *Tragelaphus strepsiceros*, topi *Damaliscus lunatus*, roan antelope *Hippotragus equinus,* and zebra *Equus quagga* (Caro, 1999; TAWIRI, 2018, 2014).

From 2000 to 2019 (the time period of our study), the area received between 350–2000 mm of annual rainfall, while the annual temperature ranged between 13–28 °C (CHIRPS, 2017). Elevation ranges from 600–2600 m asl. The vegetation mostly consists of miombo woodland, interspersed with *Acacia (Vachellia)-Combretum-Commiphora* woodland, grassland and flood plains (Douglas-Hamilton and Barnes, 1982). Miombo woodland typically forms a single storey canopy of deciduous trees dominated by species of the genera *Brachystegia, Julbernadia*, and *Isoberlinia* (Campbell, 1996). From 2000 to 2012, the human population in rural Tanzania has grown from 26,025,846 to 38,691,642 (World Bank, 2019). In the study area, human population growth is partially fuelled by immigration from other regions (NBS, 2012). The main land-use activities include agriculture and livestock keeping (NBS, 2012).

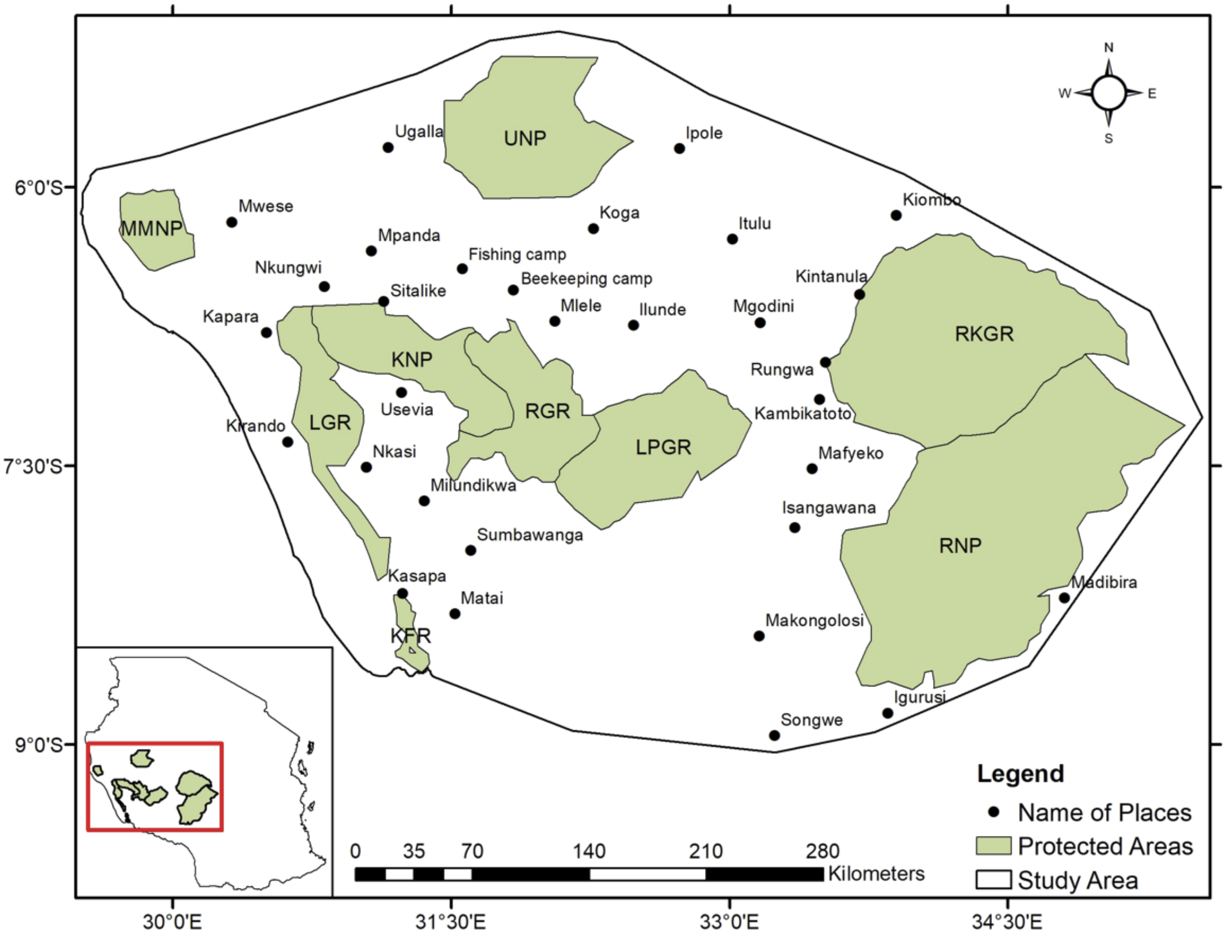

Fig. 1. Map of the protected area network of southwestern Tanzania, highlighting the spatial distribution of elephant's core areas (KNP = Katavi National Park, RGR = Rukwa Game Reserve, LPGR = Lukwati-Piti Game Reserve, LGR = Lwafi Game Reserve, KFR = Kalambo Forest Reserve, MMNP = Mount Mahale National Park, UNP = Ugalla National Park, RKGR = Rungwa-Kisigo Game Reserve, RNP = Ruaha National Park) and major towns and interview sites/villages. The inset in the lower left shows the location of the study area within Tanzania.

2.2 Elephant presence data and landscape variables

As a proxy for elephant space use across the study area, we used elephant presence data from periodically carried-out aerial surveys (Pittiglio et al., 2012). The main rationale was that such data were readily available at large temporal (three time steps during two decades) and spatial scales (TAWIRI, 2015a, 2010), and that aerial surveys relatively reliably detect elephants (Jachmann, 2002). We are aware that corridors are ideally informed by movement data from collared elephants (Poor et al., 2012; Xu et al., 2017), yet such data were not available for our study area.

We obtained 339 (year 2000), 295 (year 2011), and 293 (year 2019) geo-referenced detections of elephant groups from the Tanzania Wildlife Research Institute (TAWIRI). Aerial surveys were conducted during the dry season following the systematic reconnaissance flight technique as described by Norton-Griffiths (1978). The main rationale of using dry season data was that such data were readily available at large temporal and spatial scales. While elephants often range more widely during the wet season (Birkett et al., 2012), wet season surveys for the Katavi region are scarce (TAWIRI, 2015b) and likely fail to detect a substantial proportion of elephants due to limited visibility caused by green crown cover (Schlossberg et al., 2016). Based on established relationships between the distribution of large savanna mammals in Tanzanian ecosystems and landscape features (Bond et al., 2017; Giliba et al., 2022; Van de Perre et al., 2014), we selected the following landscape variables in our habitat suitability model: land cover (as a proxy for habitat structure and land-use), Enhanced Vegetation Index (EVI; as a proxy for primary productivity due to its advantages of reducing the background noise, atmospheric noise, and pixel saturation in most cases compared to NDVI during the dry season (Huete et al., 2002)), elevation, slope, topographic wetness index, terrain ruggedness and proximity to cropland, roads, houses, rivers, and rainfall. We obtained the global 30 m SRTM digital elevation model (DEM) for the study area from the U.S. Geological Survey (https://earthexplorer.usgs.gov) and used the DEM to derive slope, topographic wetness index and terrain ruggedness index using QGIS 3.16 (QGIS, 2020). We obtained spatial layers for houses for the years 2000 and 2011 from TAWIRI (TAWIRI, 2018) and for the year 2019 from OpenStreetMap (http://download.geofabrik.de/africa/tanzania.html). We obtained spatial layers for roads and rivers for a single time step from OpenStreetMap. For all three spatial layers, we generated distance raster surfaces at a resolution of 30 m using the Euclidian distance tool in ArcMap 10.6 (ESRI, 2018). We obtained the annual rainfall at a resolution of 5 km for each year for the study area from CHIRPS (https://data.chc.ucsb.edu/products/CHIRPS-2.0/). We generated EVI raster surface for the dry season (i.e. between July and September) of each year from Google Earth Engine - Landsat 5/8 Collection 1 Tier 1 8-Day EVI Composite (Gorelick et al., 2017). We projected all layers to the same projection and resampled them to 1 km resolution.

