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Analysis of historical and current patterns and drivers of distribution and movements of large herbivores in the Limpopo National Park

By

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A thesis submitted in partial fulfilment of the requirements for the degree of Doctor of Philosophy in Forestry Resources – Environment and Wildlife at the Faculty of Agronomy and Forestry Engineering, Eduardo Mondlane University

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DECLARATION

I declare that this thesis is my unaided work. It has not been submitted before for any degree or examination in any other University. It is submitted in partial fulfilment of the requirements for the Degree of Doctor of Philosophy in Forestry Resources – Environment and Wildlife in the Forestry Engineering Department, Faculty of Agronomy and Forestry Engineering, Eduardo Mondlane University.

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…………………………………………….

(Signature of candidate)

Maputo, December 19, 2023

DEDICATION

I dedicate this thesis to my beloved family, my wife, **Teresa Assucênia Salvador Cumaio Roque** and my children, **Alícia Dionísio Roque**, **Ágatha Dionísio Roque**, and **Árchie Dionísio Roque**. I was absent from your daily life for more than four years. However, I am deeply grateful for your amazing love, patience, support, and wisdom. You were a source soul of my aspiration, encouragement and strength. There were many falls along the way, but you always reached out and lifted me. You taught me that in life the mistake is not falling but falling and not getting up.

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ABSTRACT

The distribution, abundance, and movements of species are crucial in spatial ecology and large herbivores (LH) communities' management in human-dominated landscapes because LH populations in these environments are critically low and some species undergoing endangered. The research aimed to contribute towards a better understanding of the historical and current distribution and movement patterns of LH in the Limpopo National Park (LNP), thereby creating a basis and providing evidence for the management and further development of the Greater Limpopo Transfrontier Park (GLTP). I combined historical and current LH occurrence data (1500-2021) based on a systematic literature search, census reports, online databases, dung count transects, and camera trap surveys to reconstruct the historical distribution and movement patterns of LH species using ArcGIS 10.8.1 in five different periods: (i) prehistoric period (around 1500), (ii) peak of the colonial period (1800-1975), (iii) post-colonial/civil war period (1976-2001), (iv) post-proclamation of GLTP (2002-2018), and (v) current period (2019-2021). I assessed the distribution patterns and the relative abundance of reintroduced LH (2019-2021) through camera traps in five habitat types and the wildlife reintroduced and not-reintroduced areas. I used aerial censuses (2001-2018), camera trap surveys, and dung count transects (2019-2021) to assess how ecological and anthropogenic factors influence the distribution of LH in 5 km x 5 km grid cells through a generalized linear model (GLM). I found a dramatic collapse of LH populations between the peak of the colonial and the post-colonial periods (1800-2001), followed by a slight recovery from the post-proclamation of GLTP to the current period (2002-2021). Elephants, buffalos, and zebra appear to recover better than giraffes, eland, blue wildebeest, and white rhinos. There were LH movements in the past, which ceased in the civil war period. Currently, there is evidence of the re-establishment of wildlife movements in the LNP. The distribution and abundance of LH were associated with habitat types rather than distance to the reintroduction site. Habitat types and rainfall were the most influential factors, while cattle grazing areas were the worst factors associated with the prevalence of LH. Some species tended to avoid human settlements, while others seem attracted to human settlements. Overall, the LH distribution and movement patterns decreased over time, and currently, the restoration is in an early and vulnerable state. These findings suggest connectivity between different habitats within the LNP despite intense human presence in the core area and buffer zone. Therefore, further efforts are necessary to strengthen the slow recovery of LH in the LNP. The findings highlight the need for further research on connectivity in the larger GLTP through GPS tracking of LH species. It would also allow investigating/quantifying the potential risk of human-wildlife conflict at finer spatial scales to improve future management in the LNP and GLTP.

Keywords: anthropogenic and ecological factors, distribution and movement of large herbivores, Great Limpopo Transfrontier Park, Limpopo National Park, Old Sanctuary, species restoration, wildlife ecological corridors.

RESUMO

A distribuição, abundância e movimentos das espécies, são cruciais na ecologia espacial de grandes herbívoros (GH) em paisagens dominadas pelo homem. O estudo teve como objectivo contribuir para uma melhor compreensão dos padrões históricos e actuais de distribuição e movimentos de grandes herbívorosno Parque Nacional do Limpopo (PNL), criando uma base e fornecendo evidências para o maneio e futuro desenvolvimento do Parque Transfronteiriço do Grande Limpopo (PTGL). Combinei dados históricos e actuais de ocorrência dos grandes herbívoros (1500-2021), colectados à base de pesquisas de literatura, relatórios de censos, base de dados *online*, contagem de fezes e armadilhas fotográficas para reconstruir os padrões de distribuição e movimentos históricos dos grandes herbívoros usando ArcGIS 10.8.1 em cinco diferentes períodos: (i) periodo pré-historico (1500), (ii) pico do período colonial (1800-1975), (iii) período pós-colonial/guerra civil (1976-2001), (iv) período pós-proclamação do PTGL e (v) período actual (2019-2021). Avaliei a distribuição e abundância relativa dos grandes herbívoros reintroduzidos (2019-2021) atravês de armadilhas fotográficas em cinco tipos diferentes de habitats e em areas de reintroduções e não reintroduções dos grandes herbívoros. Usei censos da fauna (2001-2018), armadilhas fotográficas e contagens de fezes em transectos (2019-2021), para avaliar a influência dos factores ecológicos e antropogênicos na distribuição dos grandes herbívoros em grelhas de 5 km x 5 km, usando modelos lineares generalizados. Os resultados revelaram um colapso dramático dos grandes herbívoros entre o pico do período colonial e período pós-colonial (1800-2001), seguido por uma ligeira recuperação do periodo pós-proclamação do PTGL até ao período actual (2002-2021). Os elefantes, búfalos e zebras, recuperaram-se melhor do que as girafas, elandes, bois cavalo e rinocerontes brancos. Houve movimentos dos grandes herbívoros no passado, os quais cessaram no período da guerra civil. Actualmente, há evidências do restabelecimento de movimentos da fauna no PNL. A distribuição e abundância dos grandes herbivoros foram associadas aos tipos de habitat e não à distância até o local das reintroduções. Os tipos de habitat e a precipitação, foram os factores mais influentes na distribuição dos animais. Algumas espécies evitaram assentamentos humanos, enquanto outras não. No geral, a distribuição e os movimentos dos grandes herbívoros diminuíram ao longo do tempo e, actualmente, a restauração do parque está num estado inicial e vulnerável. Os resultados do estudo, sugerem existir conectividade entre diferentes habitats dentro do PNL, apesar da intensa presença humana na área central e na zona tampão. Por isso, há necessidade de esforços adicionais para acelerar a recuperação dos grandes herbívoros no PNL. Estes resultados realçam a necessidade de mais pesquisas sobre conectividades no PTGL através do rastreamento com GPS (colocação de colares) em espécies dos grandes herbívoros. Estes colares, permitiriam, também, investigar/quantificar o risco potencial de conflito homem-fauna bravia em escalas espaciais mais precisas para melhorar a gestão futura no PNL e no PTGL.

Palavras-chave: Antigo Santuário, corredores ecológicos, distribuição e movimentos dos grandes herbívoros, factores ecológicos e antropogênicos, Parque Nacional de Limpopo, Parque Transfronteiriço de Grande Limpopo, restauração das espécies.

LIST OF ABBREVIATIONS AND ACRONYMS

ACE	Abundance coverage-based estimator
AIC	Akaike’s Information Criterion
ANAC	Administração Nacional das Áreas de Conservação (National Administration of Conservation Areas)
ANOVA	Analysis of Variance
BNP	Banhine National Park
CA	Commonality Analysis
CRU	Climatic Research Unit
DINAC	Direcção Nacional de Áreas de Conservação (National Directorate of Conservation Areas)
GBIF	Global Biodiversity Information Facility
GLM	Generalized Linear Model
GLTFCA	Great Limpopo Transfrontier Park and Conservation Areas
GLTP	Great Limpopo Transfrontier Park
GNP	Gonarezhou National Park
GPS	Global Positioning System
H'	Shannon Diversity Index
HWC	Human-wildlife conflict
IUCN	The International Union for Conservation of Nature
IPZ	Intensive Protection Zone
IQR	Inter-quartile range
KFW	German Development Bank
KNP	Kruger National Park
LH	Large herbivores
LN	Lebombo North
LNP	Limpopo National Park
LRT	Likelihood Ratio Test
MICOA	Ministério para a Coordenação da Acção Ambiental (Ministry for the Coordination of Environmental Affairs)
MINAG	Ministério da Agricultura (Ministry of Agriculture)
NRA	Not-reintroductions area

NS	Nwambia Sandveld
Past	Paleontological Statistics Software
PNL	Parque Nacional de Limpopo (Limpopo National Park)
PS	Pumbe Sandveld
PTGL	Parque Transfronteiriço do Grande Limpopo
RA	Reintroductions area
RAI	Relative Capture or Abundance Index
RV	Rugged Veld
S	Species Richness
SAC	Species Accumulation Curve
SC	Shrubveld on Calcrete
SDAE	Serviço Distrital de Actividades Económicas (District Economic Activities Service)
SSC	Species Survival Commission
VIF	Variance Inflation Factor
W_m	Akaike weight
ZNP	Zinave National Park

CHAPTER ONE

1. General introduction

African savanna ecosystems hold the richest large assemblages of large herbivores (LH, with body mass ≥ 10 kg) of the world (Bell, 1971; McNaughton, 198; Lovegrove and Haine's, 2004) that drive the structure, composition, and functioning of these ecosystems (Pickup *et al*., 1998; Naiman *et al*., 2003; Shorrocks and Bates, 2015). Research on LH distribution and movement patterns in these ecosystems is crucial for management because it provides a better understanding of interrelations between LH and their environment (e.g. mass migrations or landscape shaping functions of LH) (Gaston, 2009; Morales *et al*., 2010; Venter *et al*., 2015; Kauffman *et al*., 2021). Although Africa houses 90% of the world's LH diversity (Ripple *et al*., 2016; Owen-Smith *et al*., 2020), its landscapes are changing faster than any other region on Earth, with rapidly expanding human populations, massive infrastructure development projects and changes in climatic regimes (Ogutu *et al*., 2011; Owen-Smith *et al*., 2020). Therefore, there is a need to establish relationships between herbivores' distribution, movements and their changing environments (Owen-Smith *et al*., 2010; Owen-Smith *et al*., 2020), even because this is a prerequisite for species and habitat management. Some LH species are widely distributed and occur in large numbers, while others are rare and are less abundant/occur in low density (Cromsigt, 2006).

At the landscape scale, the combined influence of abiotic factors, biotic bottom-up processes, biotic top-down processes (Grange and Duncan, 2006; Matandiko, 2016; Panebianco *et al*., 2022), and anthropogenic disturbances (Hibert *et al*., 2010) determine the distribution, abundance and movement patterns of LH. Large herbivore species face temporal and spatial environmental variability leading to the unavailability of some habitats due to seasonality, pulsed resources or human activity (Lawson *et al*., 2015; Rudolf, 2019; Laska *et al*., 2021). Dispersal or migration may be necessary due to constraints of water availability (Chamaille-James *et al*., 2007), forage abundance (Thornton *et al*., 2013), competition and thermoregulation (Fritz *et al*., 1996), whereas at smaller extents, these constraints include topography, distance from water, forage quality and quantity, and predation (Valeix *et al*., 2009; Muposhi *et al*., 2016a). In partially fenced protected areas in a restoration state, local demographic processes coupled with dispersal often lead to source-sink dynamics, in which persistence in sinks (where the population growth rate is low or negative) is contingent upon immigration from sources, i.e. areas with positive or rapid growth (Dias, 1996; Gundersen *et al*., 2001). The habitat selection at the community scale or patches should vary with the relative availability of habitat types which determines the species distribution at the landscape scale (Paton and Matthiopoulos, 2016; Holbrook *et al*., 2019). Along the body size spectrum, the high metabolism of smaller LH favour high-quality forage with minimal long-term tolerance for low-quality foods than LH with slower metabolisms can survive on (du Toit and Owen-Smith, 1989; Anderson *et al*., 2016). Furthermore, smaller herbivores face a higher predation risk (Sinclair *et al*., 2003; Owen-Smith and Mills, 2008), and therefore, they prefer areas with shrubs that allow their hiding behaviour to reduce predator encounters probability (Anderson *et al*., 2016). Herbivores of large body sizes or those that move in large, aggregated groups can use risky habitats because, per capita, their predation risk is reduced (Fritz *et al*., 2002; Fryxell *et al*., 2007).

In southern Africa, historical information suggests that until the beginning of the colonial interference (15th century), LH species were most abundant and widely distributed throughout the region (Martinho, 1934; Du Plessis, 1969; Smithers and Tello, 1976; Plug, 1982; Carruthers *et al*., 2008; Ntumi *et al*., 2009; Boshoff and Kerley, 2010; Boshoff *et al*., 2016). The movements of ungulates in this period were also common and taken in the form of massive migrations and local changes between seasonal ranges (nomadism and dispersion) (Dingle and Drake, 2007; Roche, 2008; Owen-Smith *et al*., 2020; Kauffman *et al*., 2021). However, in the early 19th century, the abundance, distribution, and movements of LH declined dramatically (Berger, 2004) owing to an increase in habitat fragmentation due to the expansion of settlements, farming, pastoralism, and urbanization (Newmark, 2008; Harris *et al*., 2009). Kerley *et al*. (2003), Skead (2007), and Boshoff and Kerley (2010) recognized the value of historical data in the reconstruction of past distribution and restoration of wildlife in southern Africa. However, the historical and current knowledge of Mozambique's large mammal fauna is highly incomplete, and species distribution data is scarce for most taxa (Smithers and Tello, 1976; Ntumi *et al*., 2009; Neves *et al*., 2018, 2019; Stalmans *et al*., 2019). The overriding reason is that Mozambique has experienced armed conflicts with significant repercussions on the knowledge and status of its biodiversity (Neves *et al*., 2018; Neves, 2020). The most recent and complete synopsis of wildlife is 46 years old (Smithers and Tello, 1976). Mozambique also experienced a long civil war in the post-colonial period (1976-1992), leading to the disruption of socio-political systems (Hatton *et al*., 2001), which made travel, exploration and scientific expeditions problematic (Monadjem *et al*., 2010; Conradie *et al*., 2016). After the peace agreement (1992), conservation areas had been abandoned, with wildlife decimated and infrastructure largely destroyed (Hatton *et al*., 2001; Hofmeyr, 2004; Lunstrum, 2016), with no management and law enforcement. This became Mozambique's wildlife poorly documented during a long period (Hatton *et al*., 2001; Ntumi *et al*., 2009; Monadjem *et al*., 2010). With the onset of peace began the restoration of wildlife populations in conservation areas such as the Limpopo and Gorongosa National Parks and the establishment of transboundary conservation areas (MICOA, 1997, 2014; DINAC, 2003).

1.1. Problem statement

Many African protected areas still have human population inside their boundaries that depend on agriculture and forestry resources for their subsistence (Newmark, 2008; Harris *et al*., 2009). As the population density increases, livestock keeping, farming, and harvesting of wildlife and flora resources increase concomitantly in these areas (Leblond *et al*., 2013; Muposhi *et al*., 2016b; Sawyer *et al*., 2018), leading to habitat loss and fragmentation (Bhola *et al*., 2012; Sawyer *et al*., 2018). These semi-natural habitats progressively become restricted to small patches (Zeller *et al*., 2017) and less suitable for occupation by LH due to limited resources and security. The long-term survival of LH in these semi-natural habitats depends on their ability to undertake dispersal and seasonal movements to areas of higher resource quality and lower predation risk (Bolger *et al*., 2008; Purdon *et al*., 2018).

The Limpopo National Park (LNP) is a protected area in Mozambique created in 2001. It is part of the Great Limpopo Transfrontier Park (GLTP) proclaimed in 2002, which also comprises the Kruger National Park (KNP) in South Africa and Gonarezhou National Park (GNP) in Zimbabwe. These three parks, together with Banhine National Park (BNP), Zinave National Park (ZNP), and the interstitial zone between these parks in Mozambique, form the Great Limpopo Transfrontier Park and Conservation Area (GLTFCA, "see Figure 2.1, Chapter II") (ANAC, 2022). The historical patterns of wildlife distribution, abundance and movements were shaped by excessive off-take of ivory, systematic expansion of sport hunting, demarcation of colonial borders, and Rinderpest (Martinho, 1934; Hoare, 1999; Mavhunga, 2003; Mavhunga and Spierenburg, 2009). Wildlife has historically taken movements from the nowadays KNP to LNP and vice versa (Pienaar *et al*., 1966; Mabunda *et al*., 2012). The KNP-LNP fence constructed in 1976 separated the wildlife population and blocked historical seasonal movements, migration routes, and other ecosystem patterns and processes between the two parks (Mavhunga and Spierenburg, 2009; Lunstrum, 2014; Purdon *et al*., 2018). Currently, wildlife movements between KNP and LNP occur only through gaps in the LNP-KNP fence, along rivers, and where elephants have damaged it (Dunham, 2004; Mabunda *et al*., 2012).

Before 2001, LNP was a trophy hunting concession –"Coutada 16" (Massé, 2016; ANAC, 2022), where wildlife had been decimated due to Mozambique's civil war (1976-1992) and decades of poaching thereafter (Hofmeyr, 2004; Lunstrum, 2016). Thus, LNP started a phased restoration program carried out from 2001 to 2008 through (i) active wildlife translocation from KNP of 4,725 LH individuals belonging to ten species [African elephant (*Loxodonta africana*), white rhino (*Ceratotherium simum*), African buffalo (*Syncerus caffer*), giraffe (*Giraffa camelopardalis*), blue wildebeest (*Connochaetes taurinus*), plains zebra (*Equus quagga*), waterbuck (*Kobus ellipsiprymnus*), roan antelope (*Hippotragus equinus*), Lichtenstein hartebeest (*Alcelaphus lichtensteinii*), and impala (*Aepyceros melampus*)] to a 300 km^2 fenced area "Old Sanctuary", and (ii) passive wildlife translocations through three sections of KNP-LNP fence removed (Figure 1.1) to allow cross-border movements of wildlife from KNP into LNP (Mabunda *et al*., 2012). The sanctuary fence was removed (2006) to allow animals to disperse and colonize the habitats in the entire park (Mabunda *et al*., 2012). However, since the beginning of the LNP restoration program, no studies have attempted to understand the restoration stage, the adaptation of reintroduced LH to the new habitats after release and their ability to invade and colonize other habitats outside the release site. The ecological parameters of reintroduced LH remain poorly explained.

The location of the LNP in the core area of GLTP is has high significant value for the full GLTFCA functioning. Although the LNP Western boundary is safe for wildlife, the Limpopo River and linkages to the parks to the East and North are not, due to human presence and habitat fragmentation in which increasing isolation of the Park from nearby natural areas reduces or prevents the movement of certain species (ANAC, 2022). The

GLTP ecological goal is to holistically manage the Limpopo ecosystem to ensure the connectivity of habitats so that the historical transboundary movements and migration routes of wildlife are re-established (Bazin *et al*., 2016; ANAC, 2022). However, there is a lack of studies providing evidence of transboundary wildlife movement in the GLTP. Furthermore, no studies attempted to reconstruct LH distribution and movement patterns over time in LNP. Currently, 30,000 people live in the LNP, of which 22,748 people with 38,280 heads of cattle live in the buffer zone. The remaining inhabitants live in the core area – Shingwedzi Valley of the park (Figure 1.1), with 9,600 heads of cattle sharing grazing and natural water sources with wildlife (Bazin *et al*., 2016; Massé, 2016; ANAC, 2022). Human activities in the LNP consist of subsistence farming along the Limpopo, Olifants, and Shingwedzi Rivers, livestock keeping and “bush meat poaching” (hunting of wildlife for local consumption) (Andresen *et al*., 2014; Bazin *et al*., 2016). The resettlement of people from Shingwedzi Valley villages into Buffer Zone is in progress (Milgroom and Spierenburg, 2008). These will likely prevent LH from accessing riparian resources along the Limpopo River in the dry season (ANAC, 2022). Wildlife and people do not coexist peacefully in human-dominated landscapes, leading to human-wildlife conflicts (Virtanen *et al*., 2021; Nad *et al*., 2022). In 2012, LNP defined six potential areas for wildlife ecological corridors, i.e. an area that provides a continuous, or near continuous, link of suitable habitat through an inhospitable environment known to be used by animals for movement (Newmark *et al*., 1993). These corridors aim to reduce human-wildlife conflicts by providing safe wildlife movements and access to water in the Limpopo River at different seasons throughout the year (PNL, 2012) and ensure potential dispersal movements to the BNP and ZNP. Nevertheless, no study assessed the current planning of proposed ecological corridors despite little evidence of their functionality. The Limpopo River is excluded and inaccessible to wildlife along much of its length due to human activities and settlements (ANAC, 2018, 2022). This is likely to impact the proposed wildlife ecological corridors and the ecological patterns and processes in the LNP because this river has productive floodplains and pans, providing water and food resources for LH in the dry season. The adjacent sandveld and mopane woodlands would supply the species in the wet season. LH species will probably rely on the few smaller habitats on the park’s western side, reducing the ecological carrying capacity in the medium-long term. Despite this, to my knowledge, no studies attempted to understand how factors related to the LH ecology and human activities shape their distribution in the landscape and habitat scale.