2.3 Spatial distribution of cropland

To produce land cover maps as inputs for land-use change analyses, habitat suitability and connectivity modelling, we acquired readily available 30 m resolution Landsat 5 and Landsat 8 imagery from U.S. Geological Survey's Earth Explorer (https://earthexplorer.usgs.gov/) for each time step. Our choice of date for satellite imagery was based on availability of aerial survey data for the dry seasons between 2000 and 2019, and imagery free from cloud cover. We used the atmospheric correction algorithm ATCOR to remove haze and calculated the top of atmosphere reflectance for Landsat 5 and Landsat 8 imagery using PCI Geomatica version 2018 (PCI Geomatics 2018). For land-use classification, we generated 600 training polygons for each year through composite imagery, high-resolution Google Earth images and field knowledge(Giliba et al., 2022). We used the scatterplot tool to evaluate our training samples to assess if there was enough separation between land cover classes using ArcMap (ESRI, 2018). Subsequently, we employed a supervised classification approach using a support vector machine algorithm to classify satellite imagery(Heydari and Mountrakis, 2019; Maulik and Chakraborty, 2017), which allowed us to condense land cover to five major categories: dense woodland, open woodland, burned areas, cropland, and water bodies. To assess the accuracy of our classified maps, we generated 1800 accuracy assessments points using stratified random sampling in ArcMap. We used high-resolution images from Google Earth and base-map layers from Google Satellite, ESRI Satellite, and Bing Satellite available in ArcMap and QGIS to validate our land cover maps (Connette et al., 2016; Hu et al., 2013; Yu and Gong, 2012). Our overall land cover classification accuracy for the three dates ranged from 96% to 98% with kappa coefficients ranging between 0.95 and 0.97 (Supplementary Information, Table S1).

2.4 Modeling habitat suitability

To avoid potential problems arising from collinearity, we tested variables for cross correlations using the corrplot package (Wei and Simko, 2017), and selected only variables with Pearson's correlation coefficient (r) ≤ 0.7 (Dormann et al., 2013). Due to a strong correlation between 'slope' and 'terrain ruggedness index', we removed the variable 'terrain ruggedness index', and used ten uncorrelated variables to fit elephant distribution models for each study period. We used elephant presence data with a background mask to generate 1000 pseudo-absences as response variable and environmental data as explanatory variables to build an ensemble model for each study period using the SDM package (Naimi and Araujo, 2019). Ensemble modelling uses multiple modelling algorithms, a strategy that minimises uncertainty associated with a single modelling approach and increases the accuracy of model predictions (Dondina et al., 2020). The ensemble model included the following algorithms: maximum entropy (Maxent), generalized boosted model (GBM), generalized additive model (GAM), and random forest (RF). We selected these algorithms based on their predictive power (high AUC values) obtained from the model run. For each algorithm, we ran 10 replications in which 75% of the presence points were used to train the model and the remaining 25% were used to test the model(Torretta et al., 2020). We used the area under curve (AUC) of the receiver operating characteristic (ROC) to evaluate the accuracy of four distribution models (Elith et al., 2006; Phillips and Dudík, 2008). To build the ensemble model, we used a weighted-averaging approach whereby individual models were weighted according to their predictive accuracy (Naimi and Araujo, 2019; Thuiller et al., 2009). We used the AUC of the ROC to evaluate the performance of the ensemble model (Marmion et al., 2009; Naimi and Araujo, 2019; Scherrer et al., 2019). Based on the output obtained from the models for the three study periods, we predicted habitat suitability for the entire landscape for each study period. To visualize the spatial and temporal dynamics of suitability maps for elephants over time, we categorized habitat suitability into three classes (high, moderate, and marginal) according to the natural breaks classification technique (Całka, 2018; Chen et al., 2019). We used the Jack-knife test to assess the relative contribution of each predictor in the final habitat suitability model for each study period.

2.5 Modeling habitat connectivity

For each time step, we modelled the connectivity across the PA network using Linkage Mapper (McRae and Kavanagh, 2011). As input data, we considered the polygon feature class containing core areas as source locations and a resistance surface map. As source locations we used the PAs (including area annexed in 2006) that are known to be occupied by elephants (i.e., all PAs that are displayed in Fig. 1). To estimate landscape resistance, we transformed the habitat suitability values into resistance values using the linear (i.e., the factor c = 0.25) transformation function (Keeley et al., 2016): $R = 100 - 99 * (((1 - \exp(-c * h))/(1 - \exp(-c)))$, where R is resistance, h is suitability, and the factor c determines the shape of the curves. For this transformation, resistance equals 1 when habitat suitability is 1 and resistance equals 100 when habitat suitability is 0. We used the linkage mapper to create least-cost corridors between PAs based on calculated cost-weighted distance (CWD)(McRae and Kavanagh, 2011). Due to a lack of empirical data on the optimum width of CWD for African savanna elephants, we tested three different maximum cost-distance values: 200, 150, 100, and 50 cost-weighted kilometers (cw-km); the 200 cw-km cutoff value (i.e. the largest default threshold in Linkage Mapper Connectivity Analysis Software (McRae and Kavanagh, 2011)) was chosen for further analysis because it resulted in reasonable corridor widths without the loss of multiple corridors connecting PAs, and it is wide enough to facilitate movement. Then, we truncated the least-cost corridors at 200 cw-km and this threshold was used to clip the least-cost corridors across the study period. To quantify the characteristics of each resulting least-cost corridor we used Centrality Mapper (which calculates the sum of all current density values) and Pinchpoint Mapper (which generates current-maps that identify and map pinch-points i.e., constrictions or bottlenecks) that utilize circuit theory (Mcrae and Shah, 2011), and treat resistance surface as the hindrance between PAs (Keeley et al., 2016). We used the Centrality mapper (McRae, 2012a) to identify the corridors most important for maintaining the connections among the networks (i.e., gatekeepers of connectivity), and Pinchpoint Mapper (McRae, 2012b) to identify bottlenecks (i.e., locations of the corridors where animal movement is restricted due to unfavorable landscape and anthropogenic features). We used two metrics to describe the quality of each corridor (Kong et al., 2021; Tobgay and Mahavik, 2020). First, the ratio of CWD to the Euclidean distance (EUD) separating each pair of PAs; this value indicates how difficult it is to move between PAs relative to how adjacent they are. Second, the ratio of CWD to the length of least critical path (LCP); this value indicates the average resistance along the optimal path between the PAs. For both metrics, high quality corridors are characterized by a ratio close to 1 (Dutta et al., 2016).

2.6 Validating habitat and corridor models

To validate our habitat suitability maps, we collected evidence for elephant presence (i.e., direct observations, elephant dung) along 105 three-kilometres transects within the Katavi-Rukwa ecosystem. We chose this subset of the study area for our validation approach as it is centrally located within the study region and allowed us to sample across a wide range of PA categories. We divided our validation study area into a 5 km by 5 km grid, so that transects were separated by 5 km to minimize spatial autocorrelation of our independent validation data. We surveyed each transect once during the dry season between July and September 2020. In each grid, we recorded centroid coordinates, and along each transect, we recorded the presence/absence of elephant dung. To validate our predictive maps, we first condensed our data to presence-absence; in 63 of the 105 transects we detected elephant dung; in the remaining 42 transects, we did not detect elephant dung. Second, we applied the specificity-sensitivity threshold (Grenouillet et al., 2011; Saupe et al., 2015) to convert our continuous suitability maps into binary maps (i.e., suitable and marginally suitable areas). Third, we superimposed presence data on the current 2019 binary map and used the extraction tool to extract the binary values to elephant presence data for accuracy assessment using ArcMap (Supplementary Information, Figure S1).

To validate our least-cost corridors, we conducted key informant interviews in sites (i.e., beekeeping and fishing camps) and villages close to the least-cost corridors generated within our study area. For each modelled corridor between two PAs, we conducted interviews at 1 to 3 villages or fishing/beekeeping camps: KNP-UNP (Uruwira fishing camp) and RGR-UNP Mlele (beekeeping camp), LPGR-UNP (Ilude-Koga), UNP-RHGR (Ipole, Itulu, Mgodini), LPGR-RKGR (Kambikatoto), LPGR-RNP (Isangawana), LGR-MMNP (Kapara, Nkungwi), LGR-KFR (Kasapa), MMNP-UNP (Ugala, Mwese), and RKR-KFR (Milundkikwa) (see Fig. 1 for the locations of the villages and camps). At each fishing/beekeeping camp, we interviewed 5 persons. In each village, we interviewed 10 persons: one village executive officer and/ or village chairperson, one beekeeper or fisherman, four members of natural resource committees or village game scouts, and four farmers and/ or pastoralists using semi-structured interviews. Prior to the fieldwork, we reported to the village office to gain permission for the interviews. We also involved the village leaders in selecting suitable interviewees (i.e. extensive wildlife knowledge; above the age of 18 years; and resident of the area since 2000). When approaching interviewee candidates, we explained the purpose of the study, promised that their identities would remain anonymous, and asked for consent to participate in an interview. The key interview questions were: i) "How many individual elephants have you seen in this area during the last year and where was this?", and ii) "What season of the year did you see the elephants?".

3. Results

3.1 Cropland cover and habitat suitability for elephants

From 2000 to 2019, the study area has experienced substantial land-use changes (Table 1). Most notable is a substantial increase of cropland cover from 6.71% (12,568 km^2) in 2000 to 13.14% (24,612 km^2) in 2019 (Fig. 2 & Table 1). On average, a total of 0.34% of surface area was converted to cropland every year (634 km^2/year). By 2019, cropland cover approached the borders of all PAs in southwestern Tanzania (Fig. 2). Our model evaluation results suggested that all ensemble habitat suitability models for each time step had good performance, with weighted average AUC scores above 0.8 (Table 2). Among the variables influencing survey-specific habitat suitability for elephants, distance to cropland consistently contributed most (Fig. 3). Based on the validation data collected in 2020, our overall predictive map accuracy for 2019 was 92.06%. Predictions of our ensemble model suggest that highly suitable elephant habitat declined over time: in 2000, 21.11% of the area was highly suitable for elephants, in 2011, this area was reduced to 20.25%, and in 2019, it was further reduced to 17.32% of the surveyed region (Fig. 4). At each time step, large portions of highly suitable habitat fell within the boundaries of PAs (2000: 16.57%; 2011: 16.28%; 2019: 14.14%; Fig. 4). Small pockets of highly suitable habitat were widely distributed in the eastern part of MMNP, the southern part of UNP, and the northern part of RKGR. Across the study period, most areas outside the PAs were classified as marginally suitable elephant habitat.

Table 1: Extent and rate of land cover changes between 2000 and 2019 in southwestern Tanzania (Area covered = 187,308 km^2).

Land cover type	**Area (%)**			**Change in land cover (%)**			**Average annual rate of change (2000-2019)**	
	2000	**2011**	**2019**	**2000-2011**	**2011-2019**	**2000-2019**	**(%)**	**(Km^2)**
Dense woodland	22.38	33.38	23.77	10.99	-9.61	1.39	0.07	136.57
Open woodland	38.43	38.45	31.17	0.03	-7.29	-7.26	-0.38	-715.36
Cropland	6.71	8.79	13.14	2.08	4.34	6.43	0.34	633.55
Burned areas	24.70	11.70	24.41	-13.00	12.71	-0.29	-0.02	-28.52
Water bodies	7.78	7.67	7.51	-0.11	-0.16	-0.27	-0.01	-26.31

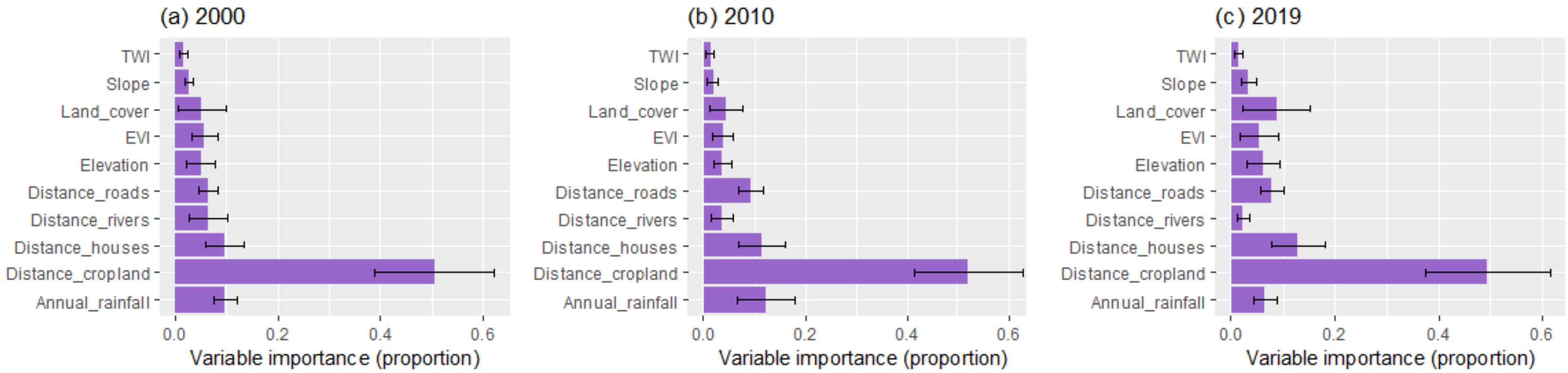

Fig. 3. Relative contribution of predictor variables for predicting the potential habitat distribution of elephants in southwestern Tanzania.

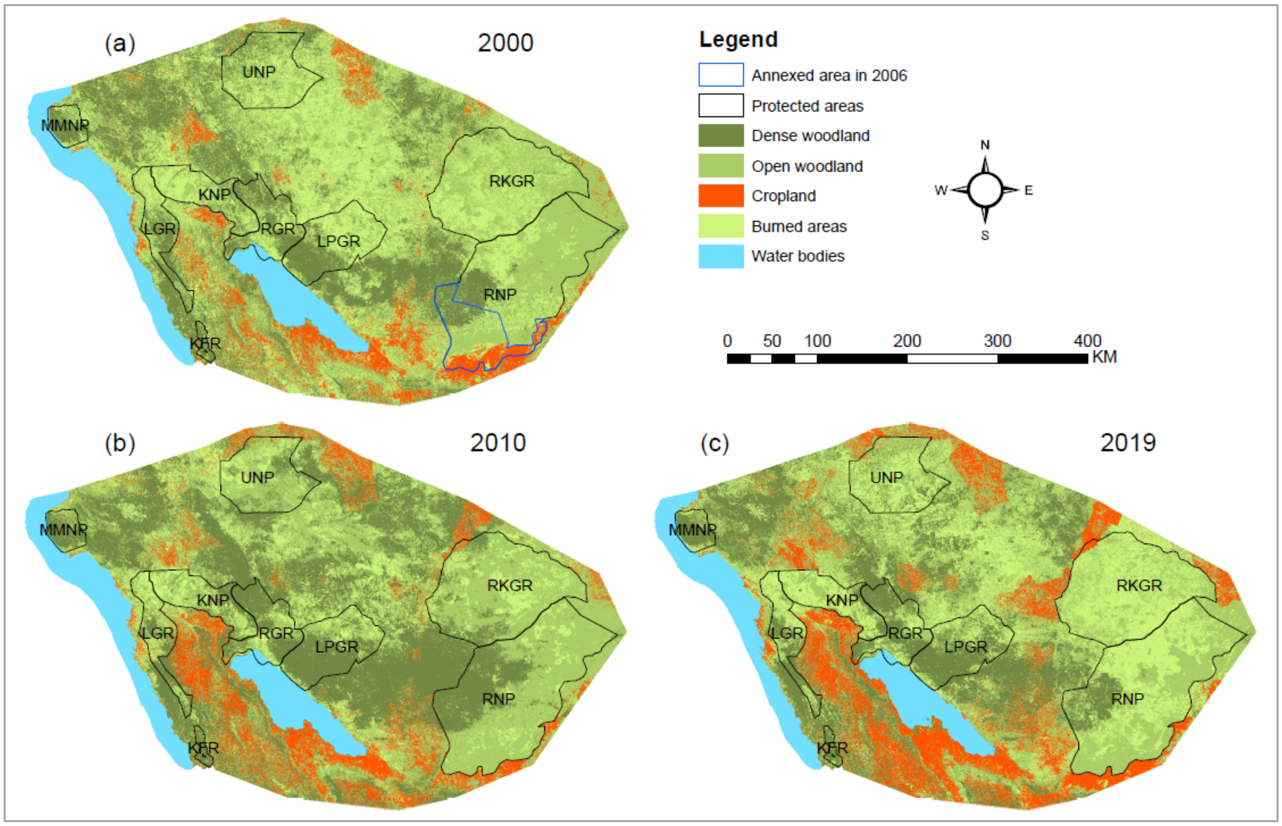

Fig. 2. Map of the study region, showing the estimated distribution of cropland in (a) 2000, (b) 2010, and (c) 2019. The polygon with the blue colour in (a) 2000 indicates area annexed by the RNP in 2006.