1.2. The need for the study

The distribution and abundance of many LH species decreased by nearly 60% between 1970 and 2005 in southern Africa (Craigie *et al*., 2010) due to habitat loss, climatic shifts, exploitation, human encroachment and wars (Gaynor *et al*., 2016; Ogutu *et al*., 2016). In Mozambique, LH decreased dramatically during the post-colonial period (1976-2001) due to civil war and poaching (Hatton *et al*., 2001; Hofmeyr, 2004; Lunstrum, 2016; Stalman *et al*., 2019). The human settlements and activities are barriers to LH dispersal and movement in the GLTP (Andresen, 2015; Bazin *et al*., 2016). The successful management of the rehabilitation of LH populations in these human-dominated landscapes needs an understanding of pre-disturbance baselines, the magnitudes of species decline, and post-disturbance LH trajectories (Venter *et al*., 2014). Limpop National Park has ecological and biophysical features (diverse ecosystems, scenic landscapes, endemic and endangered species) that require priority for conservation (Hofmeyr, 2004; ANAC, 2022). For effective dispersion and movement of wildlife to the East of the LNP, the proposed wildlife corridors should be free of human impact (ANAC, 2022). The LNP has the potential for re-wilding and absorbing wildlife from KNP. The study of LH distribution and abundance through measuring ecological and anthropogenic parameters associated with LH communities may contribute to the current knowledge of LH conservation status, support the ecological restoration of the park and assess the post-release adaptation (colonization) of reintroduced LH to new habitats. Furthermore, the political assumptions and economic beliefs concerning eco-tourism development between Mozambique, South Africa, and Zimbabwe were one of the basis for the proclamation of the GLTP (DINAC, 2003; Mavhunga and Spierenburg, 2009; Lunstrum, 2016), without scientific evidence on the ground. Thus, the study will contribute to assessing the evidence concerning wildlife transboundary movements to support the ecological goal of the GLTP.

The reconstruction of the LH historical and current distribution and movements in a human-dominated landscape gives a framework for conservation planning and the development of a complete understanding of suitable ecological corridors. This would, in turn, support the human resettlement and management plan for further development of the

GLTP. This study will produce LH distribution patterns maps based on a probability of a species occurrence according to resources, conditions, and safety at broader landscape and habitat scales creating a basis to assess future distribution changes of species and supporting management decision-making concerning habitats or locations to prioritize when conserving target species. The study can also serve as a tool for adaptive management as it may support park managers to learn from the process of managing and thereby continuously improve their management procedures concerning species restoration, people resettlement, and human-wildlife conflict mitigation. As many protected areas in Sub-Saharan Africa are also human-dominated landscapes, the study can be applied as a tool for conservation planning and management in Sub-Saharan African savannas.

1.3. Research aim, objectives, and hypotheses

The focus of this research was initially envisaged as an analysis of historical and current distribution and migration patterns of large herbivores in the Limpopo National Park, looking to create the basis for management and policy-making for further development of the GTP. For the study of migrations along the GLTP and the effects of elephants on the distribution of other LH species, the project intended to receive data from collars placed on adult female elephants covering different seasons from 2017 to 2020 by Elephant Alive Project. However, I later received only data from areas used by elephants from 2017 to 2019 without migration movements because there was an overlap with another ongoing study from Elephant Alive. Therefore, the thesis title was updated to: “Analysis of historical and current patterns and drivers of distribution and movements of large herbivores in the Limpopo National Park” to reflect the new focus. Hence, the overall aim shifted to:

- To contribute towards a better understanding of historical and current distribution and movement patterns of large herbivores in the Limpopo National Park landscape, thereby creating a basis and providing evidence for the management and further development of the Great Limpopo Transfrontier Park.

The objectives of the study were as follows:

1. To reconstruct the historical distribution and movement patterns of large herbivores species and assess the functionality of proposed ecological corridors in the Limpopo National Park;
2. To assess the distribution patterns and the relative abundance of reintroduced large herbivores in the Limpopo National Park;
3. To assess how ecological and anthropogenic factors influence the distribution of large herbivores in the Limpopo National Park landscape.

The overall research hypotheses were:

H_1. The distribution areas and movement routes of large herbivores in the LNP landscape have changed over time such that most of the suitable sites for these species in the past are no longer available;

H_2. The current distribution and abundance of large herbivores in the Limpopo National Park landscape are associated with the availability of the habitat types rather than the historical site of their resettlements (Old Sanctuary);

H_3. The ecological factors (habitat types, rainfall, and perennial rivers) influence positively the distribution of large herbivores in the Limpopo National Park, while anthropogenic factors (settlements and cattle grazing areas) influence negatively.

1.4. Literature review

1.4.1. Historical distribution and movements of wildlife in southern Africa

Most LH species are found in Africa (Ripple *et al.*, 2015), although their populations have declined throughout the continent over time (Craigie *et al.*, 2010; Ripple *et al.*, 2015; Daskin and Pringle, 2018). Data from 24 savanna ecosystems in various parts of southern Africa revealed that wildlife systems tend to be dominated by comparatively few species out of the total spectrum occurring within the savannas (Cumming, 1982; Carruthers *et al.*, 2008). Thus, impalas are the most numerous, followed by wildebeest and springbok, while in terms of biomass, elephant, buffalo, and wildebeest are the top species (Ripple *et al.*, 2015; Fløjgaard *et al.*, 2021). The centuries-old trade involving ivory and wildlife skin allows inferring a widespread distribution and abundance of LH throughout Africa (Carruthers *et al.*, 2008; Madeiros, 2017). The increases in ivory, wildlife skin and other animal trade in the 19th century began to affect the distribution and abundance of wildlife (Huffman, 1996).

Millions of ungulates have historically taken migrations and other strategic movements across southern Africa in past centuries (Pienaar *et al*., 1966; Mabunda *et al*., 2012). However, at the beginning of the 19th century, the wide distribution of LH began to narrow, and migrations dramatically decreased (Berger, 2004) due to increasing habitat fragmentation caused by human encroachment, farming, pastoralism, and urbanization (Newmark, 2008; Harris *et al*., 2009). From the mid to late twentieth, wildlife migration routes were blocked by fence construction in the borders of conservation areas (Mabunda *et al*., 2003; Mavhunga and Spierenburg, 2009; Lunstrum, 2014). Wildlife was also massively culled by veterinary services to allegedly prevent livestock diseases caused by ticks, Rinderpest, and tsetse fly (Martinho, 1934; Mavhunga and Spierenburg, 2009). Therefore, the distribution of large mammals was restricted only to conservation areas and massive ungulate migrations were disrupted (Bartlam-Brooks *et al*., 2011), and the overall species abundance decreased (Martinho, 1934; Mavhunga and Spierenburg, 2009; Madeiros, 2017). What remained from that period were only dispersal movements, local shifts between seasonal ranges, and seasonal movements to areas of higher resource quality or lower predation risk (Bunnefeld *et al*., 2011; Naidoo *et al*., 2012; Owen-Smith *et al*., 2020; Kauffman *et al*., 2021).

1.4.2. Large herbivores reintroduction in human-dominated protected areas

Reintroduction is the process that attempts to return species to parts of their historical ranges where they were decimated (Armstrong and Seddon, 2008; IUCN/SSC, 2013). When reintroduced, individuals may disperse from release sites or to the broader reintroduction site as an adaptive response to explore and select optimal habitats (Scillitani *et al*., 2013; Richardson *et al*., 2015). As large herbivores are highly mobile species (Purdon *et al*., 2018), explore large home ranges (Shannon *et al*., 2006; Göttert *et al*., 2010; Owen-Smith and Martin, 2015), and require well-connected patches (Di Minin *et al*., 2013), the adaptation/acclimatization of translocated species to a new environment after their release, the dispersal behaviour, the quality of release site, the habitat requirements of the translocated species, and the availability and quality of surrounding habitats, including connectivity and linkages at the landscape scale, play a crucial role in the reintroduction success (Armstrong et *al*., 2013; Scillitani *et al*., 2013; Richardson *et al*., 2015). However, when the habitat requirements do not meet, the post-release may also involve a stress response and produce or stimulate non-adaptive habitat selection or homing behaviour (Dickens *et al*., 2010). Reintroductions can fail in the short term due to the immediate dispersal of released individuals and in the long term due to continued dispersal away from the reintroduction site. Conversely, reintroductions might also fail due to an absence of dispersal behaviour leading to a lack of long-term genetic and demographic exchange with other populations (Hanski, 1999; Richardson *et al*., 2015).

The source-sink theory offers a basis for understanding some of the factors that influence the function of protected areas (Hansen, 2011). The source refers to the origin of a process, and the sink refers to the process's disappearance (Chen *et al*., 2008). Protected areas may be subject to source-sink dynamics for three reasons: First, protected areas are portions of larger ecosystems, and native species move out and across the larger ecosystem to obtain needed resources over the annual cycle (Hansen and De Fries, 2007). Second, protected areas are often surrounded by areas of more intense land use (Wittemyer *et al*., 2008), and the resulting gradient in land use intensity and human interaction with native species can influence birth and death rates and create source-sink dynamics (Hansen *et al*., 2005). Third, protected areas locate in landscapes with gradients in topography, climate, soils, and other biophysical factors that can lead to differential habitat quality and spatially explicit population dynamics (Hansen and De Fries, 2007). In partially fenced protected areas in a restoration state where the number of species is a result of reintroductions and migrations, local demographic processes coupled with dispersal often lead to source-sink dynamics, in which persistence in sinks (where the population growth rate is negative) is contingent upon immigration from sources, i.e. areas with positive growth (Dias, 1996; Gundersen *et al*., 2001; Bisschop *et al*., 2019).

1.4.3. A brief historical of wildlife distribution in LNP – Mozambique

Knowledge of Mozambican large herbivore diversity is hardly incomplete, and historical species distribution, movements, and abundance data are scarce (Ntumi *et al*., 2009; Monadjem *et al*., 2010; Neves *et al*., 2018) because communities and early hunters of southern Africa did not have a megafauna recording in this period (Klein, 1987) and, when available, it consisted only of rock engravings (Zeller and Göttert, 2021). The distribution and abundance of wildlife in Mozambique are associated with anthropogenic events. Mozambique's wildlife has suffered for centuries from anthropogenic activities of multiple causes such as the ivory trade, skin trade, hunting trophies, increasing human settlements, liberation war, civil conflicts, and uncontrolled hunting for bush meat by rural communities (Martinho, 1934; Dias and Rosinha, 1971; Smithers and Tello, 1976; Tello, 1977; Dias, 1981; Ntumi *et al*., 2009; Madeiros, 2017).

The pre-historic/start of the colonial period (1500) to 1700 was characterized by a high abundance and wide distribution of wildlife in Mozambique because the colonialist's interest in this period was on gold mining and trade instead of wildlife hunting and trade (Newitt, 1997; Madeiros, 2017). At the end of the colonial period (1800 to 1975), the ivory and wildlife skin trade increased and reached its peak (Martinho, 1934; Huffman, 1996; Madeiros, 2017). The Limpopo River toward the Transvaal area was one of the main routes and sources of ivory and wildlife skin in southern Mozambique. These affected the distribution and abundance of wildlife in today's LNP and KNP (Huffman, 1996). From the 1980s in the post-colonial period, the large herbivores were almost decimated due to civil war (Ntumi *et al*., 2009; Neves *et al*., 2018, 2019), and the few remaining animals have restricted their distribution along safe areas such as the border with KNP in South Africa (Stephenson, 2013; Grossman *et al*., 2014; ANAC, 2018). However, the population of LH in the nowadays LNP (former Coutada 16) could not enter South Africa due to the fence built along the entire western border with KNP (Mabunda *et al*., 2003, 2012).

1.4.4. Landscape and habitat selection

The landscape is a spatially heterogeneous geographic area composed of mosaics containing inter-linked patches of different shapes and sizes that exhibit a specific geomorphology, climate, soil, and vegetation pattern together with associated fauna (Gertenbach, 1983; Lovett *et al*., 2005; Wu, 2008). A patch is a surface area that differs from its surroundings in structure or function (Lovett *et al*., 2005). Natural landscapes contain mosaics of patches within patches over broad scales (Garshelis, 2000). According to Fahrig and Nuttle (2005), in the landscape, the matrix is not homogeneous and consists of various cover types. Different types of cover may also provide different resource types needed at different periods during the organism's life history (e.g., feeding habitat, mating habitat). Other cover types represent non-habitat, which may differ in quality, for example, in the probability of mortality of the organism while it is in the cover type. The landscape structure consists of two main components: landscape composition, which refers to the different cover types present in the landscape and the proportions of each and landscape configuration, which refers to a change in the spatial pattern of cover types independent of any change in landscape composition (Dunning *et al*., 1992). If the landscape has fewer habitat types than another and the species of interest depend only on these few habitats, the species distribution ranges will reduce. However, if the species relies on more than one kind of habitat, it may allow the species to reach a wide distribution in the landscape (Fahrig and Nuttle, 2005).

Habitat is the resources (food and water) and conditions (temperature, precipitation, shelter, safety against predators) present in an area that enable occupancy, including survival and reproduction by a given organism (Morris, 1992; Hall *et al*., 1997; Krausman, 1999). Habitat may be used for foraging, shelter, refuge, shade, nesting, drinking, resting, reproduction, predation escape, denning, or other life history traits (Litvaitis *et al*., 1996). The activities of an animal may vary on a seasonal or yearly basis because a species may use one habitat in the wet season and another in the dry season (Traill, 2004; Treydte *et al*., 2013). A habitat used more than its availability is considered to be selected for and preferred. Conversely, a habitat used less than its availability is often refered to being selected against or even avoided (Garshelis, 2000).

Habitat selection is the process by which a species chooses its habitat (Krausman, 1999) driven by resources and conditions availability (Litvaitis *et al*., 1996). Resource selection by LH occurs at different hierarchical levels (Johnson, 1980; Senft *et al*., 1987; Bailey *et al*., 1996; Owen-Smith, 2002), and the decisions made by animals at these levels influence animal movements and hence the spatial distribution of populations: the first order of selection is the broadest scale, the geographic range of the species. Within that range, second-order selection determines the home range of an individual or social group. The third order pertains to the usage of various habitat components within the home range, selecting a feeding patch. The fourth level corresponds to a feeding station characterized by the abundance of some types of food, and the fifth order of selection is the procurement of food items from those available at that site.

At the community scale, when LH select plants either from the community or from locations within a community or micro-patches, the diet selection is based on palatability and the aggregate sensory image of a potential food (Senft *et al.*, 1987). At this level, foraging should solve two problems: which plants or plant parts should be selected from the immediately available material (diet selection) and how they should move through the community (location selection). Patterns of distribution and movements at the community scale, or selection of a grazing location within it, can be explained in different ways: 1) LH may utilize “momentary maximization”, which dictates sequential acceptance of the most palatable items encountered at each feeding location until palatability decreases to some threshold level, 2) when the best remaining item at the station is below some threshold, or when the rate of forage acquisition at that station falls below a threshold, the animal moves forward, establishing new feeding station (Senft *et al.*, 1987).

Large herbivores select plant communities and other components for feeding at the landscape scale. Topography and proximity to water attract LH at this scale (Senft *et al.*, 1987). The habitat selection should vary with the relative availability of habitat types in the landscape (Holbrook *et al.*, 2019). According to Owen-Smith *et al.* (2010), foraging behaviour within the patches influences the distribution and movements of LH at landscape scales. Herbivores generally encounter food within patches constituted by clusters of plants. One or two steps taken in succession do not interrupt feeding because the time taken per step is approximately equal to the time required to process (i.e. chew and swallow) a bite. Feeding in this concentrated way can continue unbroken for many minutes, particularly for larger-body herbivores exploiting the horizontally extended patches along the landscape. Nonfood resources such as water, shelter, and protection from predators are highly localized on the landscapes, but forage resources are dispersed. Water is often concentrated at discrete locations, and selection for watering points occurs less frequently than doe’s diet or community selection (Senft *et al.*, 1987).

The daily range encompasses shifts between foraging areas and between foraging areas and resting or drinking sites. During the growing (summer or wet) season, plants can soon regenerate the parts consumed, allowing herbivores to continue foraging within the same area for successive days or weeks. During the dry season, when vegetation becomes a non-renewing resource, edible plant components are progressively depleted, prompting more frequent shifts between foraging areas (Owen-Smith *et al.*, 2010). During the African dry season, grazers may need to travel to and from places where surface water remains available every day or two (Western, 1975; Gaylard *et al.*, 2003; Cain *et al.*, 2012), leading in changes in their distribution and movements patterns. Browsers are less water-dependent than grazers through being able to secure moisture from the green leaves that persist on evergreen trees and shrubs but are forced to travel to water when conditions become so dry that few leaves remain (Owen-Smith *et al*., 2010). Within small spatial scales and home ranges, the selection of vegetation types is influenced by the quantity and quality of food resources, topography (catena position), proximity to water, and predation risk (Senft *et al*., 1987).

1.4.5. Factors determining the distribution of large herbivores

Natural ecosystems are highly complex, and their structure and composition are determined by interacting and variable natural processes such as precipitation, herbivory, predation, soil taypes, and fire, as well as by anthropogenic effects, including management interventions (van Wilgen *et al*., 2022). The distribution, movements, and abundance of LH species are affected by biotic and abiotic factors in three broad classes of mechanisms: biotic bottom-up mechanisms related to resources supply (Fryxell, 1991; Sinclair, 2003; Fryxell *et al*., 2004), biotic top-down mechanisms involving predators and diseases (Sinclair *et al*., 2003; Grange and Duncan, 2006) and the interactions of both classes (Anderson *et al*., 2010; Burkepile *et al*., 2013; Panebianco *et al*., 2022).

Water sources

The species distributions relative to water sources should correspond to their water dependence. Specifically, water-independent species should be distributed randomly concerning distance to water, whereas herds of water-dependent species should occur close to water sources (Redfern *et al*., 2003). LH's abundance and distribution will decrease with increasing distance to permanent water, and this effect will be stronger for the grazers and mixed feeders with low tolerance to water deprivation (Gaylard *et al*., 2003; Redfern *et al*., 2003) and less strong for browsers (Western, 1975; de Leeuw *et al*., 2001). Owen-Smith (1996) suggests that grazers and mixed feeders with a high biomass density at a given area are the most affected by surface-water availability because the water content of grass falls below that of browse during the dry season.

Rainfall

Populations of herbivores may increase or decline dynamically with changing rainfall patterns (Castillioni *et al*., 2022). Rainfall influences LH by determining the distribution of resources, such as forage and surface water, and habitat conditions, such as vegetation cover providing shelter, refuge and shade (Gaylard *et al*., 2003). High rainfall improves conditions by enabling rapid vegetation growth and providing ready access to surface water (Deshmukh, 1984; Castillioni *et al*., 2022), leading to increases in LH abundance and distribution (Gaylard *et al*., 2003; Castillioni *et al*., 2022). However, excess water in the form of floods may cause population declines, directly or indirectly, by reducing food availability and seasonally restricting LH distribution (Shrader *et al*., 2010).

Vegetation cover

Large herbivores select habitats with different vegetation covers (woodlands, shrublands, and grasslands) at different seasons of the year (Loarie *et al*., 2009), depending on their availability, food quality and quantity, and safety (Cornélis *et al*., 2011; Boyce *et al*., 2016). Grazers prefer to graze in habitats with short to medium (Traill, 2004) and medium to tall grasses as the body size increases (Musiega *et al*., 2006). Pure browsers select habitats with woody plant forage (Owen-Smith and Cooper, 1989), while mixed feeders prefer woodland with minimal undergrowth and low to medium-height grasslands (Botha and Stock, 2005). The vertical cover consists of deciduous and coniferous that reduces exposure to adverse climatic conditions (Ager *et al*., 2003), while lateral cover decreases predation risk by reducing prey detectability (Tufto *et al*., 1996).

Geology and soils

The soil proprieties determine vegetation patterns that provide heterogeneity in terms of food and habitat for a range of animals (e.g. from open grassy areas for grazers to densely wooded areas for browsers) (Smit and Prins, 2015). As soil quality refers to nutrient availability, poor soils support low-quality forage, which limits LH distribution and abundance (Venter *et al*., 2003). LH abundance and distribution will be greater in locations with high soil nutrient availability because these areas are related to palatable vegetation (Augustine *et al*., 2003).

Human settlements and livestock

Large herbivore species are highly mobile and sensitive to anthropogenic disturbances because they require well-connected patches (Di Minin *et al.*, 2013) to persist. LH may concentrate away from settlement areas to avoid humans and exposure to hunting risk (Leblond *et al.*, 2013; Muposhi *et al.*, 2016b). They can also persist in some human-dominated areas, however, suffering restrictions, occupying small habitat patches away from people, overlapping with people in space but not in time by adopting different day-time and night-time behaviour (Douglas-Hamilton *et al.*, 2005; Cook *et al.*, 2015).