Table 2: Accuracy evaluation of the habitat suitability for elephants between 2000 and 2019 (AUC: area under the curve of the receiver-operating characteristic).

	AUC		
Methods	**2000**	**2010**	**2019**
Maximum entropy algorithm (Maxent)	0.85	0.86	0.85
Generalized boosted models (GBM)	0.85	0.85	0.84
Generalized additive models (GAM)	0.84	0.85	0.86
Random forest models (RF)	0.95	0.94	0.94
Weighted average	0.87	0.88	0.87

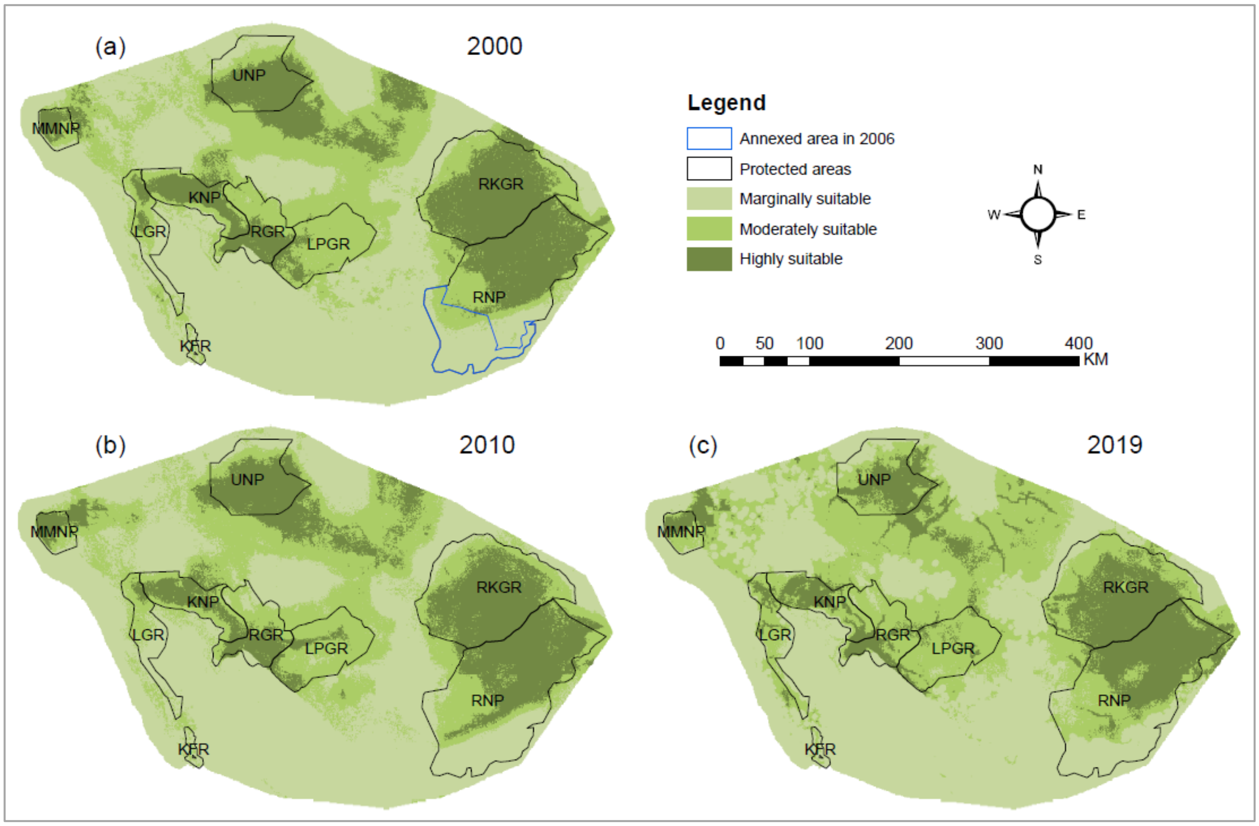

Fig. 4. Map of habitat suitability, indicating spatial and temporal distribution of potential habitat for elephant within protected areas network of southwestern Tanzania. The polygon with the blue colour in (a) 2000 indicates area annexed by the RNP in 2006.

3.2 Connectivity models for elephants

For each time step, our modelling approach identified ten elephant corridors across the PA network (Fig. 5 & Table 3). The findings of our analyses based on cost-weighted ratio metrics indicated a variation over time in the cost of elephant movement between PAs: The average resistance encountered by elephants along an optimal path between corridors varied over time (Table 3). Highest CWD:EucD ratios were recorded for the corridors linking RGR-KFR, LGR-KFR, and LPGR-KNP indicating that the cost of elephant movement between these PAs was higher than for other pairs of PAs throughout the study period (Table 3). The corridors between LPGR-UNP and RGR-UNP exhibited the lowest CWD:EucD ratios, suggesting that the costs for elephants to move between these PAs were lower than for other pairs of PAs throughout the study period (Table 3). Similarly, the highest CWD:LCP ratios were recorded for the corridors between RGR-KFR, LGR-KFR, and LPGR-RNP, indicating that the average resistance encountered by elephants along the optimal path between PAs was higher than for other corridors throughout the study period (Table 3). The lowest CWD:LCP ratio was estimated for the corridors between LPGR-UNP and RGR-UNP, indicating low resistance for elephant movement along these corridors (Table 3).

3.3 Relative corridor importance and bottlenecks

Across time, the main corridor locations remained relatively constant (Fig. 5 & 6). However, our network link centrality analyses showed that the corridors between LPGR-RNP, LGR-KFR, and LGR-MMNP recorded the highest centrality scores throughout the study period, highlighting their importance for overall connectivity in the region (Table 3). For all time steps, the lowest centrality score was recorded for the corridor between RGR and KFR, indicating its apparent minor role for overall connectivity (Table 3). Our pinch-point analyses also showed that areas with high current flow density represented corridor bottlenecks (Fig. 6). Despite the spatial location of bottlenecks remaining relatively consistent across time, its current flow density increased across corridors over time (Supplementary Information, Table S2). The corridors between MMNP-UNP, LGR-MMNP, and LGR-KFR, exhibited the highest current flow density, suggesting that elephant movement is more restricted at the corridor margins by physical barriers such as anthropogenic and topographical features than for other pairs of PAs throughout the study period (Fig. 6, Supplementary Information, Table S2). The corridors between UNP-RKGR, KNP-UNP, and LPGR-UNP recorded the lowest current flow density, highlighting that elephant movements are less restricted on the corridor margins by physical barriers throughout the study period (Fig. 6).

3.4 Validating elephant corridors

To validate our corridors, we systematically gathered local ecological knowledge from 130 interview partners in one fishing camp, one beekeeping camp and 12 villages in the vicinity of the modelled corridors. Out of 130 interview partners, 120 (i.e. 92%) reported that they saw at least one elephant during the last year (Table 3). Out of the ten modelled corridors, respondents confirmed that nine were used by elephants in the year prior to the interviews (Table 3). In five of these locations, interview partners reported that they observed elephants during the wet (October-December; March-June) and dry season (end of June to the beginning of October; January-

February) in the camp and village area (Table 3). In four locations, respondents reported elephant presence for the wet season only (Table 3). In the RGR-KFR corridor, none of the interview partners had seen elephants in the year prior to the interviews. According to the interview partners, elephants used this corridor until the 1970s. Among the active corridors, interview partners reported the highest relative numbers of elephants in areas located near corridors linking LGR-KFR, RGR-UNP, and KNP-UNP (Table 3).

Table 3: Attributes of 10 corridors mapped between PAs in southwestern Tanzania. Corridors are sorted by decreasing centrality scores to demonstrate their importance in keeping the protected areas network connected.