Fire

Fire is an important ecological process in African savanna, where it plays a central role in determining the structure, composition, function and heterogeneity of these ecosystems (van Wilgen *et al.*, 2003, 2022; Bond and Keeley, 2005). Fire is also one of the key factors in maintaining the competitive balance between trees and grasses in savanna (Higgins *et al.*, 2007). Fire depends on fuel and weather that vary over space and time and, therefore, cannot be considered in isolation. The most important sources of fire variability include soil fertility, rainfall, levels of herbivory, and variability in the conditions under which fire burns (van Wilgen *et al.*, 2003). Fire may increase the spatial and temporal heterogeneity (Hassan *et al.*, 2008), thus affecting large herbivores' distribution at different scales. Large herbivores are attracted to burned areas (Sensenig *et al.*, 2010). This preference has been mainly attributed to the new plant growth (Eby *et al.*, 2014). In the short term, fire stimulates the grass regrowth and sprouting of plants (van Wilgen *et al.*, 2003). The grass regrowth and sprouting plants have nutritious and attractive grass sward and shrub leaves containing high amounts of protein, calcium, potassium, phosphorus, and other elements (Moe *et al.*, 1990; Eby *et al.*, 2014) that attract large herbivores. In the long term, fire changes the structure and composition of the vegetation/habitat. Higher-intensity fires kill the aerial portions of trees, and they resprout only from the base, whereas less intense fires allow aerial tissues to survive, and the height growth of trees is not affected (Trollope *et al.*, 1998).

1.4.6. Human-wildlife conflict

Human-wildlife conflict (HWC) occurs when the needs and behaviour of wildlife impact negatively on humans or when humans negatively affect the needs and survival of wildlife (Madden, 2008; Mekonen, 2020). These conflicts may result when wildlife damage crops, threaten, kill or injure people and domestic animals population adjacent to wildlife habitats (Mekonen, 2020), while human beings persecute wildlife in retaliation for losses incurred and undermine their conservation and survival through poaching, illegal hunting and destruction of their habitats (Ogra, 2008). HWC today is driven by multiple factors (Hoare, 1999; Mumby and Plotnik, 2018; Pozo *et al.*, 2018). Depleted, destroyed, and fragmented habitats force wildlife to shift into other areas, changing their traditional movement and distribution patterns and spatially isolating populations (Chiyo *et al.*, 2005; Dunham *et al.*, 2010). Wildlife habitat loss is due to human population growth and land-use transformation, which changes the dynamics of social and ecological systems (Dunham *et al.*, 2010; Shaffer *et al.*, 2019). As the human population increases and the demand for resources grow, the frequency and intensity of HWC increase (Newmark *et al.*, 1993; Mekonen, 2020). The land-use transformation, coupled with climate change, increase competition for scarce water and food resources during dry periods, which pulls wildlife into human habitations attracted by highly palatable crops and permanent water reservoirs (Tiller *et al.*, 2021; Virtanen *et al.*, 2021; Nad *et al.*, 2022).

1.5. Study area and research design

The study was conducted in Limpopo National Park, a protected area in the Gaza province in Mozambique (Figure 1.1A-B). The LNP, together with the KNP and the GNP, forms the GLTP. It is also a crucial element of this transboundary protected area network because is centrally located. The GLTP can be defined as a large-scale conservation area comprising three areas which border each other across the South African, Mozambican, and Zimbabwean borders and the Makuleke communal area (ANAC, 2022). The area between the Park boundary, the Limpopo, and Olifantes Rivers forms the buffer zone of the Park (Figure 1.1C-D). The buffer zone is conceived as strips of land on park boundaries, within which the sustainable use of natural resources will be permitted (Wells and Brandon, 1993). The buffer zone in the LNP entails a 5 km strip west of the Limpopo

River and to the North of the Olifantes River and covers an area of 1,720 km^2. The area is heavily settled and farmed (ANAC, 2022).

Based on 2020 statistics, 30,000 people are living in the LNP, of which 22,748, with about 38,280 heads of cattle, live in the buffer zone. The remaining inhabitants live in four villages in the core area (Shingwedzi River) of the park (Milgroom and Spierenburg, 2008) and are scheduled to be resettled to the buffer zone (Massé, 2016, ANAC, 2022). In these villages, there are about 9,600 head of domestic cattle (ANAC, 2018, 2022) that share grazing areas with wildlife. The LNP falls within the Mopane vegetation of the Sudano-Zambezian Region and corresponds to the Veld Type 15, Mopani Veld (ANAC, 2018, 2022). Stalmans *et al*. (2004), based on woody vegetation, species composition, and physiognomy, described ten landscape types (Figure 1C) with 15 plant communities in the LNP. Although the KNP-LNP fence is still in place, some sections of the KNP-LNP boundary are still accessible for wildlife movement (Figure 1.1D). Details of study area description are presented in chapters two, three, and four.

The LNP was selected for the study because: 1) it is a crucial element of a transboundary conservation area – GLTP due to its location as a bridge between KNP and other Parks of the GLTFCA, 2) LNP has ecological and biophysical features that require priority for conservation: diverse ecosystems, scenic landscapes, endemic and endangered species (DINAC, 2003; ANAC, 2022), 3) the need of bring scientific evidence concerning the achievement of the ecological objective of the GLTP (wildlife transboundary movements and management and development of the GLTP), and 4) the need to understand the wildlife recovery process in the park since the beginning of the restoration program in 2001. I selected 16 LH species that showed some increase in their population number since 2004 (Stephenson, 2013; Grossman *et al*., 2014; ANAC, 2018). These LH species also represent different feeding guilds. Of these species, seven were actively reintroduced in the park from 2001 to 2008 (Tables 2.1 and 3.1, Chapters 2 and 3). Data collection was based on a systematic literature search, report censuses of wildlife, online databases, dung count transects, and camera trap surveys. This study covered the period from 1500 to 2021 at the broader landscape and habitat scales.

I combined historical and current LH data to reconstruct the historical distribution and movement patterns of LH species and to assess the use of proposed ecological corridors by LH in the LNP. I addressed the historical distribution and movement patterns in five different periods: (i) prehistoric/start of the colonial period (around 1500), (ii) peak of the colonial period (1800-1975), (iii) post-colonial/civil war/intense poaching period (1976-2001), (iv) post-proclamation of GLTP (2002-2018), and (v) current period (2019-2021). I assessed the distribution patterns and the relative abundance of reintroduced LH in five habitat types: (i) Nwambia Sandveld, (ii) Mopane Shrubveld on Calcrete, (iii) Rugged Veld, (iv) Lebombo North, and (v) Pumbe Sandveld. I selected these habitat types because they represent 90% of the park's surface. I combined ecological aerial surveys (2001-2018), camera trap and dung count data (2019-2021) to assess how ecological (habitat types, rainfall, and distance to rivers) and anthropogenic (distance to human settlements and cattle grazing areas) factors influence the distribution of large herbivores in the LNP landscape.

1.6. Thesis outline

The work presented in this thesis is organised into five chapters (Figure 1.2). In Chapter 1, I presented the general introduction, pointed out the problem statement, and justified the need for the study. I also presented the aim and objectives and reviewed the relevant literature on habitat selection, factors determining LH distribution in heterogeneous environments, large herbivores reintroduction, and a brief overview of the historical distribution of LH in Mozambique.

In Chapter 2, I provided a first attempt to reconstruct the historical distribution and movement patterns of large herbivore species. The chapter contains details on the historical and current data sources and the methodological approach for the compilation of species distribution and movement patterns from the pre-historic period (around 1500) to the current period (2021). The content of this chapter was published in the following article: Roque, D. V., Macandza, V. A., Zeller, U., Starik, N., and Göttert, T. (2022). Historical and current distribution and movement patterns of large herbivores in the Limpopo National Park, Mozambique. *Frontiers in Ecology and Evolution.* 10, 978397. https://doi.org/10.3389/fevo.2022.978397. Supplementary material is available in an online data repository: https://www.frontiersin.org/articles/10.3389/fevo.2022.978397/.

In Chapter 3, I assessed the distribution patterns and the relative abundance of reintroduced large herbivores using camera trap surveys. In this chapter, I presented the first systematic assessment of large herbivore communities in an area where most species were extinct followed by their restoration process. The content of this chapter was published in the following article: Roque, D. V., Göttert, T., Macandza, V. A., and Zeller, U. Assessing distribution patterns and the relative abundance of reintroduced large herbivores in the Limpopo National Park, Mozambique. *Diversity* 2021, 13, 456. https://doi.org/10.3390/d13100456. Supplementary material generated is available in an online data repository: https://www.mdpi.com/article/10.3390/d13100456/s1.

In Chapter 4, I investigated how ecological factors (distance to perennial water sources, habitat types, and rainfall) and anthropogenic factors (distance to settlements and cattle grazing areas) influence the distribution of LH species surveyed over 21 years through a generalized linear model (GLM). The content of this chapter were already accepted (in production) for publication in the *Ecosphere* and were also presented at an international conference – "Mammals of importance to the conservation of ecosystems, with special reference to the African savannas", South Africa: April 2023.

Finally, in Chapter 5, I briefly presented a general discussion of the results and synthesised the main findings of the thesis given the objectives established and pointed out the distinctions in historical and current distributions among LH species. I explore the differences in the process of wildlife recovery in the light of the restoration program started in 2001, looking at the factors that favour or not the distribution of species in the landscape. I also presented the implications of the research findings for park management.

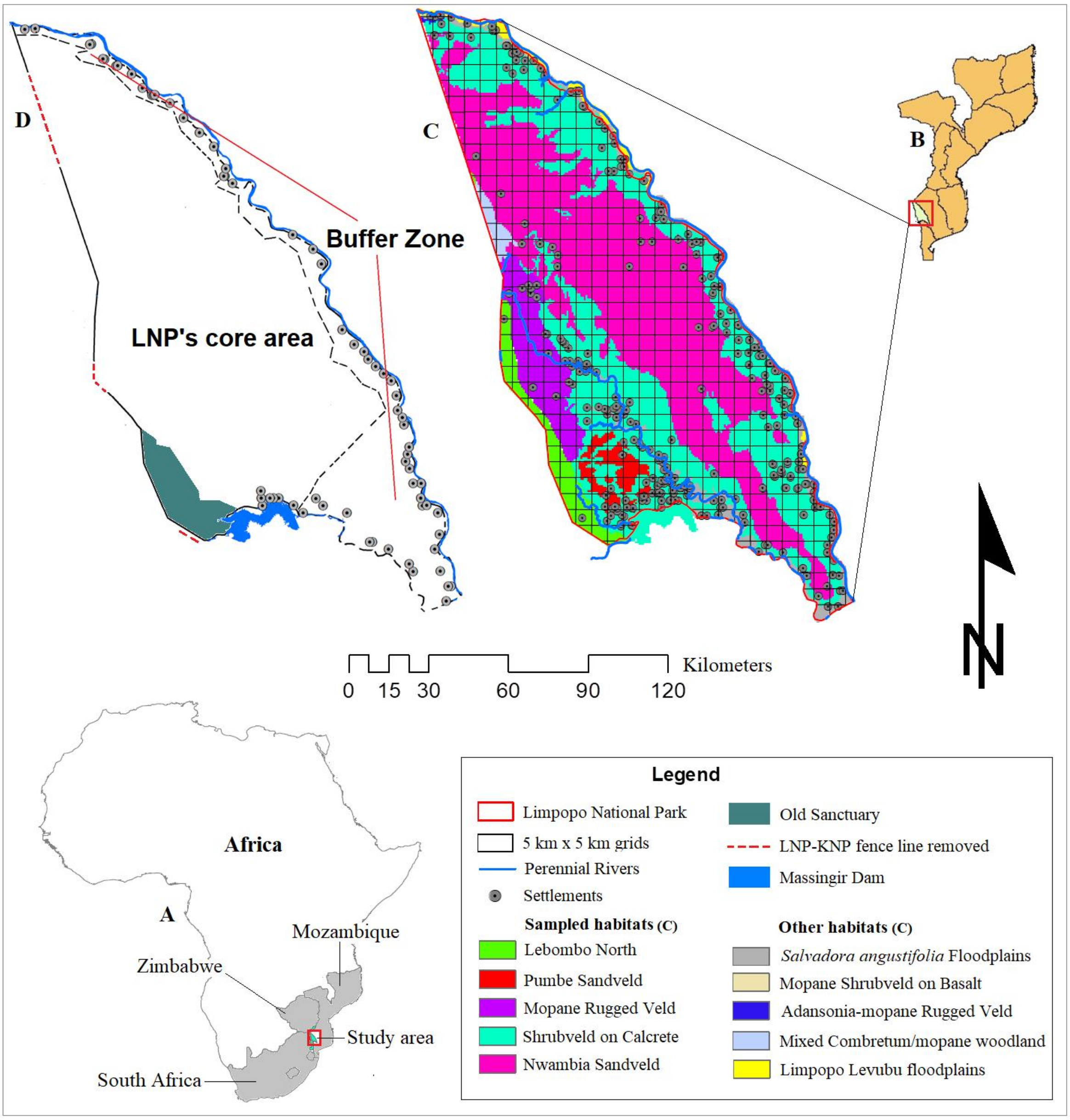

Figure 1.1. Location of the study area in the GLTP (A) and in Mozambique (B). LNP map showing the habitat types, perennial rivers, and settlements (C), Old Sanctuary, fence removed sections, Buffer Zone, and core area (D).

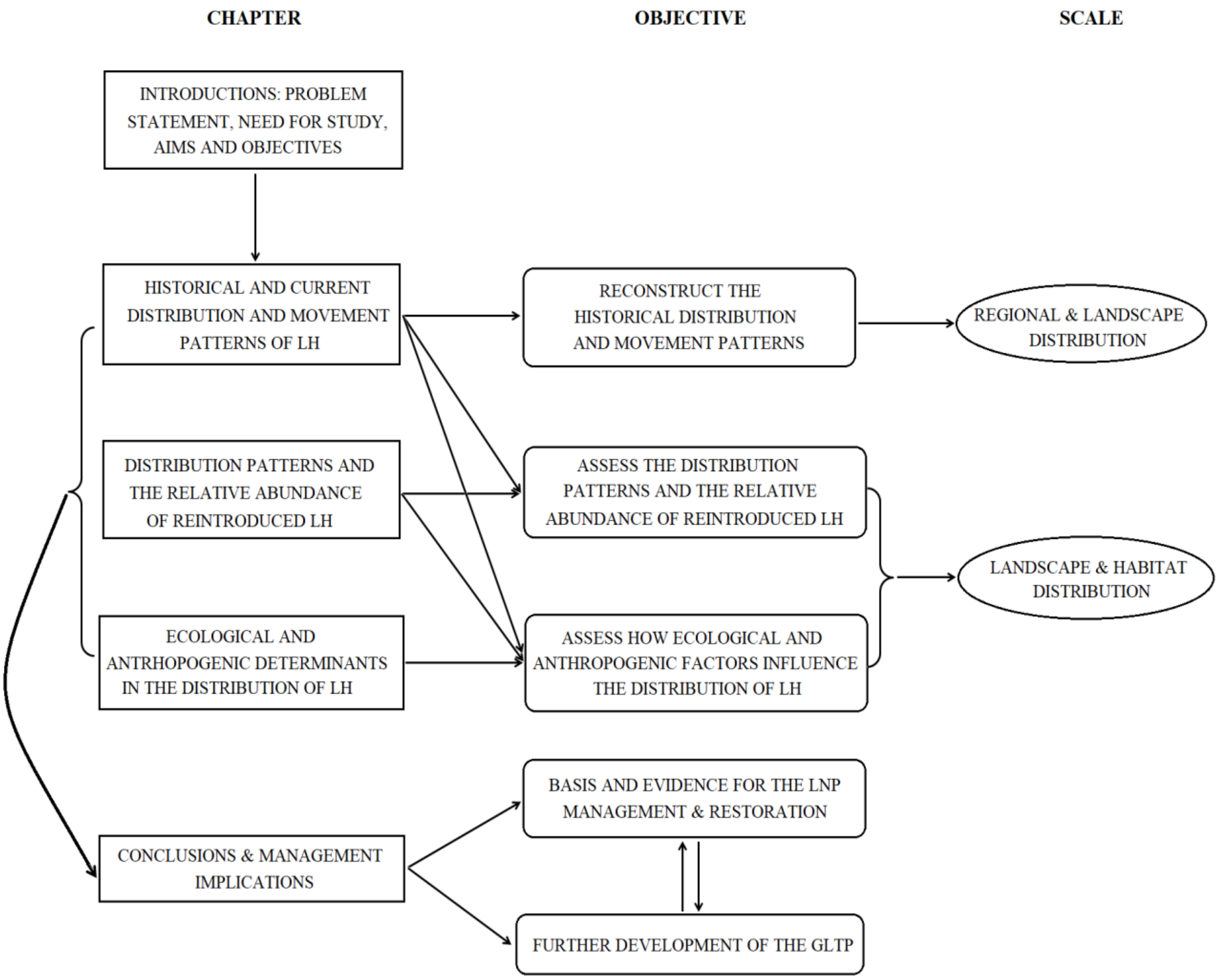

Figure 1.2. Flowchart of research objectives, scale, and thesis structure

1.7. References

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CHAPTER TWO

2. Historical and current distribution and movement patterns of large herbivores in the Limpopo National Park, Mozambique

Abstract

This study provides a first attempt to describe the historical distribution and movement patterns of selected large herbivore (LH) species in Limpopo National Park (LNP), an area in Mozambique today connected to a network of transboundary conservation areas. Between 1976 and the early 2000s, most LH species were absent in this area following the civil war in Mozambique, followed by intense poaching due to weak law enforcement capacity. Through the reconstruction of the historical and current distribution and movement patterns of seven LH species in five periods, we investigate possible changes in distribution and movement patterns over time. Data collection was based on a systematic literature search, census reports, online databases, dung count transects, and camera trap surveys. We mapped all LH observations and movements using ArcGIS 10.8.1. Our results reveal a dramatic collapse of LH populations between the peak of the colonial period and the post-colonial/civil war period (1800-2001), followed by a slight recovery from the post-proclamation of Great Limpopo Transfrontier Park (GLTP) to the current period (2002-2021). While LH population decline applied to all seven species, there are species-specific differences in the process of restoration: African elephant (*Loxodonta Africana*), African buffalo (*Syncerus caffer*), and plains zebra (*Equus quagga*) appear to recover to a greater extent than giraffe (*Giraffa camelopardalis*), eland (*Tragelaphus oryx*), blue wildebeest (*Connochaetes taurinus*), and white rhino (*Ceratotherium simum*). We found evidence of the functioning of proposed wildlife corridors in the LNP. The results give reason to assume that the restoration of populations of LH is still in a very early and vulnerable state and that further efforts are necessary to strengthen the slowly increasing LH populations. Our results highlight the importance of combining past and current data as a guide for the restoration of threatened species in African savannas impacted by human activities.

Keywords: ecological corridors, distribution of large herbivores, historical periods, Limpopo National Park, movement of large herbivores, species collapse, species restoration.

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2.1. Introduction

Historical information about the distribution, dispersal movements, and migration of wildlife refers to written records found in books, journals, reports, diaries, and letters of people, most notably explorers, settlers, hunters, missionaries, and naturalists during the period for which such records are available (Boshoff and Kerley, 2010). The value of written records is widely recognized because they help to reconstruct animal assemblages for a region (Kerley *et al*., 2003; Skead, 2007) and inform past spatial distribution of globally endangered large herbivores (LH) species in southern Africa (Knight and Emslie, 2012; Stoldt *et al*., 2020). Combining the interpretation of past written records and current data can guide the restoration of species to areas from which they have become extinct (IUCN, 2001; Kerley *et al*., 2003; Boshoff and Kerley, 2010). However, despite this, the need to be careful when interpreting these data has always been raised because most early hunters, travellers, and naturalists recorded only historical occurrences of animals along well-travelled routes, and few travelled at night, thereby missing the nocturnal species (Boshoff *et al*., 2001). Furthermore, hunters might tend to over-interpret the behaviour of certain animals termed beasts and might also have had a bias in mind and focused on species of high value for hunting and thus, leaving out certain other species.

Archaeological research has demonstrated that Iron Age communities settled in southern Africa by AD 200. The first Bantu-speaking people settled in the present-day Kruger National Park (KNP) and Limpopo National Park (LNP) by AD 400 (Plug, 1982). They built villages, collected wood, grazed animals, practised agriculture, hunted using fire, and stayed in the area until the depletion of resources (Plug, 1982; Mabunda *et al*., 2003). Because irregular rainfall in these regions limited herding and cropping, hunting for bush meat was still the major survival strategy by the twelfth and thirteenth centuries (Plug, 1982). In Mozambique, the period between the 15th and 17th centuries was one of gold production and trade, which decreased at the beginning of the 18th century, and the ivory and wildlife skin trade began (Newitt, 1997; Madeiros, 2017). The increased ivory and wildlife skin trade along the Limpopo River and Transvaal affected the distribution, migration, and other wildlife movements in today's LNP and KNP (Huffman, 1996). Migrations of millions of ungulates were common until the 19th century in Africa (Roche, 2008). However, at the beginning 19th century, these declined dramatically in both number and size, and many of those still occurring are under threat (Berger, 2004). The increase in habitat fragmentation due to human encroachment, farming, pastoralism, and urbanization (Newmark, 2008; Harris *et al*., 2009), affected the migratory populations because they require large ranges, and only a few migration routes are inside protected areas. The migratory populations rapidly decline once migration routes are blocked and seasonal ranges are no longer accessible (Bolger *et al*., 2008). Although the deployment of fences protected wildlife in some areas, many migratory movements were disrupted (Bartlam-Brooks *et al*., 2011). What remains are just other strategic movements such as nomadism, dispersal, local shifts between seasonal ranges, seasonal movements to areas of higher resource quality or lower predation risk, and movements associated with the re-establishment of historic distribution ranges (Bolger et al., 2008; Bunnefeld *et al*., 2011; Naidoo *et al*., 2012; Owen-Smith *et al*., 2020; Kauffman *et al*., 2021).

The LNP was created in 2001 as part of the Great Limpopo Transfrontier Park (GLTP), which also includes the KNP in South Africa and Gonarezhou National Park (GNP) in Zimbabwe. The LNP, KNP, GNP, together with Banhine National Park (BNP), Zinave National Park (ZNP), and the interstitial zone between these parks in Mozambique, form the Great Limpopo Transfrontier Park and Conservation Area (GLTFCA) (DINAC, 2003; Milgroom and Spierenburg, 2008). The GLTP consists of a network of transboundary ecosystems of African savannas (DINAC, 2003; Milgroom and Spierenburg, 2008) that can serve as a reference for the rest of the world because they present megafauna features close to the pre-human or near-natural situation (Zeller *et al*., 2017; Rottstock *et al*., 2020; Zeller and Göttert, 2021). Before 2001, LNP was a trophy-hunting concession called "Coutada 16" (Milgroom and Spierenburg, 2008; Mavhunga and Spierenburg, 2009; Massé, 2016). The area was affected by Mozambique's civil war from

1976 to 1992 (Hatton *et al.*, 2001) and decades of poaching, which decimated the populations of almost all LH species (Hofmeyr, 2004; Lunstrum, 2016). Patterns of wildlife distribution and movements in the current LNP from the mid to late 19th century were shaped by tsetse fly expansion, excessive off-take of ivory, systematic expansion of sport hunting, demarcation of colonial borders, and Rinderpest (Martinho, 1934; Mavhunga, 2003, 2003; Mavhunga and Spierenburg, 2009). In the early 20th century, LH populations were massively culled by veterinary services in former Rhodesia and Portuguese East Africa (present-day Mozambique) to prevent livestock diseases caused by ticks, Rinderpest, and tsetse fly (Martinho, 1934; Madeiros, 2017). Hence, Game Reserve Officials in the Transvaal (present-day KNP) began gathering wildlife from areas bordering Portuguese East Africa and Rhodesia driving them towards the safety of newly demarcated game reserves (Mavhunga and Spierenburg, 2009). However, during the dry season, wildlife frequently crossed the border in search of water, going to areas of Portuguese East Africa and Rhodesia (Pienaar *et al.*, 1964; Mavhunga and Spierenburg, 2009).

Wildlife has historically taken movements from KNP to LNP and vice versa (Pienaar *et al.*, 1964; Mabunda *et al.*, 2012). The construction of the KNP-LNP fence in 1976 negatively impacted the KNP, LNP, and GNP because it separated the LH population and blocked the historical movement routes (Mavhunga and Spierenburg, 2009; Lunstrum, 2014). The long-term survival of threatened LH depends on their ability to undertake seasonal movements to areas of higher resource quality and or lower predation risk (Bolger *et al.*, 2008; Purdon *et al.*, 2018). The KNP-LNP fence removal sections in the early 21st century (Mabunda *et al.*, 2012; Lunstrum, 2014) allowed wildlife to move freely between these parks (Mabunda et al., 2012). Therefore, wildlife is increasing in the LNP (Grossman *et al.*, 2014; ANAC, 2018). However, it still faces challenges in the medium term because the program to resettle communities living in the LNP core area is not finished yet (Milgroom and Spierenburg, 2008), and there is still intense pressure from poaching (Bazin *et al.*, 2016), leading to the concentration of LH species along the border with the KNP and in the so-called “Old Sanctuary” (Roque *et al.*, 2021) as these areas are remote from human settlements and have permanent water (Dunham, 2004; Whyte and Swanepoel, 2006). The resettlement of these communities in the “buffer zone” will likely expand and intensify the land use in the eastern LNP. These will prevent LH to access riparian resources along the Limpopo River and block movements into BNP and ZNP (Macandza and Ruiz, 2012).

Although in the 20th and 21st centuries, there has been an increasing number of publications on historical issues of LH in southern Africa (Du Plessis, 1969; Boshoff *et al.*, 2001, 2016; Plug and Badenhorst, 2001; Boshoff and Kerley, 2010, 2013, 2015), in Mozambique, information regarding historical distribution, movements, and migrations patterns of LH is scarce (Smithers and Tello, 1976; Tello, 1977; Ntumi *et al.*, 2009; Neves *et al.*, 2018, 2019; Stalmans *et al.*, 2019). An explicit goal of the GLTP is to holistically manage the Limpopo ecosystem to ensure the connectivity of habitats, landscapes, and ecological processes critical to the restoration and maintenance of biodiversity (DINAC, 2003). Currently, wildlife movements between KNP and LNP occur only through gaps in the LNP-KNP fence, along rivers, where there is no fence, and where elephants have damaged it (Dunham, 2004; Whyte and Swanepoel, 2006). In 2012, the LNP defined six potential areas for wildlife ecological corridors implementation to reduce human-wildlife conflicts, provide areas for wildlife movements to access water in the Limpopo River at different seasons throughout the year, and ensure dispersal movements to the BNP, ZNP, and the interstitial zone between these parks (Macandza and Ruiz, 2012; PNL, 2012). However, since that time, to our knowledge, no studies attempted to reconstruct the distribution and movement patterns of LH over time in LNP. Furthermore, no studies discussed the current planning of proposed ecological corridors despite little scientific evidence to suggest that LH historical movements can be restored.

Our approach has combined historical and current data aiming (i) to reconstruct the historical distribution and movement patterns of LH species, (ii) to investigate how the distribution and movement patterns of LH have changed over time, and (iii) to discuss the use of proposed ecological corridors in the LNP. We used scientific systematization to test the hypothesis that the distribution areas and movement routes of LH in the LNP have changed over time such that most of the suitable sites for these species in the past are no longer available. Linking LH distribution and movement patterns in the past and present (i) would assist the current restoration of the LNP, (ii) would inspire park managers to choose the most suitable ecological corridors, and (iii) would allow gaining knowledge of the state of the park in the past, and this would support the human resettlement and management plan for further development of the GLTP.

2.2. Materials and methods

2.2.1. Study area

The study area incorporates the present-day Limpopo National Park (LNP) (22°25'S – 24°10'S, 31°18'E – 32°39'E), a 10.000 km^2 protected area in Gaza province in Mozambique. The LNP is a crucial element of a transboundary protected area network that, together with the KNP and the GNP, forms the GLTP. The western boundary of the LNP is formed by the border between Mozambique and South Africa and northern side of the Massingir Dam basin boundary. The Zimbabwean border touches on the northernmost tip of the area. The eastern boundary is formed by the Limpopo River, whilst the Olifants River is the southern boundary. The climate of the LNP is warm and dry tropical with two seasons, the wet season (November to April) and the dry season (May to October). The mean annual temperature fluctuates between 24 ºC and 30 ºC. Rainfall is low and highly variable, ranging from 300 mm/year in the North to 500 mm/year in the South. Rainfall is also markedly seasonal, with 95 per cent of the yearly rainfall occurring in the wet season (DINAC, 2003; Brito and Julaia, 2007; ANAC, 2022). The altitude in the park varies between 260 and 840 m above sea level. Geologically, LNP is dominated by rhyolite volcanic rock in the southern region, while the North consists of the red sand mantle, whereas alluvium and clay sediments characterize the Limpopo floodplains (DINAC, 2003).

LNP has three main river systems with crucial impacts on land use and wildlife distribution: (1) the Limpopo is the largest, perennial river, although water becomes restricted to pools along the river bed at the end of the dry season, (2) the Olifants remains perennial throughout the season, and (3) the Shingwedzi is a much smaller non-perennial river. As Shingwedzi drains the central portion of the LNP, it affects wildlife distribution. (DINAC, 2003). Subsistence farming, free grazing of livestock, and “bush meat poaching” (hunting of wildlife for local consumption) characterize the settlements in the LNP (Andresen *et al.*, 2014). Based on 2020 statistics, about 30,000 people live in the LNP, of which 22,748 people organized in 51 communities of 5,155 households with about 38,280 heads of cattle, living in the buffer zone. The remaining inhabitants live in four villages of 1,380 households in the core area (Shingwedzi River) of the park (Milgroom and Spierenburg, 2008) and are slated to be resettled in buffer zone (Figure 2.1) (Massé, 2016, ANAC, 2022). In these villages, there are about 9,600 head of domestic cattle (SDAE, 2012; ANAC, 2018, 2022) that share grazing areas with wildlife. The continuous matrixes of agricultural resettlements along the Limpopo River and Shingwedzi Valley (Hatton *et al*., 2001; Lunstrum, 2016), and the KNP-LNP fence act as barriers to wildlife distribution and movements in the GLTP.

Although wildlife populations were almost decimated, LNP has already shifted from an almost wildlife-empty area to an area in the early-intermediate stage of restoration (Roque *et al*., 2021). This is due to a restoration program carried out from 2001 to 2008 through (i) active wildlife translocation from KNP of 4,725 LH individuals belonging to ten species (African elephant, white rhino, African buffalo, giraffe, blue wildebeest, plains zebra, waterbuck, roan antelope, Lichtenstein hartebeest, and impala) to a 300 km^2 fenced area (Old Sanctuary) in the south-western corner of the LNP (Hofmeyr, 2004; Mabunda *et al*., 2012), and (ii) passive wildlife reintroductions through three sections of KNP-LNP fence removed in the North, Center, and South (Figure 2.1A) to allow wildlife cross-border movements from KNP into LNP (Mabunda *et al*., 2003). Between 2010 and 2014, the GLTP was impacted by large-scale poaching of white rhinos and elephants primarily in the KNP, where the majority of poachers entered Kruger from the Mozambican borderlands (Lunstrum, 2014). The poaching crisis has stalled efforts to remove further sections of the international border fence (Büscher and Ramutsindela, 2015). Although the KNP-LNP historical migrations routes are still blocked (Mabunda *et al*., 2003, 2012), there is little scientific evidence of LH movements through fence gaps (Andresen *et al*., 2012; Grossman *et al*., 2014; Everatt, 2015).

2.2.2. Study design

Spatial and temporal scales

For the distribution patterns of LH, the study area was restricted within the LNP park boundaries. However, because the ungulates exhibited a diversity of movement strategies, such as the local changes between seasonal ranges (nomadism and dispersion) and massive migrations (classical, long-distance, altitudinal, facultative, mixed, and partial migrations) (Dingle and Drake, 2007; Bunnefeld *et al*., 2011; Avgar *et al*., 2014; Owen-Smith *et al*., 2020; Kauffman *et al*., 2021), the study area for LH movements includes 10 km beyond LNP limits on the western border with KNP, the northern border with GNP (Sengwe corridor), the eastern border with Limpopo River, and the southern border with Olifants River (Figure 2.1). We addressed the historical distribution and movement patterns in five different periods: (i) prehistoric/start of the colonial period (around 1500), (ii) peak of the colonial period (1800-1975), (iii) post-colonial/civil war/intense poaching period (1976-2001), (iv) post-proclamation of GLTP (2002-2018), and (v) current period (2019-2021). The time spans used were determined by the availability of data and the dynamics of colonial trade that directly or indirectly affected LH in Mozambique: the prehistoric and start of the colonial period was the era of gold production and trade without wildlife pressure; at the beginning of the 18th century (peak of the colonial period), gold production decreased, and the wildlife pressure through ivory, wildlife skin, and hunting trophies trade began and increased as the time advanced (Newitt, 1997; Madeiros, 2017); the post-colonial/civil war/intense poaching period was a period of wildlife extinction, where the hunting law enforcement capacity was weak countrywide after the peace agreement in 1992 (Hatton *et al*., 2001; Dunham, 2004). Furthermore, after 1992, conservation areas had been abandoned, with wildlife decimated and infrastructure largely destroyed (Hatton *et al*., 2001; Ntumi *et al*., 2009), with no management and law enforcement. Therefore, wildlife in all conservation areas in Mozambique, including Coutada 16, was poorly documented from 1992 to the beginning of the 2000s (Hatton *et al*., 2001; Hofmeyr, 2004; Lunstrum, 2016); in the post-proclamation of GLTP to the current period, began the wildlife restoration in the LNP (Dunham, 2004; Whyte and Swanepoel, 2006; Mabunda *et al*., 2012).

Selection of species

We selected seven species of LH (body mass > 150 kg) with the availability of historical records of their occurrence and movements in the study area as many explorers, settlers, hunters, missionaries, and naturalists would focus on these species due to their high hunting value and thus, leaving out certain other species (Elton, 1872; Erskine, 1874; Sealous, 1908; Martinho, 1934; Pienaar *et al*., 1964; Sidney, 1965; Smithers and Tello, 1976; Dias, 1981). These species also represent different residence guilds (Table 2.1).

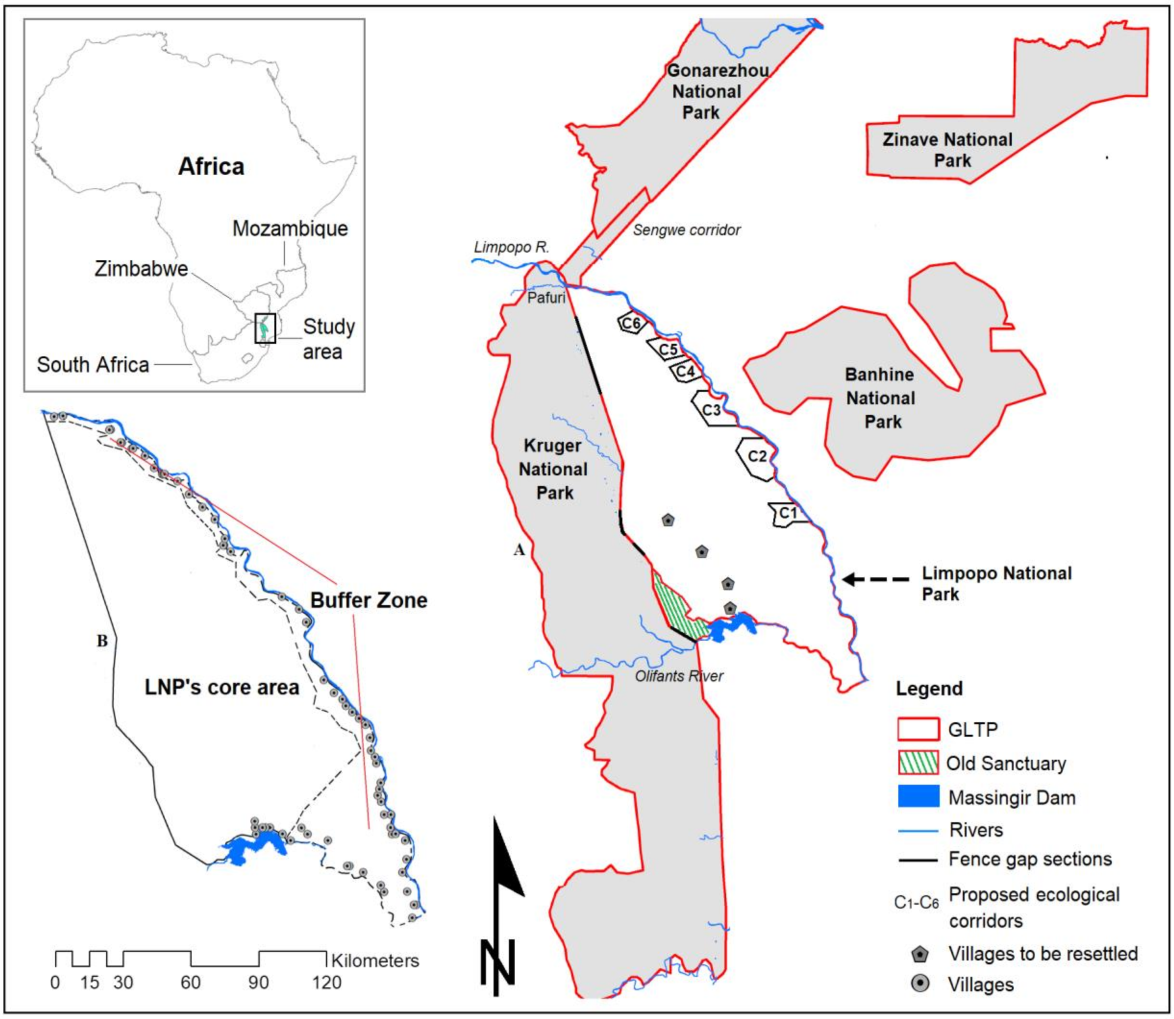

Figure 2.1. Overview of the study area showing (A) the Great Limpopo Transfrontier Park and Conservation Area (GLTFCA), removed fence sections, "scape sites," proposed ecological corridors (C_1-C_6), villages in the core area to be resettled in the buffer zone, and (B) the buffer zone with villages

Table 2.1. Large herbivore species (body mass > 150 kg) selected for the study in the LNP (the upper and lower limit of weight corresponds to variations between adult males and females)

Common name	**Scientific name**	**Body mass (kg)** (Skinner and Chimimba, 2005; Estes, 2012)	**Feeding guild** (Skinner and Chimimba, 2005)
Blue wildebeest	*Connochaetes taurinus*	180 – 250	Grazer
Plains zebra	*Equus quagga*	290 – 340	Grazer
African buffalo	*Syncerus caffer*	580 – 700	Grazer
White rhino	*Ceratotherium simum*	1,700 – 2,300	Grazer
Giraffe	*Giraffa camelopardalis*	970 – 1,400	Browser
Eland	*Tragelaphus oryx*	400 – 900	Mixed feeder
African elephant	*Loxodonta Africana*	2,800 – 6,300	Mixed feeder

2.2.3. Data collection

Historical data

For the prehistoric/start of the colonial period (1500), we relied on sporadic written records that covered a small area of present-day LNP. For the peak of the colonial period (1800-1975) and post-colonial/civil war/intense poaching period (1976-2001), we systematically searched the literature sources for written records of the historical incidence and movements of LH in the study area. The written records comprise mainly hand-drawn maps, digitalized maps, maps related to archaeological information, journal articles, reports, mammals atlas, and books written by some of the literate pioneers – notably European explorers, travellers, naturalists, and big game hunters. Our primary sources of literature information include Mozambique's Historical Archive, Eduardo Mondlane University Library, and Systematic Zoology Library at Humboldt – Universität zu Berlin. Despite the interpretational challenges inherent to information quality as well as quantity, the use of historical records is a valuable tool widely used to assist in the reconstruction of past LH assemblages (Skead, 2007; Harris *et al.*, 2009; Boshoff and Kerley, 2010, 2013, 2015) and provides the past distribution of animals with some reliability (Plug and Badenhorst, 2001). We also searched an online open-access biodiversity database "Global Biodiversity Information Facility – GBIF" (GBIF, 2021), which provides extensive and immediate access to species data and aggregates both historical and recent occurrences of LH from a variety of sources worldwide (Nelson and Ellis, 2018). To verify and improve findings from the historical distribution of the post-colonial/civil war period, we talked to two Game wardens and one experienced former hunter who worked in the present-day LNP when it was a hunting concession. For the post-proclamation of the GLTP period (2002-2018), we relied on (i) aerial wildlife censuses data (2006, 2007, 2008, 2010, 2013, 2014, and 2018) and (ii) digitalized maps, journal articles, reports, and books. The wildlife censuses of 2006 and 2007 covered only 30% of the park (Whyte and Swanepoel, 2006), while the rest covered the entire park (Stephenson, 2010, 2013; Grossman *et al.*, 2014; ANAC, 2018).

Current data

For the current period, we walked for three years (2019-2021), 70 dung counts transects of 2 km established from 140 random points 5 km apart. Two observers counted and recorded the dung presence of study species within one meter on each side of transects using a handheld GPS. We walked each transect six times with a mean interval between the walks of 80 days. During this period, we also randomly deployed in ~2 km^2 grid cells (Woog *et al.*, 2010; Rovero *et al.*, 2013), 24 infrared wildlife camera traps (Foxelli Outdoor Gear Oak's Eye Trail Cam® -14 MP 1080 Full HD) in a 60 x 108 km^2 grid cells surveyed. We deployed one camera trap in each grid (Rovero *et al.*, 2014; Debata and Swain, 2018) at 0.50 to 1.5 meters in height on trees and shrubs. The cameras were active 24 hours a day and took bursts of two successively high-resolution photos, 14 MP (4426 x 3312P), with a delay of 60 seconds between trigger activations. Each camera trap location or station constituted a sampling unit (Mena *et al.,* 2020). We moved the cameras from one station to another six times and collected LH data in 146 sampling units. The average length of camera deployment at each sampling unit was 69.5 days (SD = 31.2; min = 28; max = 122). Each camera traps station was also recorded using a handheld GPS. To capture LH movements, we deployed 20 camera traps in "gap sites" along the KNP-LNP fence. We covered 6,000 km^2 out of 10,000 km^2 of the park with the camera traps and dung count transects.