PA		**[a]CWD:EUCD**			**[b]CWD:LCP**			**Current flow centrality (Amps)**			**Sightings**	**[c]Sightings**	**Interview partners**	**Corridor**
From	**To**	**2000**	**2010**	**2019**	**2000**	**2010**	**2019**	**2000**	**2010**	**2019**	**Mean ± SD**	**Season**	**N**	**status**
LPGR	RKGR	84.90	85.54	89.86	77.51	78.09	82.03	7.34	7.31	7.09	7.80 ± 2.20	Wet and Dry	10	Active
LGR	KFR	96.05	89.21	91.25	88.88	77.43	82.18	6.91	6.90	6.93	21.90 ± 3.81	Wet	10	Active
LGR	MMNP	82.69	71.51	66.88	78.03	67.48	59.37	6.37	6.62	6.78	8.40 ± 3.44	Wet and Dry	20	Active
LPGR	RNP	86.65	86.27	86.07	81.54	81.79	81.00	4.79	4.82	4.92	10.40 ± 3.80	Wet and Dry	10	Active
RGR	UNP	64.48	63.85	68.40	61.13	56.63	56.25	3.62	3.54	3.60	18.40 ± 1.67	Wet	5	Active
UNP	RKGR	71.44	72.97	69.85	58.77	63.22	62.41	3.44	3.36	3.33	10.00 ± 3.15	Wet	30	Active
MMNP	UNP	71.21	71.77	72.26	64.09	65.16	65.74	3.28	3.05	3.00	11.50 ± 3.05	Wet and Dry	20	Active
KNP	UNP	72.23	68.58	70.67	62.79	63.06	64.70	3.03	3.09	3.09	16.60 ± 2.15	Wet	5	Active
LPGR	UNP	60.16	61.98	61.48	56.21	54.66	53.36	2.25	2.11	2.19	13.70 ± 1.88	Wet and Dry	10	Active
RGR	KFR	98.04	90.97	96.11	89.70	83.23	87.93	1.25	1.23	1.21	0	-	10	Inactive

[a] Index describes the cost of elephant movement between PAs relative to how adjacent they are.
[b] Index represents the average resistance encountered by elephants along an optimal path between PAs.

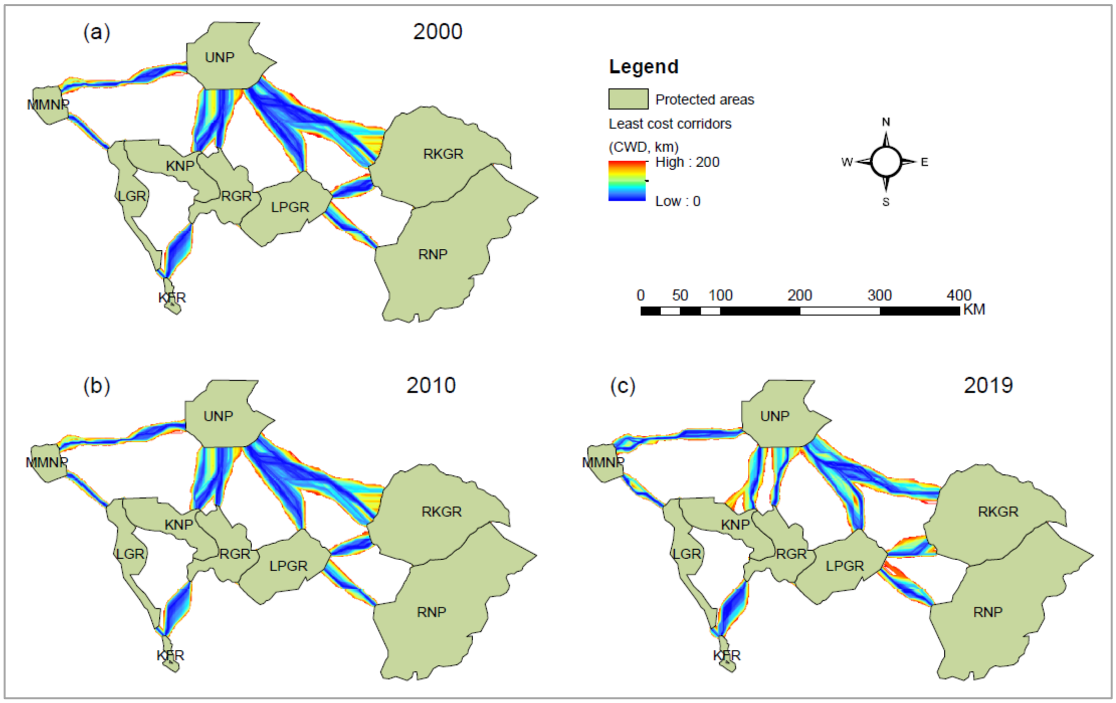

Fig. 5. Map of least-cost corridors clipped at cost-weighted distance (CWD) of 200 km, depicting spatial and temporal distribution of elephant corridors.

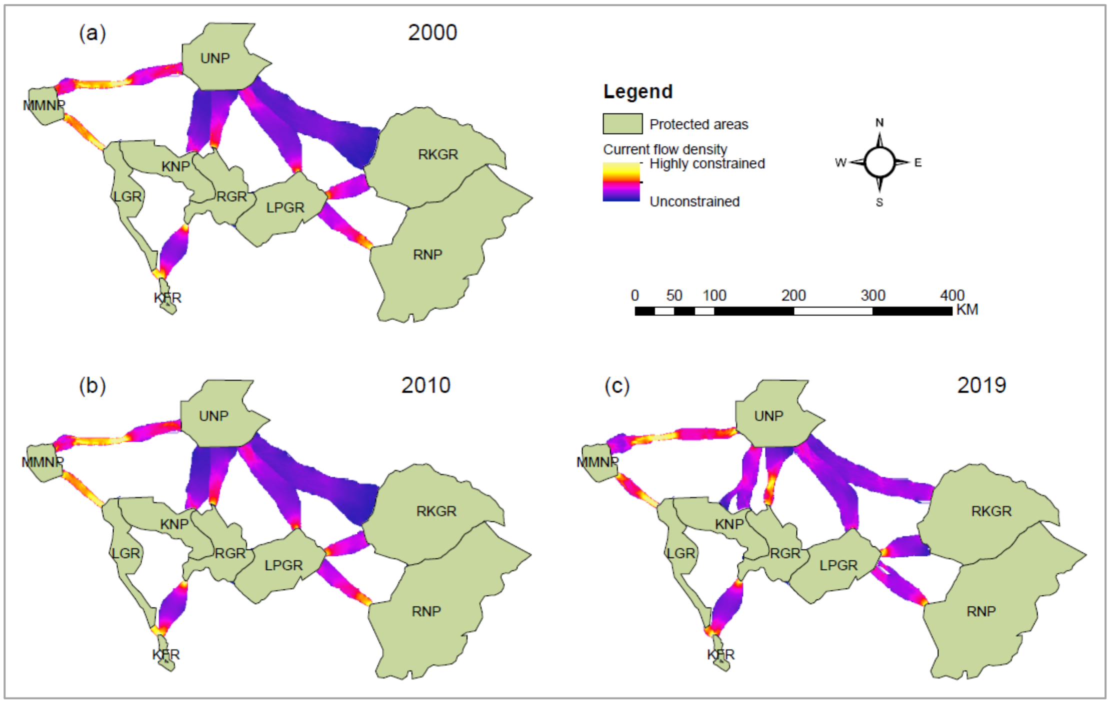

Fig. 6. Pairwise pinch point maps indicating where the current flow is highly restricted between the two protected areas.

4. Discussion

Our data-driven and field-validated models of elephant habitat and corridors over two decades suggest that functional connectivity for elephants is largely persisting in this region of southwestern Tanzania. However, the loss of at least one elephant corridor and the observed rapid pace of land-use change calls for timely conservation action to protect and partly restore the functional connectivity in this landscape.

4.1 Drivers of habitat suitability and functional connectivity

Our results indicate that the habitat suitability for elephants in our study area is more determined by anthropogenic variables than by environmental variables. Among the variables influencing habitat suitability, distance to cropland and houses consistently contributed most (Fig. 3). These findings echo results of other studies which have shown that elephants and other large East African mammals avoid cultivated and settled areas (Giliba et al., 2022; Morrison and Bolger, 2014; Ogutu et al., 2010; Riggio et al., 2022), highlighting that the expansion of human settlements and agriculture pushes and compresses the distribution of large wildlife species further into the core areas of PAs. This pattern has previously been shown for large herbivores in the Katavi-Rukwa ecosystem in western Tanzania (Giliba et al., 2022) and the Serengeti ecosystem in northern Tanzania (Veldhuis et al., 2019). While an evaluation of connectivity typically relies on movement data, our results on habitat suitability and elephant corridors derived from two independent presence/absence datasets (dung survey and local ecological knowledge) mirror elephant-habitat relationships [e.g. avoidance of human influence (i.e., settlements and cropland)] that were found in elephant movement-habitat studies (Wall et al., 2021). However, as our analyses were based on elephant space-use during the dry season, our models may not fully capture elephant movement. In some ecosystems of East Africa, elephant movements outside of PAs mostly occur during the rainy seasons (Kiffner et al., 2022; Pittiglio et al., 2012) and thus dry season distributions may provide rather conservative models for landscape-scale distribution and functional connectivity. Nevertheless, interview-based data suggest that the modelled corridors [which were based on imperfect data – a common issue for documenting dynamic processes such as long-distance migrations (Sawyer et al., 2009) are used by elephants during both dry and wet seasons (Table 3). Additional research could elucidate which areas of the ecosystem are primarily used for connectivity and which patches are additionally used as stop-over or longer-term habitat (Green et al., 2018).