2.2.4. Data processing and analysis

To plot the distribution and movement patterns of study species on the LNP shape file, we defined: (i) observation as each record of the species occurrence in a place, (ii) location as each place where the species was observed, and (iii) reference as each source of species occurrence record. Thus, each reference can be a source of several records of the species and several record locations of species during many years. We assumed each census, each camera trap, and each transect as one reference. Since no information on past LH occurrence had been digitalized for GLTP, all the written records extracted from the literature were geo-referenced and plotted into a GLTP shape file. We used a similar system to that used by Skead (2007) and Boshoff and Kerley (2010, 2013) to map the written records because they were based not only on direct observation of LH but also on sightings, vocalizations, and signs. Thus, we only mapped species occurrence and movements on the "acceptable identification" and "precise locality categories" which are considered most suitable for mapping (Skead, 2007; Boshoff and Kerley, 2010, 2013; Boshoff *et al.*, 2016): (i)"acceptable identification category" – species in which there were a certainty, or, occasionally, reasonable certainty about the animals' identity (taxon) and (ii) "precise locality category" – species located at an identifiable place, or within a roughly circular area with a diameter of approximately 5 km.

The hand-drawn maps were also geo-referenced and created a new ArcMap layer from the indicated occurrence and movement of species in the maps. The density of points and arrow directions related to the LH occurrence and movements in the new ArcMap layer arises from the pattern the authors used to geo-reference their hand-drawn lines. Although hand-drawn maps are biased and do not reflect the exact locations of today, they can still provide valuable information to support historical wildlife reconstruction (Kerley *et al.*, 2003; Stoldt *et al.*, 2020). For the digitalized maps, the density of points in the new LH occurrence layer generated is a replica of historical digitalized sightings. For the post-proclamation of the GLTP period, the latitude, longitude, and number of individuals recorded are available in all censuses. We used the software "Camera Base – Adobe Bridge 2020 for Windows (Adobe systems)", an access database designed for managing camera trap data (Tobler *et al.*, 2009; Rovero *et al.*, 2010). We sorted all photographs by species, date, and time and converted them to camera-independent observation (independent events). We defined independent events as (i) consecutive photographs of individuals of different species; (ii) consecutive photographs of individuals of the same species taken more than 0.5 h apart; and (iii) non-consecutive photos of individuals of the same species (O'Brien *et al.*, 2003; Tobler *et al.*, 2008). For the dung count transect, we considered independent events the dungs 50 m apart. From camera trap and dung data, we generated maps of species distribution in ArcGIS.

Records that mention the occurrence of LH and allude to movements by one or more study species were mapped using ArcGIS 10.8.1. All points and arrows used to display LH ranges in the maps have a 5 km buffer, as we assume that the species will also occur within 5 km of the sighting because they explore large home ranges (Smuts, 1975; Shannon *et al.*, 2006; Göttert *et al.*, 2010; Owen-Smith and Martin, 2015). We followed an empirical approach based on a visual assessment of the number of observations (records) and the number of individuals observed to assist in the generic interpretation of the species distribution patterns. We depicted the LH occurrence in graduated symbols of four classes in ArcGIS 10.8.1 according to the absolute values of individuals observed in each period. The lack of uniformity in the periods among the species depicted in the maps and figures is related to the differences in the periods of observation of each species. Each species observation corresponds to a spatial unit occupied by the species such that the greater the observation numbers in a period, the more widely distributed the species. Thus, we calculated the species observations by reference as the total species records in a period divided by the total reference number. However, the sampling effort is not the same throughout the study periods because some of the historical observations (prehistoric/start of the colonial, the peak of the colonial, and post-colonial/civil war/intense poaching period) were taken in a non-systematic sampling exercise, we determined the precise area covered by the references in each period based on the total area of the park (10,000 km^2) to allow comparability between data from different periods. We plotted the values of species observations by area using Microsoft Excel 2010 in different periods taking into account the total area of the park to assess the patterns of species distribution in km^2.

For movement patterns, all LNP's borders (North, South, West, and East) were considered potentially suitable except for the present-day KNP-LNP border that was fenced in 1976 (Mabunda *et al*., 2003, 2012). After this year, the movements occurred only through fence-removed sections and "gap sites". We generated movement maps for each LH species from written records, hand-drawn maps, and photographs. As historical migration routes are blocked, and seasonal ranges are no longer accessible in the LNP (Mabunda *et al*., 2003; Mabunda *et al*., 2012) due to the fence and encroachment of people (Milgroom and Spierenburg, 2008; Lunstrum, 2014), we classified them as being nomadism, dispersal, local shifts between seasonal ranges, and movements associated with the re-establishment of historic distribution ranges. We used a single arrow in ArcGIS 10.8.1 to indicate the movement areas and their direction. Each movement area depicted on the maps represents a 5 km radius, as we assumed the species disperses within 5 km of the sighting (Stoldt *et al*., 2020). To assess the use of proposed ecological corridors for species movements, we overlaid the movement shape files of each species in different study periods on the proposed ecological corridors shape files and compare whether there is an overlap in the use of these corridors. The corridors were defined in 2012 and allow movements from LNP to BNP, ZNP, community areas, private concessions, and other areas between the two parks (Macandza and Ruiz, 2012; PNL, 2012). A total of 70 historical literature passages (Tables 2.S1-S2), six hand-drawn maps, 13 digital maps, 36 online records from the Global Biodiversity Information Facility (GBIF), 1,459 records from camera traps, 386 from dung counts and 1,162 from censuses which mention, or allude to LH occurrence and movements, were found in the study area.

2.3. Results

The taxa dealt with in this study (seven LH species with a body mass > 150 kg) are listed in Table 2.1. Species distribution and movement patterns are grouped and described based on their degree of similarity concerning diet or movement guild. We also consider significant zones (North, South, Center, West, and East) of the Limpopo National Park (LNP).

2.3.1. Prehistoric and start of the colonial period (1500)

In this period, all species except the white rhino were sporadically recorded in the present-day LNP. African elephants and eland were recorded in the Pafuri region of the LNP. African buffalo, plains zebra, and blue wildebeest were sporadically recorded in the Pafuri region of the present-day LNP and the extreme northwest of the present-day LNP. Giraffes were recorded only in the extreme northwest. The movements into and outside present-day LNP for plains zebra, blue wildebeest, eland, elephant buffalo, and giraffe occurred mainly along the Pafuri region of the present-day LNP. However, plains zebra, blue wildebeest, buffalo, and giraffe also migrated through the extreme northwest of the park (Figures 2.2A-2.7A).

2.3.2. The peak of the colonial period (1800-1975)

At the peak of the colonial period, all seven study species were frequently and widely recorded in high abundance throughout the present-day LNP. Movements into and outside present-day LNP also took place along all boundaries for all study species. However, plains zebra, blue wildebeest, eland, and elephant showed much more movements and used areas that overlap all the proposed ecological corridors (Figures 2.2B-2.8B).

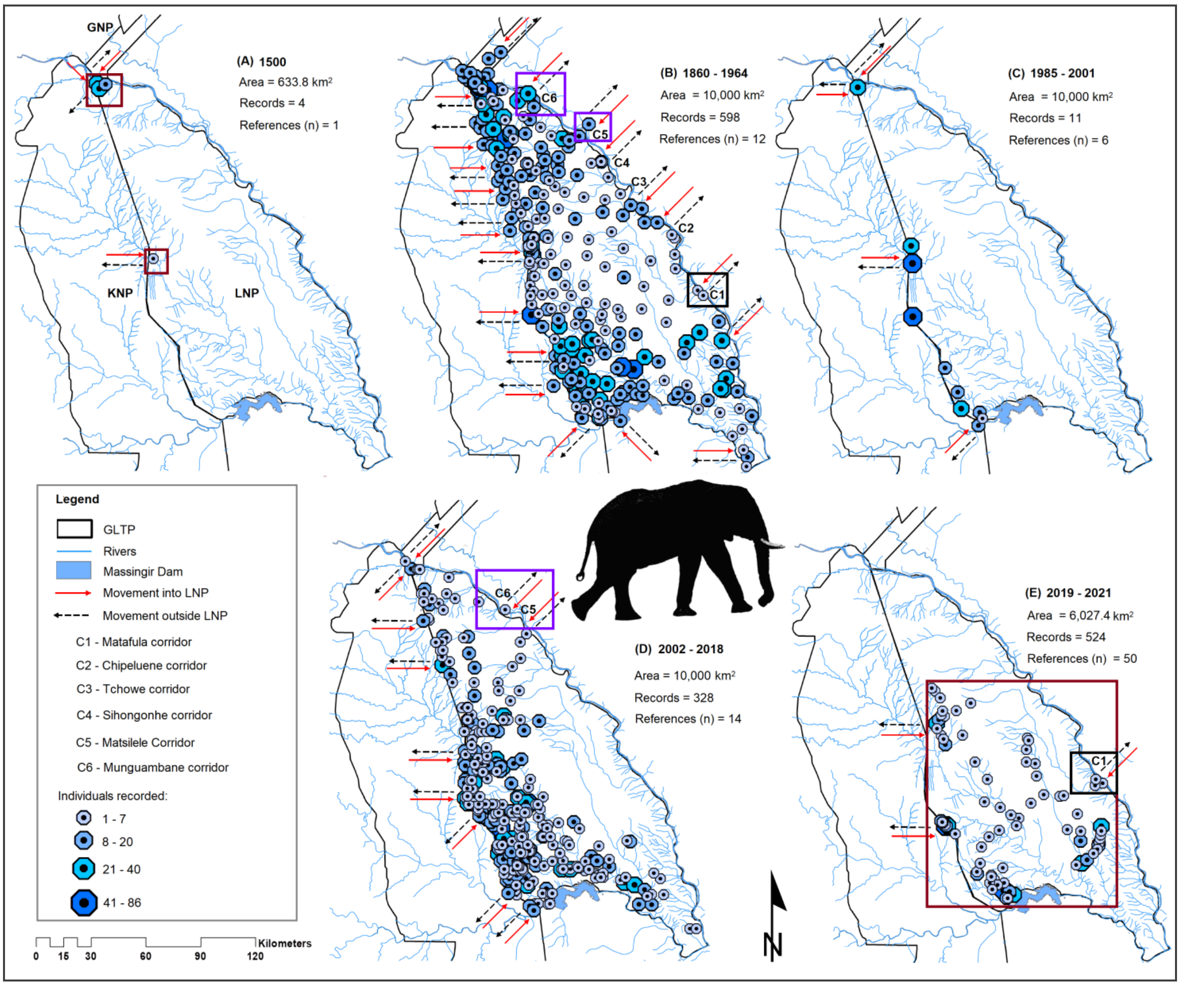

Figure 2.2. African elephant distribution and movement patterns in the LNP, (A) prehistoric/start of the colonial period, (B) peak of the colonial period, (C) post-colonial/civil war/intense poaching period, (D) proclamation of GLTP period, and (E) current period. The area (km^2) represents the spatial covered by the references, the record is the observation of the species, the reference is the species observation source, dark red rectangles represent the area covered by reference in periods (A, E), and black and purple rectangles represent the use of corridors in the period (B, D, E). GLTP – Great Limpopo National Park; GNP – Gonarezhou National Park; KNP – Kruger National Park; LNP – Limpopo National Park.

2.3.3. Post-colonial/civil war/intense poaching period (1976-2001)

Elephants and giraffes were sporadically recorded in the southern (Pafuri region), midwestern and northwestern parts of the present-day LNP. Buffalo and eland were sporadically recorded in the vicinity of Massingir Dam, although eland was also recorded on the southeast side. Plains zebra and blue wildebeest were recorded in the southwest (former Old Sanctuary), midwest, and northwest of present-day LNP. Elephants, plains zebras, and blue wildebeests showed some movements along the extreme northwest, midwest, and southwest while the eland dispersed along the extreme southeast and North (Massingir Dam region) of the present-day LNP. Eland is the only species that used one of the proposed ecological corridors (Munguambane corridor) in this period (Figures 2.2C-2.7C).

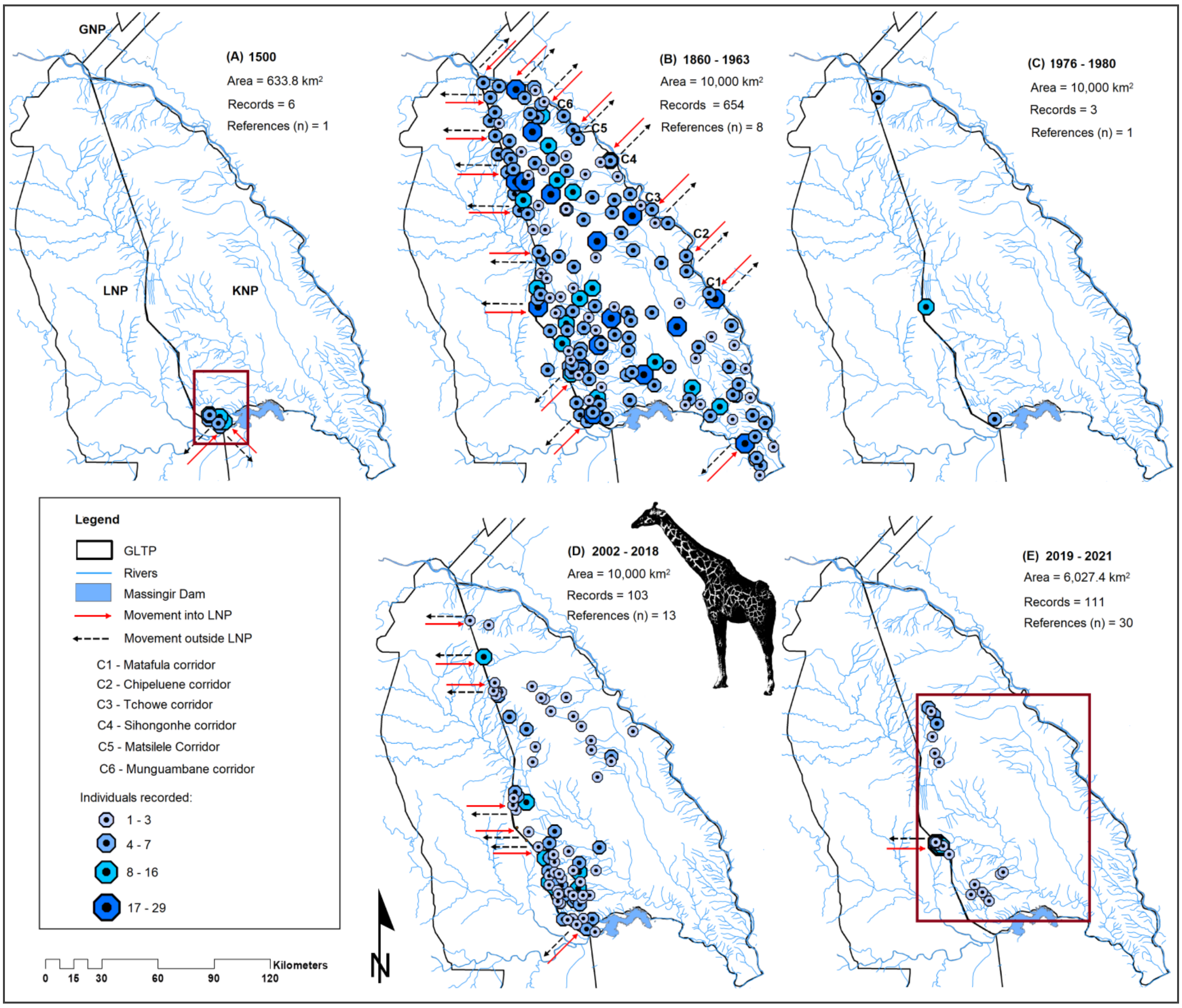

Figure 2.3. Giraffe distribution and movement patterns in the LNP, (A) prehistoric/start of the colonial period, (B) peak of the colonial period, (C) post-colonial/civil war/intense poaching period, (D) proclamation of GLTP period, and (E) current period. The area (km^2) represents the spatial covered by the references, the record is the observation of the species, the reference is the species observation source, and dark red rectangles represent the area covered by reference in periods (A, E). GLTP – Great Limpopo National Park; GNP – Gonarezhou National Park; KNP – Kruger National Park; LNP – Limpopo National Park.

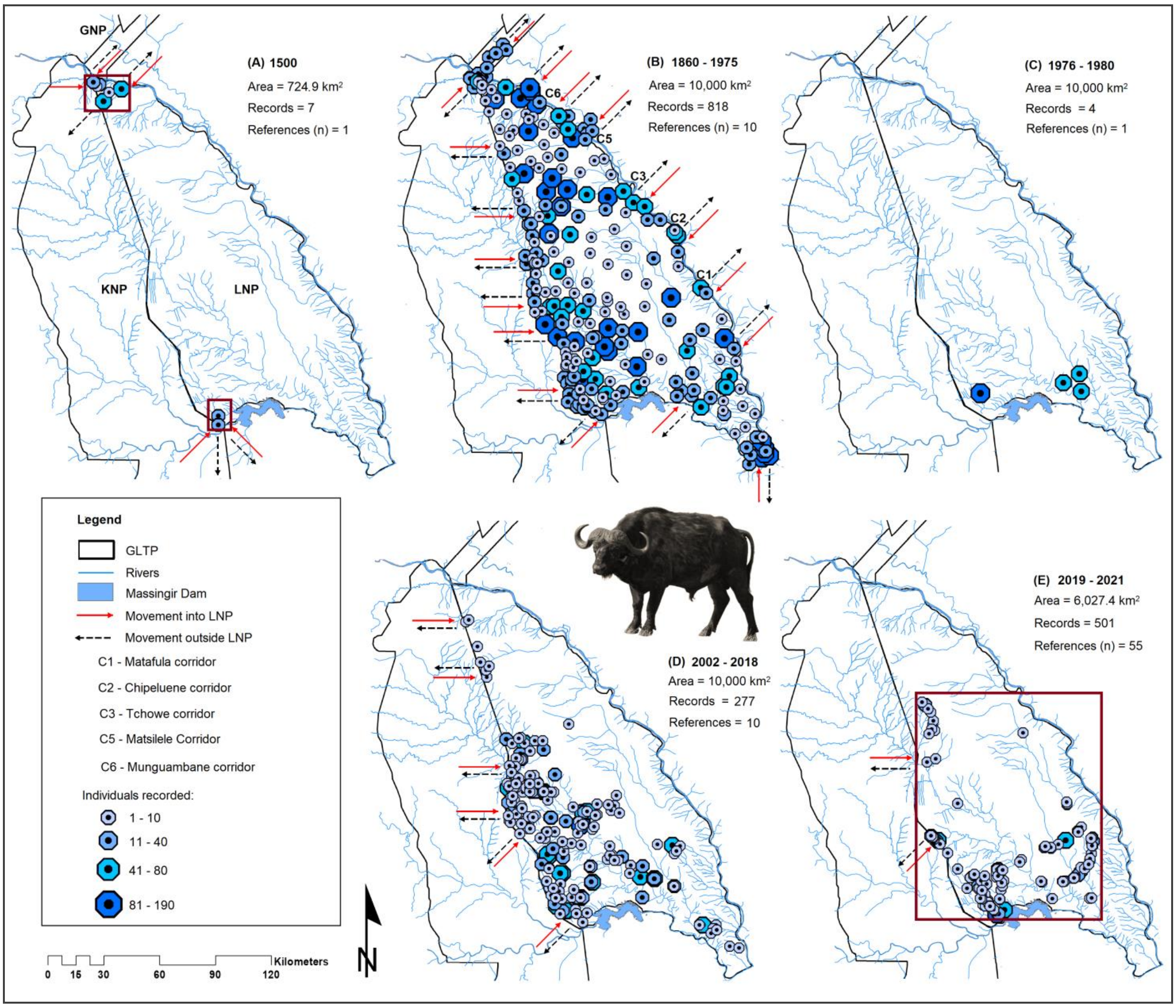

Figure 2.4. African buffalo distribution and movement patterns in the LNP, (A) prehistoric/start of the colonial period, (B) peak of the colonial period, (C) post-colonial/civil war/intense poaching period, (D) proclamation of GLTP period, and (E) current period. The area (km^2) represents the spatial covered by the references, the record is the observation of the species, the reference is the species observation source, and dark red rectangles represent the area covered by reference in periods (A, E). GLTP – Great Limpopo National Park; GNP – Gonarezhou National Park; KNP – Kruger National Park; LNP – Limpopo National Park.

2.3.4. Post-proclamation of Great Limpopo Transfrontier Park (2002-2018)

Elephants and buffalos were frequently and widely recorded in high numbers throughout the park except in the central-eastern portion. Giraffes were frequently recorded along the West side of LNP. White rhino, plains zebra, and blue wildebeest were recorded along the LNP-KNP border, especially in the former "Old Sanctuary." Eland was sporadically recorded in the South LNP-KNP border. Movements of all species occurred through fence gaps and rivers on the West side of the park. Elephants and wildebeest used some of the proposed ecological corridors – Chipeluene, Matsilele, and Munguambane corridors that were also used in the historical period (Figures 2.2D-2.8D).