Anthropogenic change such as expansion of human settlements and agriculture towards PAs are often associated with habitat destruction, encroachment and blockage of wildlife corridors (Kauffman et al., 2021; Wall et al., 2021). Among the ten key corridors identified, one was inactive and had been blocked by human settlements and agriculture before the start of our study. The remaining 9 active corridors were characterized by increasing movement costs over time and contraction caused by expansion of human settlements and agriculture (Supplementary Information, Fig. S2). Albeit still being in use, our land-use change analyses demonstrated that by 2019 most of our corridors (7 out of 10, i.e., RGR-KFR, LPFR-RKGR, LPGR-RNP, UNP-RKGR, MMNP-UNP, LGR-MMNP, and LGR-KFR) were encroached by cropland in the study region (Supplementary Information, Fig. S2c). Between 2000 and 2019, cropland cover increased by 634 km^2 per year, mostly at the expense of natural vegetation (i.e., dense and open woodlands) around PAs (Fig. 2). This land-use change in the region is likely associated with an increase of the rural human population (World Bank, 2019), which is partially elevated by immigration from other regions (NBS, 2012). Agriculture (e.g., rice, maize, cotton, tobacco) and livestock keeping are the main land-use activities in the region (NBS, 2012); the former is practiced in an unsustainable manner (i.e., shifting cultivation) particularly for tobacco production. Low fertility of the regions' soils (Chidumayo, 1999) and the nutrient-demanding nature of tobacco (Baris et al., 2000), as well as demand for biomass energy to dry the tobacco leaves (Jew et al., 2017) are the primary reasons for shifting cultivation in the region. Such shifting cultivation likely contributed to land-use change near elephant corridors and near core protected areas in the study region (Supplementary Information, Fig. S2a-c).

Importantly, the expansion of the RNP in 2006 resulted in further displacement of Usangu farmers and Sukuma pastoralists from Mbarali District to frontier areas around the western part of the park (Sirima, 2016). Likely, such migration to frontier areas around the western part of RNP contributed to the observed encroachment within LPGR-RNP and LPGR-RKGR corridors (Supplementary Information, Fig. S2a-c). If the observed trend in land-use change continues, elephant movements within the study region will most likely be hampered further in the near future (e.g., through RGR-KFR, LPFR-RKGR, LPGR-RNP, UNP-RKGR, LGR-KFR, and MMNP-UNP corridors), with anticipated negative consequences on population viability of elephants.

4.2 Conservation implications

The study region is one of the few regions in Africa where large scale movements of elephants seem to persist (Dejene et al., 2021; Zacarias and Loyola, 2018), yet our results suggest that this functional connectivity is increasingly threatened by anthropogenic land conversion for human settlements and cropland. A recent study recorded evidence of genetic differentiation among the elephant populations from the Ruaha-Rungwa and Katavi-Rukwa ecosystems in the study region (Lobora et al., 2018). Although the levels of genetic differentiation recorded were low and mainly concerned the younger cohort, it still indicates a recent divergence likely caused by habitat connectivity loss between the two ecosystems in the study region (Lobora et al., 2018). Linking PAs with corridors is a cost-effective way to safeguard functional connectivity within and across ecosystems and requires relatively little land as corridors do not necessarily need to be very wide. The importance of wildlife corridors is also reflected by the Wildlife Corridor Act of the Tanzanian government (MNRT, 2018, 2013). Based on our analyses, we recommend the following conservation actions to retain, restore or enhance ecological connectivity in the study region.

First, in areas where corridors get narrower (e.g., MMNP-UNP, LGR-MMNP, and LGR-KFR) and encroached (e.g., LPFR-RKGR, LPGR-RNP, UNP-RKGR, MMNP-UNP, and LGR-MMNP), delineation of the corridor would be a first crucial step in conserving wildlife corridors. This also requires enforcing land-use plans and having alternative and sustainable forms for generating income from the land without impairing wildlife habitat. One possible avenue for implementation would be generating a forest and wildlife-based economy from the modelled corridors (e.g., income from selling carbon credits, beekeeping, and ecotourism) in seeking to generate benefits from nature to outweigh the costs associated with wildlife conservation. For example, Carbon Tanzania established a REDD+ project that secures habitat in the corridor linking MMNP and KNP corridor through

LGR and provides adjacent communities with income through the sale of carbon credits. Second, in highly degraded areas within some modelled corridors (e.g., RGR-KFR, LPGR-RKGR, MMNP-UNP) due to human encroachment from arable farming, restoration may be an option through natural regeneration of miombo from roots and cut stumps (Luoga et al., 2004; Shirima et al., 2015; Syampungani et al., 2017). However, despite a high regeneration potential, long-term reforestation of native miombo species planning is required (Montfort et al., 2021) to restore highly degraded areas that cannot regenerate naturally. Third, our models provide spatially explicit locations of wildlife corridors, thus any future development projects (e.g., upgrading earth roads to tarmac roads) and activities impairing wildlife habitat should be prioritized outside of the modelled corridors to avoid further impacts on connectivity. In sum, a long-term strategy would be to incorporate PA networks into land-use plans that integrate the needs of both people and wildlife (Grass et al., 2019; Kremen and Merenlender, 2018). Our modelled elephant corridors and land-use change maps for the two past decades could offer valuable inputs for such landscape planning.

Conclusions

Conserving functional connectivity is vital for the long-term persistence of wide-ranging mammals, such as elephants. Our findings on connectivity in the Miombo region of southwestern Tanzania could help in the delineation, restoration, and conservation of elephant corridors. Elephant connectivity can be maintained or restored by reducing further anthropogenic cropland expansion towards the modelled corridors through implementation and enforcement of site-specific land-use planning. Our analysis integrates several temporal data sources (from remote sensing and aerial wildlife surveys), models (ensemble species distribution models, least-cost and circuit theory approach) and validation techniques (local ecological knowledge and ground wildlife surveys) to model spatially explicit wildlife corridors for effective PA network land-use planning and conservation. The approach can also be reproduced in other regions and for other wildlife species.

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Supplementary Information

Table S1: Cross-tabulation error matrix for 2000, 2010 and 2019 land cover classification in southwestern Tanzania.

Land cover 2000	Dense woodland	Open woodland	Burned area	Cropland	Water bodies	Total	User accuracy
Dense woodland	118	2	0	0	0	120	0.983
Open woodland	1	117	2	0	0	120	0.975
Burned area	0	2	117	1	0	120	0.975
Cropland	0	0	2	118	0	120	0.983
Water bodies	0	0	0	0	120	120	1.000
Total	119	121	121	119	120	600	
Producer accuracy	0.992	0.967	0.967	0.992	1.000		
Overall accuracy							0.983
Kappa							0.979

Land cover 2010	Dense woodland	Open woodland	Burned area	Cropland	Water bodies	Total	User accuracy
Dense woodland	117	3	0	0	0	120	0.975
Open woodland	2	114	3	1	0	120	0.950
Burned area	0	2	116	2	0	120	0.967
Cropland	0	2	2	116	0	120	0.967
Water bodies	0	0	0	0	120	120	1.000
Total	119	121	121	119	120	600	
Producer accuracy	0.983	0.942	0.959	0.975	1.000		
Overall accuracy							0.972
Kappa							0.965

Land cover 2019	Dense woodland	Open woodland	Burned area	Cropland	Water bodies	Total	User accuracy
Dense woodland	117	3	0	0	0	120	0.975
Open woodland	2	114	3	1	0	120	0.950
Burned area	0	4	114	2	0	120	0.950
Cropland	0	1	3	116	0	120	0.967
Water bodies	0	0	0	1	119	120	0.992
Total	119	122	120	120	119	600	
Producer accuracy	0.983	0.934	0.950	0.967	1.000	0.000	
Overall accuracy							0.967
Kappa							0.958

Table S2: Distribution of current flow density (Amps/cell) within the modelled corridors between PAs across three time steps (2000, 2010, and 2019) in southwestern Tanzania.

PA		**Current flow density (Amps/cell)**					
		2000		**2010**		**2019**	
From	**To**	**Min**	**Max**	**Min**	**Max**	**Min**	**Max**
MMNP	UNP	0.04	0.13	0.04	0.15	0.03	0.20
RGR	KFR	0.03	0.14	0.33	0.15	0.03	0.16
LGR	MMNP	0.09	0.12	0.09	0.13	0.06	0.15
LGR	KFR	0.08	0.11	0.09	0.12	0.09	0.14
LPGR	RNP	0.03	0.11	0.04	0.12	0.04	0.13
LPGR	RKGR	0.04	0.10	0.05	0.11	0.02	0.12
RGR	UNP	0.02	0.09	0.02	0.10	0.02	0.12
LPGR	UNP	0.03	0.08	0.03	0.09	0.03	0.07
KNP	UNP	0.02	0.04	0.02	0.50	0.23	0.06
UNP	RKGR	0.01	0.03	0.01	0.04	0.03	0.05

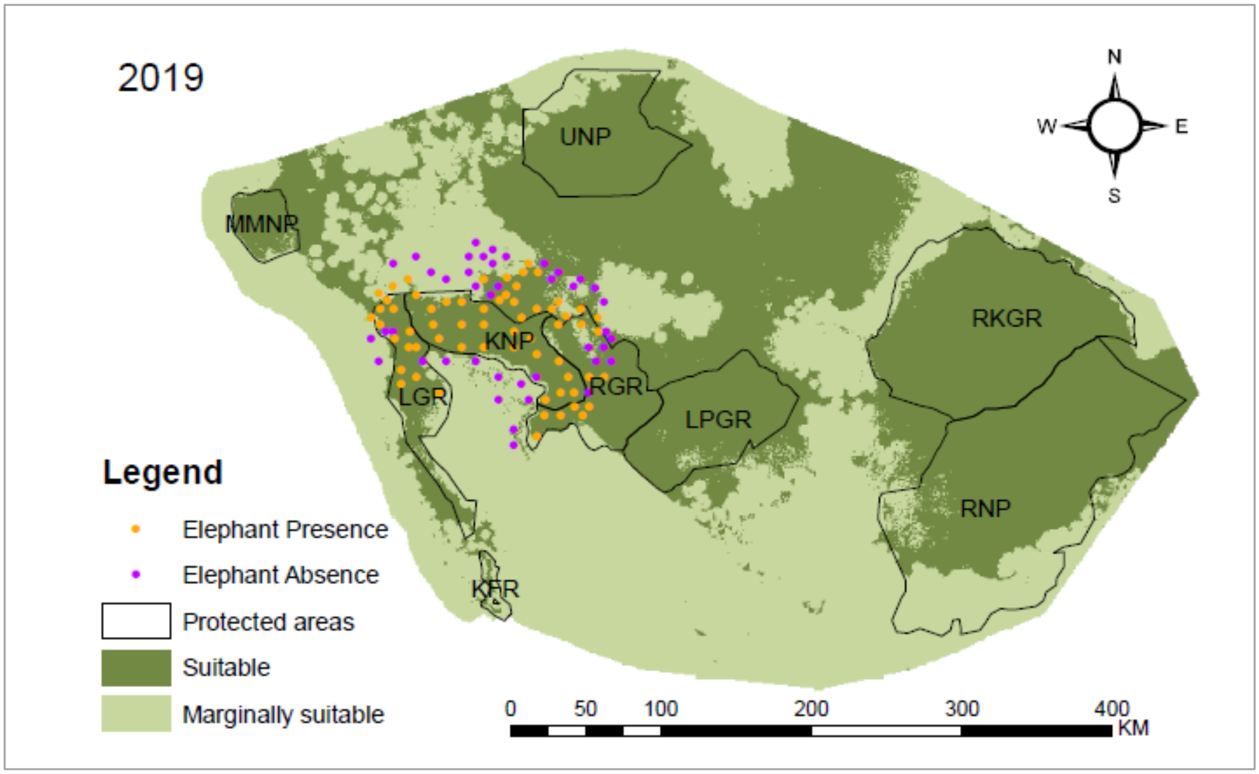

Figure S1. Validation map, presenting presence and absence of elephants within our predicted binary maps (i.e., suitable and marginally suitable areas) in 2019. Each dot represents a three kilometer long transect.

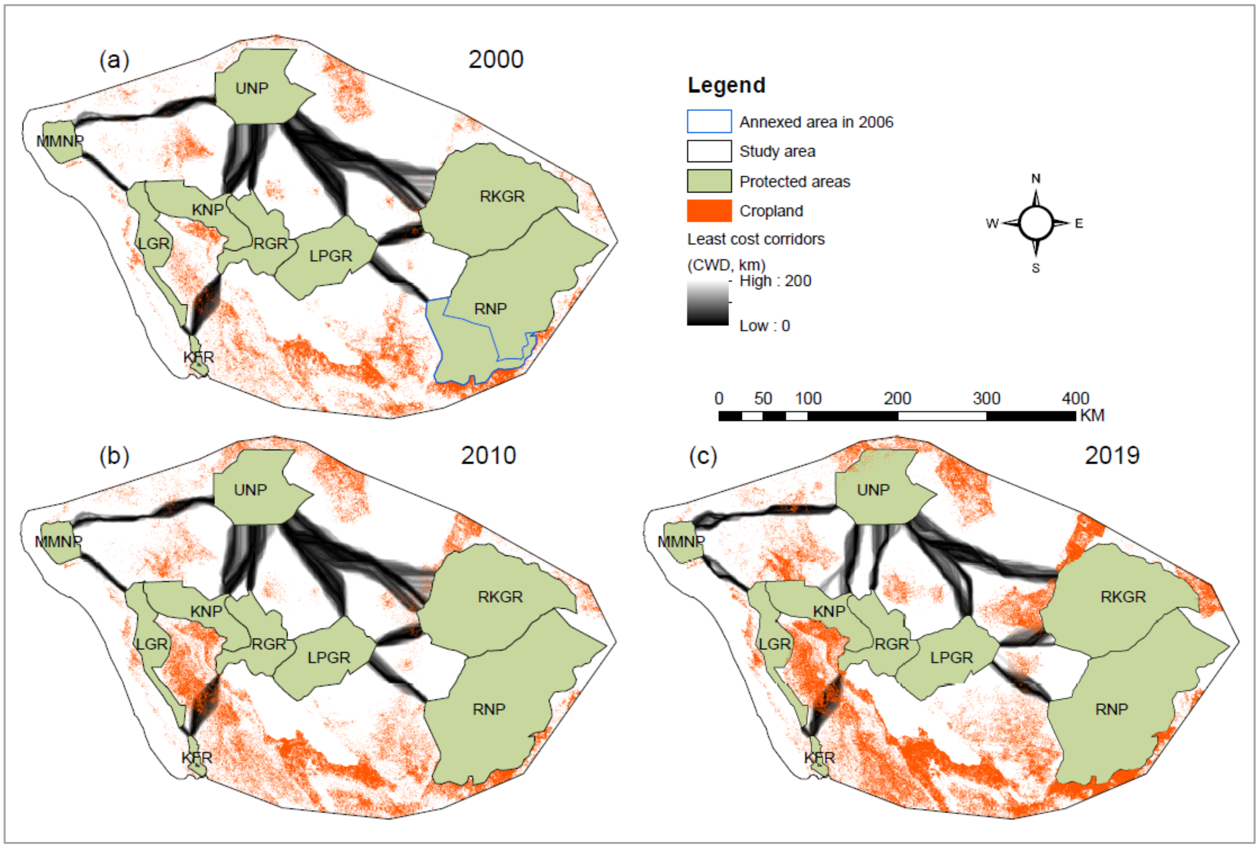

Figure S2. Map of the study region, showing the cropland distribution within and around the modelled corridors in (a) 2000, (b) 2010, and (c) 2019. The polygon with the blue colour in (a) 2000 indicates area annexed by the RNP in 2006.

Curriculum vitae Mr. Richard Alphonce Giliba (Msc.)