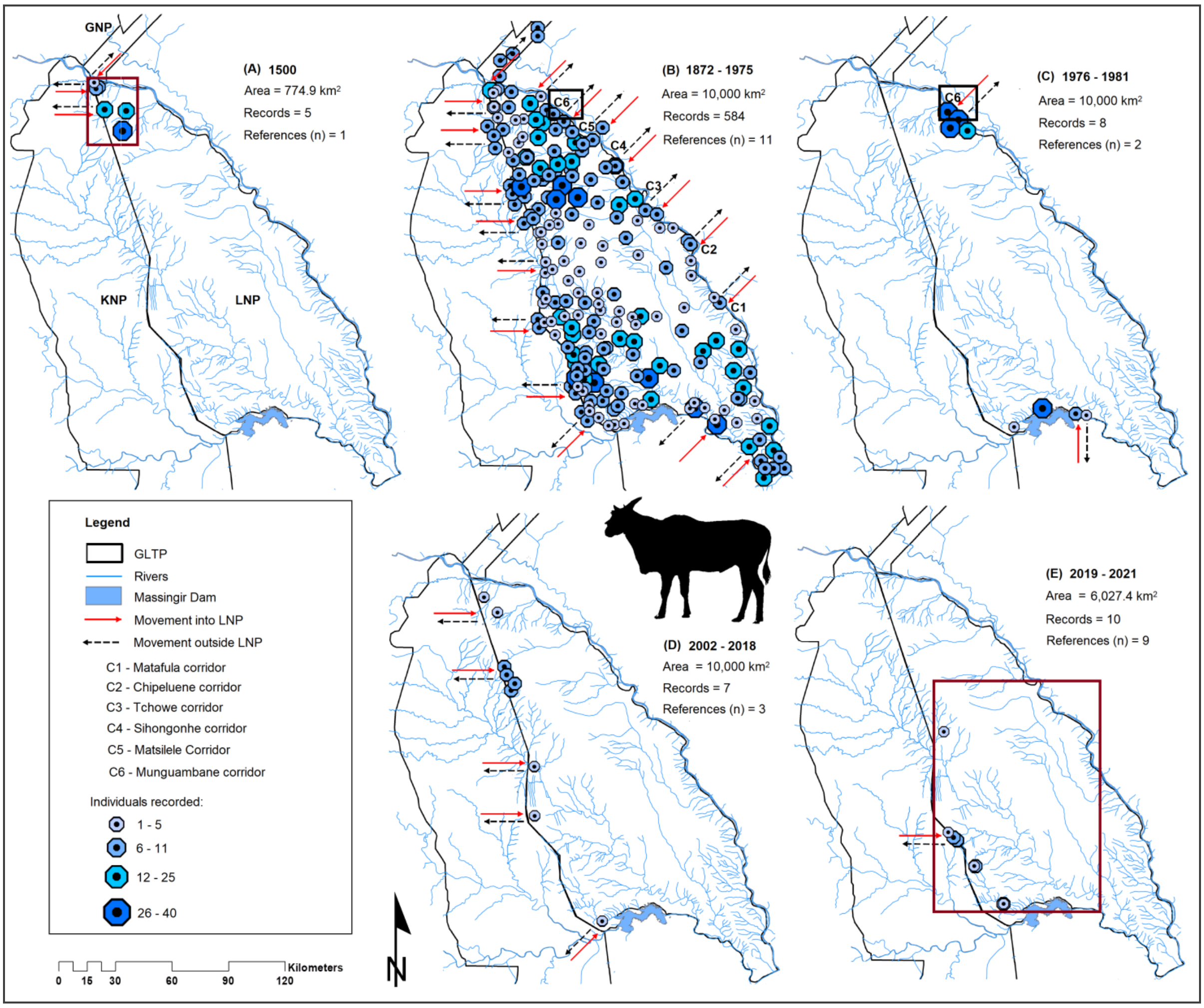

Figure 2.5. Eland distribution and movement patterns in the LNP (A) prehistoric/start of the colonial period, (B) peak of the colonial period, (C) post-colonial/civil war/intense poaching period, (D) proclamation of GLTP period, and (E) current period. The area (km^2) represents the spatial covered by the references, the record is the observation of the species, the reference is the species observation source, dark red rectangles represent the area covered by reference in periods (A,E), and black rectangles represent the use of corridors in the periods (B, C). GLTP – Great Limpopo National Park; GNP – Gonarezhou National Park; KNP – Kruger National Park; LNP – Limpopo National Park.

2.3.5. Current period (2019-2021)

Elephants and buffalos were frequently recorded in the northwest (former Old Sanctuary), midwest, and northeast side of the LNP. Plains zebra and blue wildebeest were recorded along the LNP-KNP border, mainly in the former “Old Sanctuary region.” Giraffes and elands were sporadically recorded in the northwest (Old Sanctuary) and Midwest portions of the LNP. Movements of all study species except the white rhino took place through fence gaps. The elephant is the only species that still uses one of the proposed ecological corridors (Matafula corridor) that was also used in the historical period (Figures 2.2E-2.7E).

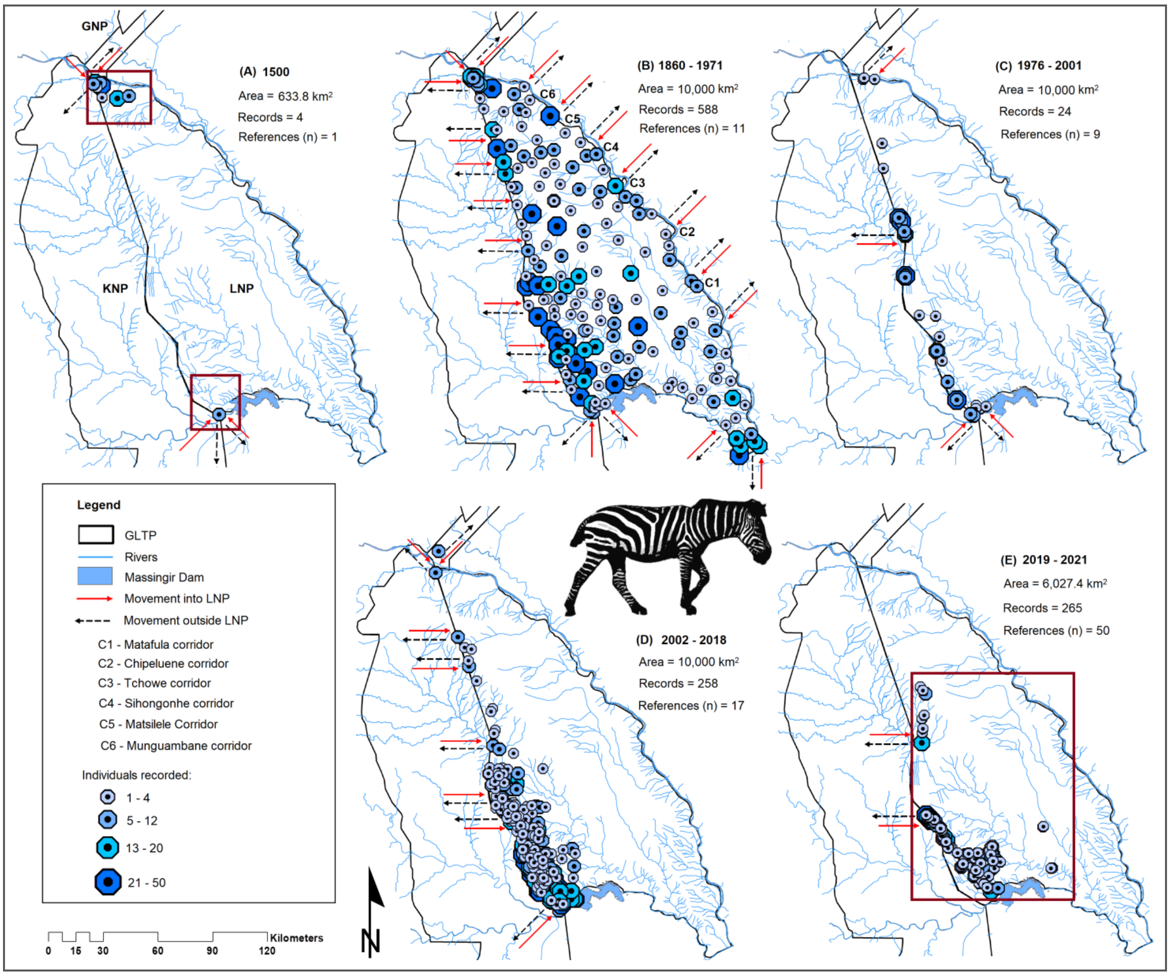

Figure 2.6. Plain's zebra distribution and movement patterns in the LNP, (A) prehistoric/start of the colonial period, (B) peak of the colonial period (C), post-colonial/civil war/intense poaching period, (D) proclamation of GLTP period, and (E) current period. The area (km^2) represents the spatial covered by the references, the record is the observation of the species, the reference is the species observation source, and dark red rectangles represent the area covered by reference in periods (A, E). GLTP – Great Limpopo National Park; GNP – Gonarezhou National Park; KNP – Kruger National Park; LNP – Limpopo National Park.

Furthermore, the comparison of species distribution patterns by reference (sources) and area in different study periods reveals a dramatic population decrease between the peak of the colonial period and post-colonial/civil war for all study species, followed by a slight recovery from the post-proclamation of GLTP to the current period. However, there are species-specific differences in the LH recovery process: elephants, buffalos, and plains zebras appear to recover to a greater extent than giraffes, elands, and wildebeests. The white rhinos were not recorded in the post-colonial/civil war period and the current period (Figure 2.9).

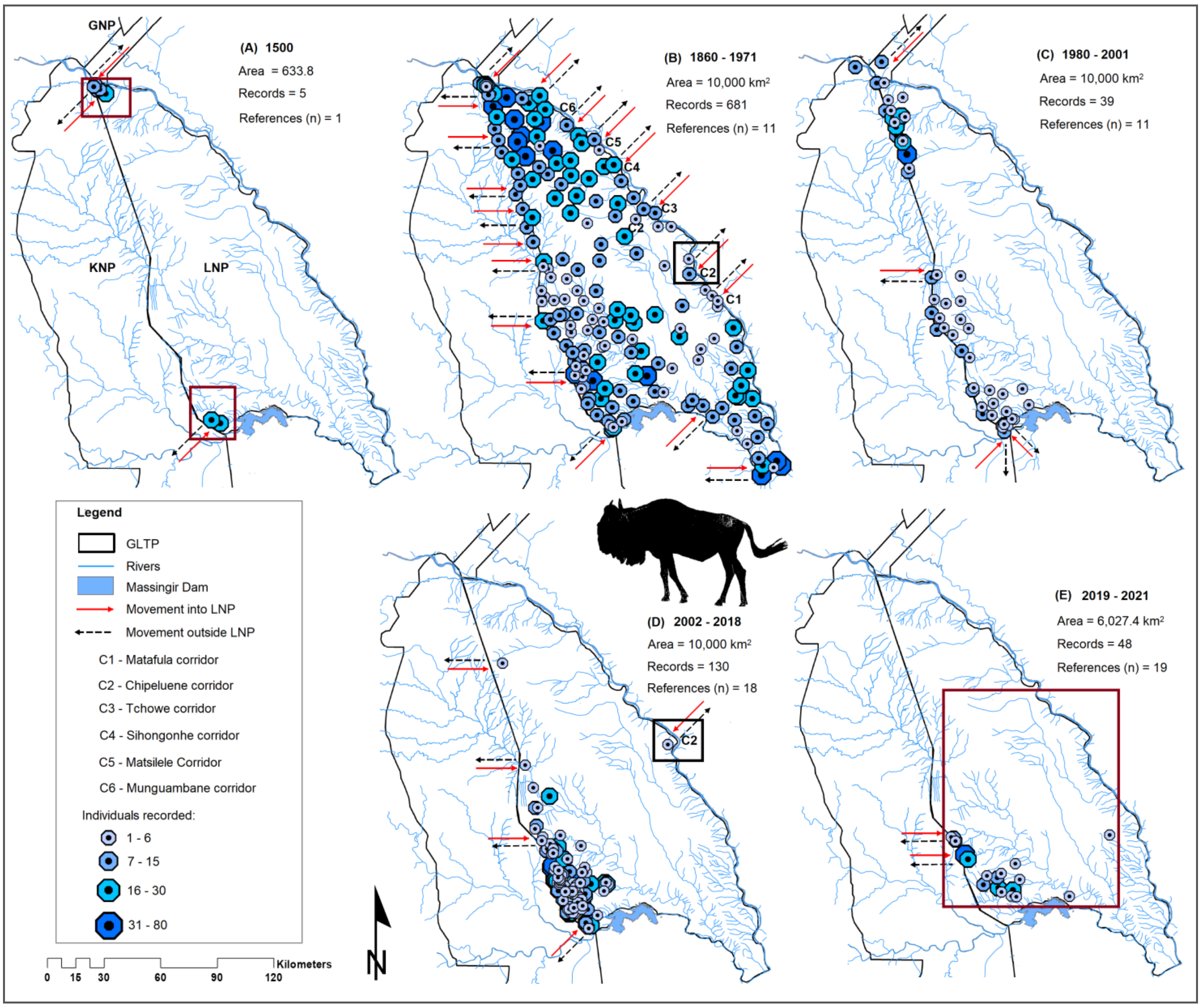

Figure 2.7. Blue wildebeest distribution and movement patterns in the LNP, (A) prehistoric/start of the colonial period, (B) peak of the colonial period, (C) post-colonial/civil war/intense poaching period, (D) proclamation of GLTP period, and (E) current period. The area (km^2) represents the spatial covered by the references, the record is the observation of the species, the reference is the species observation source, dark red rectangles represent the area covered by reference in periods (A, E), and black rectangles represent the area covered by reference in periods (B, D). GLTP – Great Limpopo National Park; GNP – Gonarezhou National Park; KNP – Kruger National Park; LNP – Limpopo National Park.

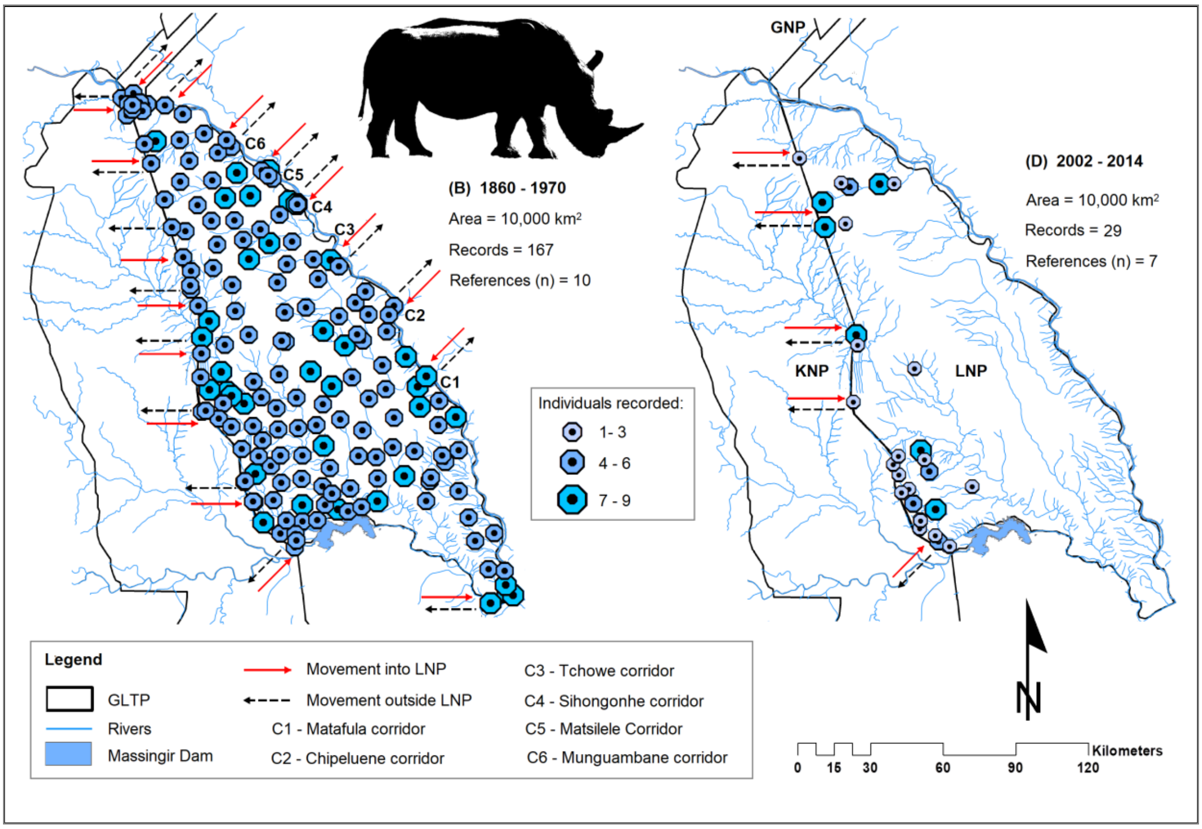

Figure 2.8. White rhino distribution and movement patterns in the LNP, (B) peak of the colonial period, and (D) proclamation of GLTP period. The area (km^2) represents the spatial covered by the references, the record is the observation of the species, and the reference is the species observation source. GLTP – Great Limpopo National Park; GNP – Gonarezhou National Park; KNP – Kruger National Park; LNP – Limpopo National Park.

2.4. Discussion

This study provides the first attempt to describe the historical distribution and movement patterns of selected LH species in LNP. Owing to the non-systematic manner in which the written records were collected, their quality and quantity vary, especially in terms of the areal coverage achieved and of the information that comprises each record. Moreover, the study area was not always a conservation area throughout the five periods studied, and therefore, it underwent different forms of pressure and land use throughout its history. There may also be potential sources of error associated with comparing data generated using different methods and tools, particularly after the proclamation of GLTP (censuses data) and the current period (camera traps and dung count data). These aspects must be considered in any interpretation and comparison between the distribution and movement patterns within and among the study species. Therefore, we have tried to interpret and discuss the results with due caution. Our reconstruction of the historical distribution and movement patterns of LH species gives (i) a valid estimation of the degree of LH population collapse over time and (ii) reveals, on the other hand, the differentiated restoration course of these species. The overriding reason is that Mozambique's wildlife has suffered for centuries from the uncontrolled destruction of multiple causes. These vary from the ivory trade, skin trade, hunting trophies, increasing human settlements, liberation war, guerrilla hostilities, and civil conflicts to uncontrolled hunting for bush meat by rural communities (Martinho, 1934; Dias and Rosinha, 1971; Smithers and Tello, 1976; Dias, 1981; East, 1999; Ntumi *et al*., 2009; Madeiros, 2017).

Our results give reason to assume that there is scientific evidence of the functionality of proposed ecological corridors for wildlife movements due to an overlap in the use of these areas over time. We recorded clusters of historical movements through these corridors for all study species in the peak of the colonial period, which is the period with features closest to natural African savannas. After the proclamation of GLTP, three proposed corridors (Matafula, Matsilele, and Munguambane) are still used by elephants and blue wildebeests. As blue wildebeests are migratory (Morrison and Bolger, 2014) and elephants are highly mobile (Purdon *et al*., 2018), these species probably have an evolutionary adaptation that allows them to cross the continuous matrixes of agricultural resettlements along the Limpopo River and Shingwedzi Valley. However, owing to the expansion of land use by humans along the Limpopo River (Andresen *et al*., 2014), movements are reduced in the current period. From the peak of the colonial period to the post-colonial/civil war period, the Munguambane corridor also was used by elands. Three corridors (Sihongonhe corridor, Matsilele corridor, and Munguambane corridor) in the far North of the park appear to have not been used in the current period (2019-2021) because our study area did not cover these corridors.

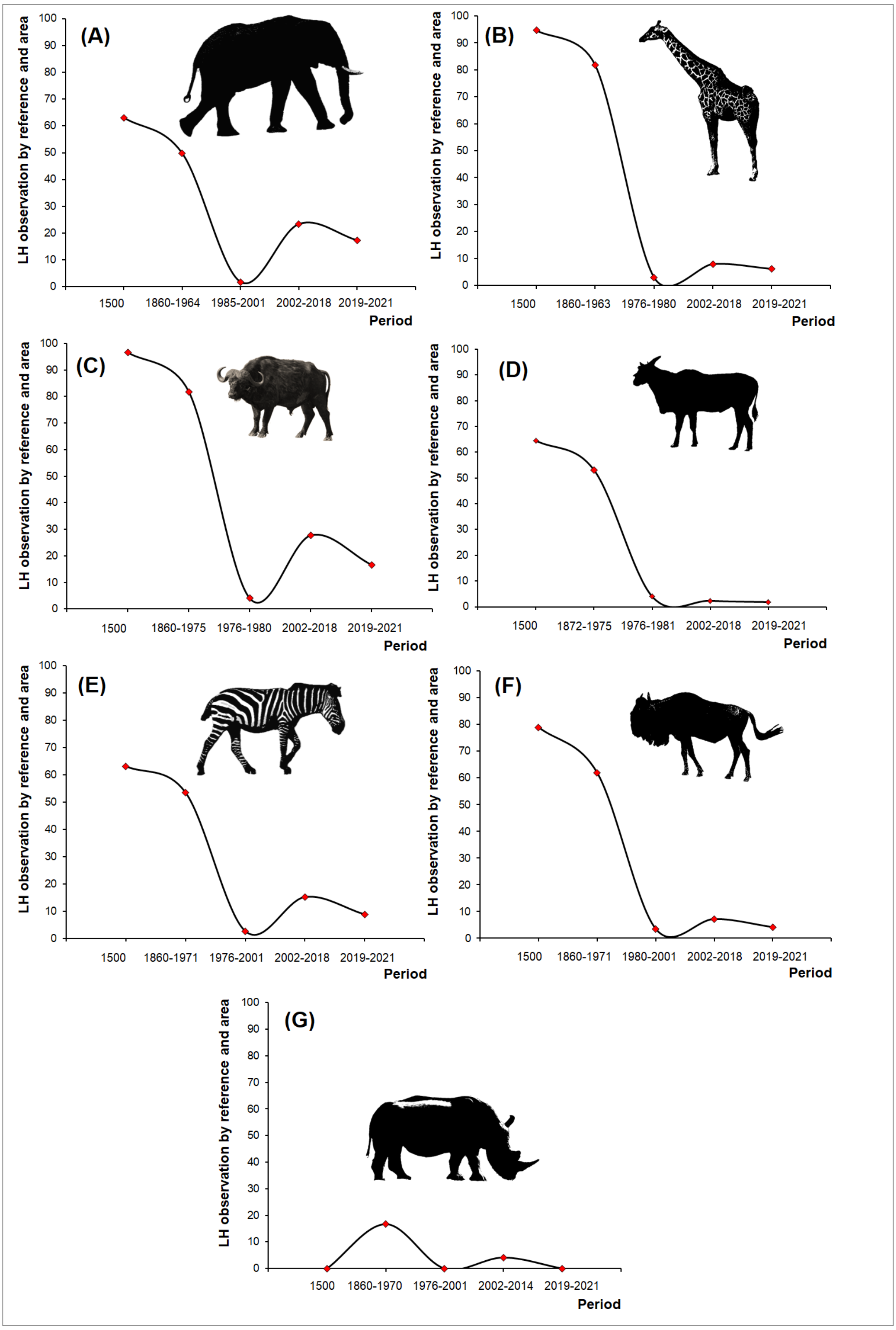

Figure 2.9. Relationship between species observation by references and the total area covered in different study periods of (African elephant, (B) giraffe, (C) African buffalo, (D) eland, (E) plains zebra, (F) blue wildebeest, and (G) white rhino. Species observation/reference – total records of species in a period/total number of references; area – the total area covered by the references in each period.

2.4.1. Prehistoric/start of the colonial period – Sporadic observations

Six of the seven study species (African elephant, African buffalo, giraffe, eland, plains zebra, and wildebeest) were reported to occur sporadically in the present-day LNP in this period. However, our references did not report white rhino occurrence. References that reported the LH occurrence in this period are scarce and only provide much more details regarding small areas of the present-day KNP (Plug and Badenhorst, 2001). Although our only reference reveals few sporadic observations of LH in restricted areas (about 700 km^2 out of a total of 10,000 km^2) of the northwest and southwest of the present-day LNP, this does not necessarily mean that large herbivores did not occur or distribute throughout the park in the prehistoric/start of the colonial period. The communities and early hunters of southern Africa did not have a megafauna recording and efficient hunting systems (Klein, 1987; Owen-Smith, 1999) in this period and, when available, it consisted of rock engravings (Zeller and Göttert, 2021). Even though the ivory and wildlife skin trade had begun during this period, gold mining and trade were the main activities (Newitt, 1997; Madeiros, 2017). This further increased the lack of records on large herbivores. Therefore, information about LH in present-day LNP in this period is rare. Consequently, any interpretation, comparison, extrapolation, and attempt to reconstruct the large herbivores' historical assemblages based on the prehistoric/start of the colonial period in the LNP should be avoided. However, the LH observations in this period although sporadic, are valuable.

2.4.2. The peak of the colonial period – Reference for near-natural African savanna

All study species were relatively common and widely distributed throughout the present-day LNP in this period. Increases in the ivory and wildlife skin trade and extensive wildlife hunting expeditions in Mozambique in the eighteenth century support the hypothesis that large herbivores were likely numerous and widespread throughout the country (Huffman, 1996; Ntumi *et al.*, 2009). Similarly, Sheriff (1983) indicated that by the mid-eighteenth century onward, as European markets have influenced the ivory trade since the thirteenth century, extensive hunting had been expanded between Maputo and Zambezia with 200 tons of ivory taken per year by Portuguese, Arab, and native traders. The movements into and outside present-day LNP also took place in clusters along all boundaries. These patterns of LH distribution and movements give scientific evidence to assume that this period describes the closest features of African savannas in their intact natural state. Thus, any attempts to reconstruct the large herbivores’ historical assemblages based on the peak of the colonial period in the LNP can accurately be done. Therefore, we consider the peak of the colonial period as the reference for the restoration of the park. However, we acknowledge it is impossible to reach this state as the landscape of the present-day GLTP has been modified by human settlements.

Despite this, the rise of the ivory and wildlife skin trade and extensive wildlife hunting at the end of the eighteenth century (Sheriff, 1983; Huffman, 1996; Ntumi *et al.*, 2009), the land transformation from 1900 onward that involved the killing of big game as part of settlement policies, increasing human native population, Europeans settler, and expansion of farming activities (Du Plessis, 1969; Ntumi *et al.*, 2009) began to gradually decrease LH numbers at the end of the nineteenth century. The approach for the eradication of cattle diseases such as tick-borne diseases, Rinderpest, and tsetse fly transmitted diseases from the 1940s (Ntumi *et al.*, 2009; Madeiros, 2017) may also have contributed to the historical decline in LH numbers. Most of the areas cleared of tsetse fly through the massive slaughtering of LH were soon occupied by people and cattle, preventing the growth of wildlife populations (Ntumi *et al.*, 2009). Furthermore, at the beginning of the 1950s, wildlife from the present-day LNP dispersed and populated the KNP (Pienaar *et al.*, 1966; Whyte *et al.*, 2003; Mavhunga and Spierenburg, 2009). Likewise, Dias and Rosinha (1971); Mavhunga and Spierenburg (2009); Madeiros (2017) indicated that from the 1940s to 1970s, about 3,000 elephants and countless species of other LH were killed in many areas in the former Rhodesian and Portuguese East Africa (present-day LNP area) as campaigns to eradicate tsetse flies and took complete refuge in safe areas of Transvaal. Child and Savory (1964); Sidney (1965) pointed to the destruction and degradation of habitat as the prime reason for the decline in the number of LH in the middle of the nineteenth century in all of southern Africa. This was to such an extent that certain LH species could not inhabit or occupy it any longer (Du Plessis, 1969).

2.4.3. Post-colonial/civil war period –The drastic reduction of wildlife

In this period, the results reveal that the populations of all LH species studied were almost decimated and the few remaining animals concentrated their distribution along the

LNP-KNP border. Four events or factors can explain these patterns, (i) the conversion of the area as hunting concession "Coutada 16" in the early 1970s, (ii) the independence of Mozambique in 1975 followed by (iii) the outbreak of the civil war from 1976 to 1992, and (iv) after 1992 there was no civil war, but conservation areas including the hunting concessions had been abandoned, with no management, no law enforcement, poaching was intense, leading to dramatic LH declines. This sequence of events further reduced the wildlife and pushed them to safer places (LNP-KNP fence and where the fence crosses rivers) where they could easily escape to KNP (Piennar, 1963; Dunham, 2004; Whyte and Swanepoel, 2006). After Mozambique's independence, there was further expansion of cultivation areas because many families returned to their villages and started growing crops (Smithers and Tello, 1976; Tello, 1977; Hatton *et al.*, 2001; Ntumi *et al.*, 2009). This further reduced the large herbivores' range.

The civil war (1976-1992) ended up with the rest of the wildlife as it forced the government's abandonment of most protected areas, they were militarily occupied and the various armies slaughtered most of the country's remaining wildlife (East, 1999; Madeiros, 2017). The persecution and hunting that the eland, buffalo, and zebra were subjected to during the civil war made these species scarce and patchily distributed only in safer areas (Dias, 1981). Likewise, studies conducted in entire Mozambique on antelopes (East, 1999), historical trends in the distribution and abundance of elephants (Ntumi *et al*., 2009), terrestrial mammals (Neves et al., 2018), and large mammals in Gorongosa National Park (Stalmans *et al*., 2019), confirm a severe decline in the abundance and distribution ranges of some study species in the LNP during the civil war. Although some white rhinos from the reintroduced population in KNP had wandered eastwards across the international border into present-day LNP (Pienaar *et al*., 1966), there was no record of this species in this period. This can be explained by (i) excessive hunting during the civil war in the present-day LNP (Dunham, 2004; MINAG, 2008) that may have prevented the entering of rhinos in the former "Coutada 16" coming from Zimbabwe and South Africa (Dunham, 2004), and (ii) absence of records in this period due to the lack of expeditions to the area caused by the civil war.

2.4.4. Proclamation of GLTP to current period – Slow recovery and vulnerable large herbivore population

Our results reveal a slight increase in the abundance and range expansion of elephants, buffalo, and plains zebra in opposite to giraffe, eland, and blue wildebeest that show the poorest restoration. After the proclamation of GLTP as LNP was almost an empty wildlife area, a restoration program took place between 2001 and 2008 (Hofmeyr, 2004; Mabunda *et al.*, 2012). During this period, 111 elephants, 98 buffalos, 759 blue wildebeests, 1,024 plains zebras, 61 giraffes, 12 white rhinos, and other species not included in this study were actively translocated from KNP to the former "Old Sanctuary" (Dunham, 2004; Hofmeyr, 2004). During the same period, some sections of the LNP-KNP international border were also removed to allow passive wildlife reintroduction and wildlife cross-border movements from KNP into LNP (Mabunda *et al.*, 2003; Dunham, 2004). This contributes to a slight increase and restoration of LH species in the park. Elephants recover well due to their ability to tolerate human settlement areas (Grossman *et al.*, 2014; Roque *et al.*, 2021) and could even invade agricultural fields and villages although increasing human-elephant conflicts. Buffalos, although avoiding livestock (Hibert *et al.*, 2010) may use the same grazing areas with livestock at different times (Chigwenhese *et al.*, 2016). Likewise, Stephenson (2010, 2013); Grossman *et al.* (2014); ANAC (2018); Roque *et al.* (2021) reported increased abundance activities and distribution patterns of these species in places with human resettlements.

Surprisingly, blue wildebeest, the migratory species (Morrison and Bolger, 2014) that was reintroduced in the highest numbers (759 individuals) with few historical hunting records in the LNP (Whyte and Swanepoel, 2006; Stephenson, 2010, 2013; Grossman *et al.*, 2014; ANAC, 2018), revealed the lowest abundance and didn't expand their range out of "Old Sanctuary" because this area has availability of permanent surface water throughout the year. This area is also remote from the human settlement (Dunham, 2004; Whyte and Swanepoel, 2006). The giraffes and elands also show behaviour similar to blue wildebeest. However, these species according to LNP Park Warden, have suffered from intense poaching for meat and traditional ceremonies at least ten years after the establishment of the LNP. This was because by that time the number of anti-poaching control posts was low, and the park had not yet implemented the Wildlife Intensive Protection Zone (PNL, 2012; Grossman *et al.*, 2014). Furthermore, eland was not reintroduced in the LNP and this can further explain the poorest restoration. This is consistent with findings by Whyte and Swanepoel (2006); Roque *et al*. (2021), who recorded the above-mentioned species to occur only in the "Old Sanctuary." Intensive studies conducted in the LNP after the proclamation of GLTP (aerial censuses 2002 – 2018, elephant movements monitoring from Elephants Alive, and camera traps systematic assessment 2019-2021) reveal a slow and vulnerable LH restoration process. Similarly, Stalmans *et al*. (2019) documented post-war asymmetric recovery rates across LH species in Gorongosa National Park, Mozambique.

After the proclamation of LNP, about 12 white rhinos were reintroduced into LNP (Hofmeyr, 2004; Whyte and Swanepoel, 2006; Mabunda *et al*., 2012), and a small number of white rhinos have moved from KNP to LNP through gaps in the fence (Dunham, 2004). Despite this effort to repopulate white rhinos, they did not ever reach a distribution beyond the limits of the "Old Sanctuary" due to the intensification of poaching. According to Stephenson (2010); Lunstrum (2014); Büscher and Ramutsindela (2015); Ferreira *et al*. (2015), the GLTP was impacted by the unprecedented increase in white rhino poaching, mainly in the KNP. The threat of poaching prevented movements from KNP into LNP. The camera assessment carried out from 2019 to 2021 in LNP (Roque *et al*., 2021) did not record any white rhinos.

Our findings, which result from combining different natures of references and interpretations significantly, enhance our knowledge in this regard, as they may improve the wildlife restoration and other conservation strategies and plans for the study species in the Great Limpopo Transfrontier Park (GLTP). The results of this study have advanced our knowledge of the topic in question as it simultaneously revealed the dramatic collapse of large herbivores in the Limpopo National Park and the process of their restoration. These findings suggest connectivity between different habitats within the LNP despite intense human presence in the core area and buffer zone. Therefore, further efforts are necessary to strengthen the slow recovery of LH in the LNP. The findings highlight the need for further research on connectivity in the larger GLTP through GPS tracking (collars fitting) of LH species to improve future management in the LNP and GLTP. However, as this study is the first historical reconstruction of LH distribution and movements in the area, its results should be viewed as being of a preliminary nature, since the indicated patterns can be strengthened and gaps filled if and when new written records for the different periods under study are discovered. Our results highlight the importance of combining the interpretation of past and current data as a guide for the restoration of threatened species in African savannas impacted by human activities. Failure to recognize how much of a species' range has been lost in the past represents a failure to recognize the full extent of man's impact on that species in the future. This is a key aspect of conservation biology and restoration ecology.

It has been 20 years since the LH reintroductions and the opening in the LNP-KNP fence took place. However, the restoration process remains slow and vulnerable. Our results provide evidence that it is not enough to simply perform LH reintroductions and open sections of the fence to have a spontaneous increase in wildlife. It is necessary to put a continuous effort into the restoration process. The distribution and movement patterns of LH provided here offer a framework for conservation planning and management and the development of a more complete understanding of suitable wildlife ecological corridors and human resettlement areas for further development of the Great Limpopo Transfrontier Park. For such, there is a need to extend the coverage achieved by this study to include the entire Great Limpopo Transfrontier Park. There is also a need to monitor and mitigate the drivers and implications of the observed changes in the distribution and movement patterns.

Acknowledgments

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2.5. Supplementary material

Table 2.S1. Some examples of passages in the early literature that refer to large herbivores occurrence in the Great Limpopo Transfrontier Park

date	Location	Excerpt	Source	Pages
1860	Northwest of Limpopo National Park (LNP)	"…The moment I arrived I saw Manova and the hunter Macindana coming along, each bringing the tail of a buffalo which he had killed, fastened to their muskets. The hunter Maxotil had killed a zebra, and Mabana, a tuongonlie…." "They ate the insides of all the five animals, and the whole of the zebra…"(Das Neves, 1879)	Primary	46-48
1860	Northwest of LNP	"…Maxotil and the hunters returned in the afternoon with the carriers bringing the three buffaloes, part of the rhinoceros and part of the giraffe…."(Das Neves, 1879)	Primary	70
1860	Northwest of LNP	"…The number of elephants killed amounted to fifty-five. The tusks were all despatched to the house of Senhor Albazini…"(Das Neves, 1879)	Primary	124
1861	Northeast of LNP	"...On coming close to the place, a buffalo suddenly sprang out from among the tall reeds, and escaping along the bank, up the river (Letaba River), crossed over…"(Das Neves, 1879)	Primary	213
1862	Northeast of LNP	"…resting only for a short time during the day near a waterfall of the river Imbelule… And in truth they were not far distant, for we soon came upon a herd of five buffaloes"(Das Neves, 1879).	Primary	228-229
1870	LNP river	"…During 1870, both the white rhino and the black rhino were reported west of the Limpopo River, between its confluences with the Elefantes and Nuanetsi Rivers…" (Dunham, 2004)		
1872	Northeast and Southeast of LNP	"……noted the presence of white rhino west of the Limpopo River, between the confluence of the Limpopo and Elefantes Rivers, and the confluence of the Limpopo and Nuanetsi Rivers (Dunham, 2004)	Secondary	4
1930s	LNP	Location of large-scale hunting in the Lourenço Marques District in the 1930s (present-day Limpopo National Park) (Martinho, 1934)	Primary	4-23
1953	East of LNP	"…*Lododonta africana* distributions …commoner north of the Olifants River; Shingwedzi, Letaba……Portuguese East Africa…. Southern Rhodesia"(Ellerman *et al*., 1953)	Primary	156

1953	East of LNP	"…*Equus burchelli* distributions: Transvaal, where it is widely distributed (Punda Maria,- Shingwedzi, Letaba, Satara, Skukuza, Pretorius Kop, Toulon, etc…Southern Rhodesia... parts of Portuguese East Africa"(Ellerman *et al.*, 1953)	Primary	166
1953	South of LNP	"…*Connochaetes taurinus* distribution: Shingwedzi, Satara, Skukuza, Pretorius Kop, Toulon, etc. Very common south of the Olifants River). Zululand…Southern Rhodesia ….Southern Portuguese East Africa"(Ellerman *et al.*, 1953)	Primary	205
1953	Western LNP	"…*Tragelaphus oryx* distribution: North of the Olifants River, and in the Giants Castle Reserve, Natal. Parts of Southern Rhodesia, and western Portuguese East Africa..."(Sealous, 1908)	Primary	210
1953	East of LNP	"…*Syncerus caffer* distribution: Transvaal (districts of Shingwedzi, near Crocodile River in the Skukuza region where it occurs in large numbers), Toulon, etc… Southern Rhodesia… …Portuguese East Africa, recorded from districts of Gazaland…"(Ellerman *et al.*, 1953)	Primary	211
1958	Northeast of LNP	"…Buffalos along the Nuanetsi river about 10 miles from the Portuguese border; along the Limpopo and Bubye river…" (Fraser, 1958)	Secondary	256
1964	South LNP (Sengwe corridors), Nuanetsi river	"…Buffalos are most numerous in the south east,…The latter may be buffalo which enter the territory from Portuguese East Africa…"(Child and Savory, 1964)	Primary	13
Early 1970s	Between the Limpopo River and KNP	"…By the early 1970s white rhino had been eliminated from most of its former range, and the few surviving animals were restricted to the area between the Limpopo River and Kruger National Park (KNP) on the South African border…" (Dunham, 2004)	Primary	98
1970s	North and South of LNP	The location of distribution of white rhinos in Mozambique (present-day LNP) in the 1970s (Dunham, 2004)	Secondary	7

Table 2.S2. Some examples of passages in th early literature taht mention, or allude to movements behaviour by large herbivores in the Great Limpopo Transfrontier Park

Date	**Direction of movement**	**Excerpt**	**Source**	**Pages**
1900s	From KNP to LNP	"…In 1905 the Sabi Game Reserve and Shingwidzi Reserve (KNP) had only 10 elephants but the number grew in 1912 to 25 elephants as results of immigration from adjoining Portuguese East Africa (Mozambique)…"(Pienaar *et al.*, 1964)	Secondary	1
1902	From KNP to LNP	"…Game (elephants, rhinos and elands) movements from areas bordering Mozambique (current southeast of Limpopo National Park) and Rhodesia [current Gonarezhou National Park (GNP)] to Shingwitsi and Sabi game reserve (current Kruger National Park) in 1902…" (Mavhunga and Spierenburg, 2009)	Primary	46-47
1903	From KNP to LNP	"The recolinization of KNP by elephants from Mozambique (present-day Limpopo National Park) after the arrival of the first warden in 1903 through Olifant's River" (Whyte *et al.*, 2003)	Secondary	337
1900-1945	From LNP to KNP	"…Figure 16.1 shows the recolonization of Kruger by elephants, giraffe, eland…..Northward colonization took until 1945……Southward was slightly slower, taking until 1958…"(Whyte et al., 2003)	Secondary	337
1950-1970		"…Elephant numbers increased rapidly from perhaps 50 to over 1000 in 1959, to nearly 9000 in 1970, due largely to immigration from Mozambique…"(Walker *et al.*, 1987)	Primary	385
1960-1967	From LNP to KNP	"…immigration from Mozambique probably contributed to dramatic increase of elephant population between 1960 and 1967"(Whyte *et al.*, 2003)	Secondary	336
1964	From KNP to LNP and vice-versa	"Temporary or permanent immigration from Portuguese East Africa and even Southern Rhodesia, could likewise have added to the increase"(Pienaar *et al.*, 1966) "Two elephants herds of 42 and 34, respectively, were seen during March, to enter KNP from Portuguese East Africa at Kalabyene Spruit in the	Primary	43

		Lebombo Mountains"(Pienaar *et al*., 1966) "The possibility is not excluded that in consequence of severe drought, a considerable number of immigrant elephant entered the park (KNP) from adjoining sandveld, leaving again after sufficient rain had fallen (cf i.a 86 bulls elephant counted at Pafuri during the census)"(Pienaar *et al*., 1966)		
1964	From Southern Rhodesia and Mozambique	"….but the surplus male animals represents an influx of nomadic elephant bulls over the year from Southern Rhodesia (cf. Pafuri) and Mozambique (cf. the Lebombo Flats" (Whyte *et al*., 2003)	Primary	35
1964-1969	Along LNP western border	White rhinos re-population movements from Kruger National Park to Limpopo National Park between 1964 and 1969 (Pienaar, 1970)		
1976	From LNP to KNP	"After the isolation of park (KNP) through fencing in 1976, this rate (7.5% per year) declined to 6.6%, suggesting that elephant population growth may have been enhanced by immigration from Mozambique"(Whyte *et al*., 2003)	Primary	338
2003	LNP – KNP border	The eastern boundary fence of KNP prevented the movement of rhinos from the mid- 1970s until the end of the 20th century, but within the last few years, white rhinos have again moved from KNP into LNP, crossing the international border either through a 14-15 km gap that was deliberately opened in the fence during 2003, or through gaps where the border fence crosses rivers and floodwaters have recently damaged the fence (Dunham, 2004)	Primary	4
2008-2013	LNP to GNP	Movements of buffalos from KNP to GNP between 2008 and 2013 in the GLTP (Caron *et al*., 2016).	Primary	278
2018	From KNP to LNP and vice-versa	Movements of elephants from KNP to LNP and vice versa between 2002 and 2014 (Purdon *et al*., 2018)	Primary	5

2.6. References

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CHAPTER THREE

3. Assessing distribution patterns and the relative abundance of reintroduced large herbivores in the Limpopo National Park, Mozambique

Abstract

This study is the first systematic assessment of large herbivore (LH) communities in Limpopo National Park (LNP) in Mozambique, an area where most LH species were extinct until the early 2000s. We investigate whether LH community parameters are linked with the availability of habitat types or the distance between sampling sites and the origin of LH resettlement (Old Sanctuary). We placed camera traps in five habitat types and on the reintroductions and not-reintroductions areas to compare species richness, relative abundance index, grazers-browsers-mixed feeder ratio, and naïve occupancy of 15 LH species. While the richness decreased along the distance gradient of the LH reintroductions area, the relative abundance index strongly responded to habitat features. Among habitat types, the browsers ratio oscillated, while from reintroductions areas to not-reintroductions areas, the ratio increased. Most species showed a wider distribution range among habitat types. The associations of most large herbivore community parameters with habitat types rather than distance to the initial release site of LH, together with the species-specific and guild-specific response patterns of LH, suggest Limpopo National Park to already be in an early-intermediate stage of restoration. Our results highlight the importance of post-release monitoring of reintroduced wildlife as a tool to assess the success of ecological restoration initiatives in transboundary conservation areas.