Part A: Personal History

Surname	Giliba
Given names	Richard Alphonce
Sex	Male
Date of birth	7th February; 1977
Marital status	Married (3 children)
Nationality	Tanzanian
Mobile	+255 767 710 622
Languages	Fluent English (written, spoken), Swahili (written, spoken)
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Part B: Brief overview

I have been working for over 10 years in the field of Ecology, Climate change mitigation (REDD+) and adaptation, Remote sensing and Geographical information sciences. I have worked extensively and intensively in the forest and wildlife resources planning and conservation. I hold a degree of a Bachelor's of Science in Forestry from Sokoine University of Agriculture, Tanzania obtained in 2005. I further hold three Masters Degrees one in Human Ecology from Vrije Universitiet Brussel, Belgium obtained in 2010; the second one is Advanced Studies in Human Ecology from Vrije Universitiet Brussel obtained in 2011; and the third one is Geographical Information Science from Lund University, Sweden obtained in 2018. I have published over 20 scientific papers including journal articles, guide books, and book chapters.

Part C: Academic Background

Basic education

1. Moringe Sokoine Secondary School, 1999 – 2001, Advanced Cert. Sec. Edu., Manyara, Tanzania
2. Singe Secondary School, 1994 -1997, Ordinary Cert. Sec. Edu., Arusha, Tanzania

Professional education

1. MSc. Geographical Information Science major in species distribution modelling, Lund University, Sweden, 2018

   Research work: Predicting the impact of climate change on the geographical distribution of plant species in the Eastern Arc Mountains forests of Tanzania.
2. MSc. Advanced Studies in Human Ecology major in Forest Ecology and Management, Vrije Universiteit Brussel, Belgium, 2011

Research work: Impact of Human activities in the Miombo woodlands of Northern Tanzania using Remote sensing and GIS, techniques

3. Msc. Human Ecology major in Environment and Development, Vrije Universiteit Brussel, Belgium, 2010
   Research work: Influence of socio-economic factors on deforestation in the protected areas of Northern Tanzania
4. BSc. Forestry, Sokoine University of Agriculture, 2005
   Research work: Laboratory analysis of Heavy Metals in Some Edible and Fodder Plants of Mazimbu Village, Tanzania

Academic awards

1. A best Overall Student in BSc. Forestry – 2005
2. Best Third Year Student in BSc. Forestry - 2005
3. Best Third Year Student in Forest Management and Administration - 2005
4. Best Third Year student in Forest Management Plan – 2005

Part D: Employment History

July 2020 - date	The Nelson Mandela African Institution of Science and Technology, Arusha Tanzania- Assistant Lecturer responsible for teaching, conducting research and consultancy
June 2006 – June 2020	Forestry Training Institute, Olmotonyi, Ministry of Natural Resources and Tourism- Tutor responsible for teaching, conducting research and consultancy
July 2005 – May 2006	FORCONSULT, SUA, Tanzania –Research assistant responsible for biophysical data collection and analysis
June 2001 – July 2002	Mbugwe Secondary School–Teacher responsible for teaching Biology and Chemistry

Part E: Professional Linkages

1. Alumni Member: Tropical Biology Associations
2. Members of Tanzania Association of Foresters
3. Member of Society for Conservation GIS

Part G: List of Publications

Journal Articles

1. **Giliba, R. A**., Fust P., Kiffner, C., & Loos, J. (2022). Using density surface models to assess the ecological effectiveness of a protected area network in Tanzania. Under review *Diversity and Distributions.*
2. **Giliba, R. A**., Fust P., Kiffner, C., & Loos, J. (2022). Modelling elephant corridors over two decades reveals opportunities for conserving connectivity across a large protected area network. Under review *Scientific Reports.*
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12. Mwendwa, P.M, **Giliba, R.A.,** (2012). Climate Change Impacts and Adaptation Strategies in Kenya. *Journal of Population Resources and Environment, 10: 22-29.*
13. Mwendwa P.M, **Giliba, R.A.,** (2012). Benefits and Challenges of urban green spaces. *Journal of Population Resources and Environment, 10: 73-79*

14. **Giliba, R.A.,** Boon, E.K., Kayombo, C.J., Chirenje, L.I., Musamba, E.B., Kashindye A.M., Shayo, P.F. (2011). Species Composition, Richness and Diversity in Miombo Woodlands of Bereku Forest Reserve, Tanzania. *Journal of biodiversity, 2:1-7*
15. **Giliba, R.A.,** Boon, E.K., Kayombo, C.J., Chirenje, L.I., Musamba, E.B. (2011). The Influence of Socio-economic Factors on Deforestation: A Case of the Bereku Forest Reserve, Tanzania. *Journal of Biodiversity, 2:31-39*
16. **Giliba, R.A.,** Mafuru C.S., Mary, P., Kayombo, C.J., Kashindye A.M., Chirenje, L.I., Musamba, E.B. (2011). Human Activities Influencing Deforestation on Meru Catchment Forest Reserve, Tanzania. *Journal of Human Ecology, 33: 1 – 9*
17. **Giliba, R.A.,** Boon, E.k., Kayombo, C.J., Chirenje, L.I., Musamba, E.B., Kashindye A. Mushi, J.R. (2011). Assessment of Heavy Metals in some Edible and Fodder Plants from Mazimbu Village, Morogoro, Tanzania. *Journal of Life Sciences, 3: 93-96*
18. **Giliba, R.A.,** Lupala J.Z., Kayombo, C.J., Kiungo, Y.M., Mwendwa P.M, (2011). The role and effectiveness of Local Institutions in the Management of forest biodiversity in New Dabaga-Ulongambi forest reserve, Iringa Region-Tanzania. *Journal of Population Resources and Environment, 10: 111-115*
19. Musamba E.B., Ngaga Y.M., Boon E.K., **Giliba R.A.,** Sirima A. and Chirenje L.I. (2011) Economics of Water in Paddy and Non-paddy Crop Production around the Kilombero Valley Ramsar Site, Tanzania: productivity, costs, returns and implication to poverty reduction. *Journal of Agricultural Sciences, 2:17-27*
20. Musamba, E.B., Boon, E.K., Ngaga, Y.M., **Giliba, R.A**. and Dumulinyi, T. 2012. The Recreation Value of Wetlands: A Case Study of Lake Victoria in Musoma Municipality, Tanzania. *Journal of Human Ecology 37: 85-92*
21. Musamba, E.B., Boon, E.K, Ngaga, Y.M and **Giliba, R.A**. 2011. Impact of Socio-economic Activities around Lake Victoria: Land Use and Land Use Changes in Musoma Municipality, Tanzania. *Journal of Human Ecology 35: 143-154*

Book Chapters and Guide Books

1. Mwakalukwa, E. E. **Giliba, R. A**. Kitereja S. N. and Woiso D. A. ed (2019). Silvicultural Practices. In: Handbook for Forestry Practitioners (in Press). E and D Publishing LTD, Dar es Salaam
2. Woiso, D.A. Giliba, R.A. Mongo S. and Kitereja S. N. ed (2019). Forest Botany. In: Handbook for Forestry Practitioners (in Press). E and D Publishing LTD, Dar es Salaam
3. Mugasha, W.A. Kashindye, A., Katani, J.Z., **Giliba, R.A**., Kingwere, S.R.J. and Zahabu E. ed (2019). Forest Resources Assessment In: Handbook for Forestry Practitioners (in Press). E and D Publishing LTD, Dar es Salaam practitioners

4. Augustino S., Silayo D.A, **Giliba R.A**. and Mawinda S. ed (2017). Forests and Climate Change Adaptation. In: Climate Change and Forestry Practices for the Technical Professionals, ISBN 978-9987-08-304-6. Mkuki na Nyota Publishers. p.37.
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7. Kayombo C.J., **Giliba R.A**. (2015). Identification guide for some fruits and green vegetables of Tanzania, Karljamer Print Technology ISBN 9789987030903
8. Kayombo C.J., **Giliba R.A.** (2015). Field guide to the plant species of urban forestry of Tanzania, Vilex enterprises ISBN 9789987031079
9. **Giliba R.A.,** Boon E.K., Kasindye A.M. (2012). Impact of Human Activities on the Miombo Woodlands of Bereku Forest Reserve. Lambert Academic Publishing ISBN 978-3-8484-9334-0

Declaration

I hereby certify that the submitted dissertation entitled "Biodiversity responses to a protection gradient in Tanzania" has been written by me without using unauthorized aids. I did not use any aids and writings other than those indicated. All passages taken from other writings either verbatim or in substance have been marked by me accordingly.

I hereby confirm that in carrying out my dissertation project I have not employed the services of a professional broker of dissertation projects, nor will I do so in the future. This dissertation, in its present or any other version, has not yet been submitted to any other university for review. I have not taken or registered to take another doctoral examination elsewhere.

Lüneburg,

Richard Alphonce Giliba