Keywords: ecological parameters, camera trap, colonization, distribution patterns, relative abundance, habitat types, large herbivores reintroduction, Limpopo National Park, Old Sanctuary.

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3.1. Introduction

Large herbivores are one of the components determining the structure, composition and function of ecosystems in African savannas (Winnie *et al.*, 2008; Anderson *et al.*, 2016). In the Sub-Saharan African savannas, wildlife shares pastoral landscapes with people and livestock (Sawyer *et al.*, 2018). As long as this phenomenon persists, these semi-natural habitats progressively become smaller and less available (Zeller *et al.*, 2017; Stoldt *et al.*, 2020) and confine the distribution of wildlife to areas that are still safe and suitable. As large herbivores explore large home ranges (Smuts, 1975; Shannon *et al.*, 2006; Göttert *et al.*, 2010; Owen-Smith and Martin, 2015), landscape-scale monitoring is needed, although it is costly because the distributions patterns are affected by processes which operate at multiple scales (Jones, 2011), so methods that provide robust information at low-cost are particularly valuable.

Habitat availability and the quality and quantity of food are determinants in the distribution and abundance of LH (Chirima, 2009; Cornélis *et al.*, 2011; Boyce *et al.*, 2016). Habitat choice and LH distribution also depend on water and shelter availability, topography, human settlements, predator occurrence and abundance (Sinclair, 1985; Redfern *et al.*, 2003), social interactions between individual animals, breeding and territorial behaviour (Roath and Krueger, 1982). The landscape is heterogeneous concerning the habitat types forcing large herbivores to move according to habitat characteristics and their needs for energy and safety (Duparc *et al.*, 2019; Holbrook *et al.*, 2019). Herbivores with smaller body sizes require relatively less forage but of higher nutritional quality, whereas larger herbivores tolerate low-quality food, provided that it is of sufficient quantity (Bell, 1971; Jarman, 1974; Olff *et al.*, 2002; Hopcraft *et al.*, 2012; le Roux *et al.*, 2020). As a result of body-size-related nutrient requirements (Riginos and Grace, 2008), larger species exploit a higher diversity of habitat types than smaller species (Olff *et al.*, 2002; Cromsigt *et al.*, 2009) and are therefore more evenly distributed in the landscape than smaller species (du Toit and Owen-Smith, 1989). Body size and feeding guild interactions also influence the distribution of LH. Grazers [e.g., warthog (*Phacochoerus africanus*), blue wildebeest, and plains zebra] prefer to graze in habitats with short-to-medium grasses (Traill, 2004) and medium-to-tall grasses (African buffalo) as the body size increases (Skinner and Chimimba, 2005; Musiega *et al.*, 2006). Pure browsers [e.g., greater kudu (*Tragelaphus strepsiceros*) and giraffes] select mainly habitats with woody plant forage (Owen-Smith and Cooper, 1989), while mixed feeders [e.g., impala (*Aepyceros melampus*), nyala (*Tragelaphus angasii*) and sable antelope (*Hippotragus niger*)] prefer woodland with minimal undergrowth and low to medium height grasslands (Botha and Stock, 2005; Skinner and Chimimba, 2005).

The Limpopo National Park was established in 2001 (DINAC, 2003). Before that time, it was a hunting concession called "Coutada 16" (Mavhunga and Spierenburg, 2009; Massé, 2016). The area was affected by Mozambique's civil war (1976-1992) (Hatton *et al*., 2001) and decades of poaching, which decimated the populations of almost all large herbivore species in the region (Hofmeyr, 2004; Lunstrum, 2016). The LNP is part of the Great Limpopo Transfrontier Park (GLTP) initiative that links the LNP in Mozambique, Kruger National Park (KNP) in South Africa and Gonarezhou National Park (GNP) in Zimbabwe (DINAC, 2003). Communities that had fled during the war gradually returned in the 1990s, and by the time the area was declared a national park, it was home to some 20,000 people (Bazin *et al*., 2016). An explicit goal of the GLTP is to rehabilitate wildlife populations in the area to allow wildlife transboundary movements in the Great Limpopo Transfrontier Park (DINAC, 2003). For this purpose, a 300 km^2 fenced area (Old Sanctuary), easy to patrol and allow wildlife adaptation and growth, was built in the southwestern corner of the LNP. Afterwards, a total of 4,725 large herbivore individuals belonging to 10 species (African elephant, white rhino, waterbuck, roan antelope, Lichtenstein hartebeest, African buffalo, giraffe, blue wildebeest, plains zebra, and impala) were actively translocated from KNP to LNP between 2001 and 2008 (Hofmeyr, 2004; Mabunda *et al*., 2012). The fence of the sanctuary was later removed in 2006 to allow animals to disperse and colonize the rest of the park. Some sections of the LNP-KNP international border also were removed to allow passive wildlife reintroduction and wildlife cross-border movements from KNP into LNP (Mabunda *et al*., 2003). The reintroduction success depends on the adaptation/acclimatization of translocated animals to a new environment after their release (Scillitani *et al*., 2013) and their dispersal behaviour (Richardson *et al*., 2015). Species of LH may disperse from reintroduction sites as an adaptive response to explore and select high-quality habitats surrounding or away from release sites (Scillitani *et al*., 2013; Richardson *et al*., 2015). However, human presence limits habitat use by large herbivores and their ability to disperse to other habitats in the landscape (Larkin *et al*., 2004). Around 30,000 people live inside LNP. Twenty-three per cent (23%) of these people are waiting to be resettled in an area outside the current park borders that is termed a “buffer zone” (Milgroom and Spierenburg, 2008; Bazin *et al.*, 2016). These villages block the use of the habitats by large herbivores in the Limpopo National Park landscape.

Understanding the large herbivores’ spatial distribution and abundance in African savanna ecosystems is critical for the adaptive management of species and their habitats (Murwendo *et al.*, 2020; Muposhi *et al.*, 2016). Since the beginning of the LNP restoration program in 2001 (Hofmeyr, 2004; Mabunda *et al.*, 2012), to our knowledge, there are no studies to understand the stage of its course, the adaptation of reintroduced LH to the new habitats after release and their ability to invade and colonize other habitats outside the release site. The important ecological parameters (occurrence, relative abundance, species richness, diversity index, grazer-browser-mixed feeder-ratio, ungulate-potential predators and spatial occupancy) of reintroduced LH that can indicate the re-establishment of processes and patterns in the LNP landscape remain poorly explained. Because the LNP is considered one of the core areas for the development of GLTP (DINAC, 2003), these parameters may indicate the functionality of GLTP. Some parameters (population trends and density, spatial distribution of selected species) are still estimated only through the aerial census data (Whyte and Swanepoel, 2006; Stephenson, 2013; Grossman *et al.*, 2014). Furthermore, no study has yet attempted to compare these parameters concerning the habitat features at the origin of LH resettlement (Old Sanctuary). Our study aimed to investigate whether ecological parameters associated with large herbivore communities in Limpopo National Park (e.g., occurrence, relative abundance, species richness, diversity index, grazer-browser-mixed feeder ratio, ungulate-potential predators and naïve occupancy) are explained by (i) the availability of habitat types or (ii) the distance between sampling site and the “origin of large herbivore reintroductions (Old Sanctuary)”. Thus, we hypothesized that the ecological parameters (1) will decrease with an increasing distance of the sampling site from the so-called “origin of LH reintroductions” (“Old Sanctuary” Figure 3.1A-B), (2) will decrease from Lebombo North (West of LNP) to Nwambia Sandveld (East of LNP) (Figure 3.1C), and (3) that mixed feeders and species of larger body size will use a wider range of habitats. The study results can be a suitable tool for the ecological restoration of the park by measuring (i) its success or failure or (ii) the post-release adaptation (colonization) of reintroduced large herbivores to new habitats in the

Limpopo National Park. This will ultimately support the development of a comprehensive conservation management and monitoring plan for the further development of the Great Limpopo Transfrontier Park.

3.2. Material and methods

3.2.1. Study area

The study was carried out from December 2019 to March 2021 in LNP (22°25'S - 24°10'S, 31°18'E - 32°39'E), a 10.000 km² protected area in Gaza province in Mozambique (Figure 3.1A-C). The LNP is a crucial element of a transboundary protected area network which, together with KNP in South Africa and GNP in Zimbabwe, forms GLTP. The western boundary of the LNP is formed by the border with South Africa. The Zimbabwean border touches on the northern-most tip of the area. The Limpopo River forms the eastern boundary, whilst the Olifants River is the southern boundary. The climate is classified as warm dry tropical with mean annual precipitation increasing from 360 mm to over 500 mm from northern to southern. The mean annual temperature fluctuates between 24 ºC and 30 ºC. Rainfall occurs in the wet season extending from November to April. The dry season extends from May to October (DINAC, 2003). The annual rainfall average that falls in the wet season is about 60% (Brito and Julaia, 2007). The altitude in the park varies between 260 and 840 m above sea level. Geologically, LNP is dominated by rhyolite volcanic rock in the southern region, while the North consists of a red sand mantle, whereas alluvium and clay sediments characterize the Limpopo floodplains (DINAC, 2003).

Hydrologically, the LNP is dominated by three river systems with an overwhelming impact on the land use of the region, which influences wildlife distribution: (1) the Limpopo is the largest, perennial river, although water becomes restricted to pools along the river bed at the end of the dry season; (2) the Olifants remains perennial throughout the season; and (3) the Shingwedzi is a much smaller not-perennial river system. As Shingwedzi drains the central portion of the LNP, it has a large effect on wildlife distribution (DINAC, 2003). Settlements in the LNP are characterized by subsistence farming, free livestock grazing, and “bush meat poaching” (illegal hunting of wildlife for local consumption) (Andresen *et al.*, 2014). About 30,000 people live in the park in 50 villages. Most of the population (around 20,000 people) is concentrated in 42 villages along the right bank of the Limpopo River and the left bank of the Olifants River, where the alluvial soils are suitable for agriculture (Bazin *et al*., 2016). The remaining inhabitants live in eight villages along the Shingwedzi Valley (Milgroom and Spierenburg, 2008). These continuous matrixes of agricultural resettlements along the Limpopo River and Shingwedzi Valley act as barrier to wildlife distribution and movements. Free livestock grazing and bush meat poaching are the main threats in the most extensive habitats (Sandveld habitats) in the LNP (Andresen *et al*., 2014; Andresen, 2015). There are over 7,000 heads of cattle along Shingwedzi Valley and more than 10,000 in the buffer zone grazing with wildlife (ANAC, 2018). People hunt with large packs of 10-20 domesticated dogs (*Canis lupus* f. familiaris), and large herbivores are displaced by these activities, particularly in the open grasslands in the Sandveld (Andresen, 2015). The encroachment of people in the park modifies the composition and structure of habitats and reduces safety, forcing wildlife concentration away from agriculture and settlement areas.

Based on woody vegetation, species composition and physiognomy, Stalmans *et al*. (2004) described ten landscape types with 15 plant communities in the LNP: (i) Nwambia Sandveld, (ii) Pumbe Sandveld, (iii) Rugged Veld, (iv) Lebombo North, (v) Shrubveld on Calcrete (*Combretum* sp/*Colophospermum mopane*), (vi) Shrubveld on Basalt, (vii) Woodland, (viii) Limpopo Levubu Floodplains, (ix) Rugged Veld (*Adansonia digitata*/ *Colophospermum mopane*) and (x) *Salvadora angustifolia* floodplains. Since the establishment of the LNP, there has been an increase in the wildlife population, and at least 26 LH species have been documented (Whyte and Swanepoel, 2006; Stephenson, 2013; Grossman *et al*., 2014) as a result of active reintroductions through capture and release of LH from KNP to LNP and passive reintroductions through dropping of three sections of the fence between these two parks to allow transboundary wildlife movements in the context of the establishment of the GLTP (Whyte and Swanepoel, 2006; Mabunda *et al*., 2012; Bazin *et al*., 2016).

3.2.2 Study design

<u>Selection of species</u>

We selected 15 large herbivore species (body mass > 10 kg) that show some increase in their population number since 2004 (Stephenson, 2013; Grossman *et al*., 2014).

These LH species also represent different feeding guilds. Seven of these species were actively reintroduced in the park from 2001 to 2008 (Table 3.1), and together with the rest of the species, are believed to have crossed the borders through the dropped fence sections (Mabunda *et al*., 2012) such that the current number of LH species in the park is an obvious result of reintroductions, dispersal movements, migration and intrinsic population growth.

Table 3.1. Large herbivore species (body mass > 10 kg) selected for the study in the Limpopo National Park (the upper and lower limit of weight corresponds to variations between adult males and females)

Common name	Scientific name	Body mass (kg) (Skinner and Chimimba, 2005; Estes, 2012)	Feeding guild (Skinner and Chimimba, 2005)
Warthog	*Phacochoerus africanus*	60 – 72	Grazer
Waterbuck	*Kobus ellipsiprymnus***	180 – 220	Grazer
Blue wildebeest	*Connochaetes taurinus***	180 – 250	Grazer
Plains zebra	*Equus quagga***	290 – 340	Grazer
African buffalo	*Syncerus caffer***	580 – 700	Grazer
Common duiker	*Sylvicapra grimmia*	18 – 21	Browser
Bushbuck	*Tragelaphus scriptus*	32 – 64	Browser
Greater kudu	*Tragelaphus strepsiceros*	190 – 250	Browser
Giraffe	*Giraffa camelopardalis***	970 – 1400	Browser
Steenbok	*Raphicerus campestris*	12 – 14	Mixed feeder
Impala	*Aepyceros melampus***	40 – 70	Mixed feeder
Nyala	*Tragelaphus angasii*	100 – 126	Mixed feeder
Sable antelope	*Hippotragus niger*	180 – 230	Mixed feeder
Eland	*Tragelaphus oryx*	400 – 900	Mixed feeder
African elephant	*Loxodonta Africana***	2800 – 6300	Mixed feeder

****** Actively reintroduced species in the Limpopo National Park

Selection of habitats

Based on an assessment made from a helicopter, we selected sites corresponding to five of the ten habitat types (Stalmans *et al*., 2004), which represent 90% of the park surface: (i) Nwambia Sandveld, (ii) Mopane Shrubveld on Calcrete, (iii) Rugged Veld, (iv) Lebombo North, and (v) Pumbe Sandveld (Figure 3.1C). Due to the increase in poaching activities since 2010, the park has been implementing an Intensive Protection Zoning (IPZ) since 2013, which excludes villages and land-use areas for livestock grazing and agriculture from the protected area (Stephenson, 2013). The IPZ is ecologically preserved (Hofmeyr, 2004) and is where the "Old Sanctuary" and fence-dropped sections of the KNP-LNP international border were located. The IPZ is also crucial for the active and passive restoration processes because, historically, wildlife undertook seasonal movements between KNP and Mozambique before the construction of the Eastern boundary fence of KNP (Mabunda *et al*., 2012). Thus, we consider the IPZ (KNP fence, Old Sanctuary and reintroductions area) as the origin of LH reintroductions and the area outside IPZ, excluding the buffer zone as a not-reintroductions area (Figure 3.1A-B). By overlapping the IPZ map (Figure 3.1B) and the sampling sites map (Figure 3.1C), we calculated the average distances between the sampling site and the "origin of LH reintroductions area" using ArcMap 10.8.1, a Geographic Information System. In the next step, we established the gradient in the following order: (1) Lebombo North (inside the IPZ); (2) Pumbe Sandveld, and (3) Rugged Veld (partially within the IPZ); (4) Shrubveld on Calcrete (16 km from the IPZ) and (5) Nwambia Sandveld (21 km from the IPZ).

(i) Lebombo North: covers 398.78 km^2 (3.5 % of LNP) and has high richness in its grass composition (44 species) but lower average biomass (2,076.5±569.83 kg/ha) than Nwambia Sandveld and Shrubveld on Calcrete. The ecologically important trees are *Colophospermum mopane* and *Combretum apiculatum*. The tree's average height is 2.9 m (Ribeiro *et al*., 2019). *Heteropogon* sp, *Digitaria* sp, and *Uroclhoa mossambicensis* are the most dominate grasses (Stalmans *et al*., 2004).

(ii) Pumbe Sandveld: covers 256.08 km^2 (2.3 % of LNP) and has a relatively higher floristic composition (87 species) than Lebombo North, Rugged Veld, Pumbe Sandveld and lower than Nwambia Sandveld. It is dominated by *Combretum apiculatum* and *Terminalia sericea*. The grass layer is dominated by *Panicum maximum* and *Eragrostis pallens* (Stalmans *et al*., 2004).

(iii) Rugged Veld: covers 699.11 km^2 (6.21% of LNP) and is relatively rich (81 species) in botanic composition. The most ecologically important trees are *C. mopane, Acacia nigrescens*, *Sclerocarya birrea* and *Combretum imberbe*. The grass layer is dominated by *P. maximum*, *Uroclhoa mossambicensis* and *Schmidittia pappaphoroides* (Stalmans *et al*., 2004).

(iv) Shrubveld on Calcrete: covers 4,158.9 km^2 (38.8% of LNP) and, similar to Lebombo North, has the highest richness in its grass composition (44 species), however with low average biomass (2,968 kg/ha±635.63). *Digitaria eriantha*, *Penisetum glaucum* and *P. maximum* are the most dominant grass species. Calcrete is almost homogeneous concerning the species composition; shrubby *C. mopane* is the overwhelmingly dominating species. The tree's average height is lower (~ 2.25 m) compared to other habitats (Ribeiro *et al*., 2019).

(v) Nwambia Sandveld: the most extensive habitat covering 4,586.41 km^2 (41.1% of LNP) and is relatively richer than others with 99 species in overall botanic composition (Stalmans *et al*., 2004). Although the grass composition is relatively low (35 species), the average biomass is higher (3,630.5±298.62 kg/ha) than in other habitats. *Digitaria eriantha* and *Uroclhoa mosambicensis* are the most dominant grass. The most ecologically important trees are *Combretum apiculatum*, *Sclerocarya birrea* and *Xeroderris stuhlmannii*. The average tree height in this landscape is the highest, with ~ 4.25 m (Ribeiro *et al*., 2019).

3.2.3. Data collection

We deployed 24 infrared wildlife camera traps (Foxelli Outdoor Gear Oak's Eye Trail Cam$^{®®}$ – 14MP 1080 Full HD) in 146 sites from December 3, 2019, to June 4, 2021. We used a stratified random design with habitat types as the main strata, and we randomly selected ~2 km^2 grid cells (Woog *et al*., 2010; Rovero *et al*., 2013) in 60 × 108 km^2 grid cells surveyed. We deployed one camera trap in each grid (Rovero *et al*., 2014; Debata and Swain, 2018) at 0.50 to 1.5 meters in height on trees, and shrubs. Areas that were difficult to access and there was a high risk of cameras being stolen (close to roads or settlements and cattle grazing areas) were not covered for sampling. All cameras worked on a passive infrared-triggered basis. The cameras were active 24 hours a day and took bursts of two successively high-resolution photos, 14 MP (4426 x 3312P), with a delay of 60 seconds between trigger activations. The cameras had eight long-lasting alkaline batteries (Amazon Basics AA High-Capacity Rechargeable) and one Micro Transcend$^{®®}$ SD memory card (SanDisk 32 GB micro SDHC memory card). Each camera trap location or station constituted a sampling unit (*n*) (Mena *et al*., 2020). We moved the cameras from one station to another six times and collected LH data in 146 sampling units at average intervals of 69.5 days.

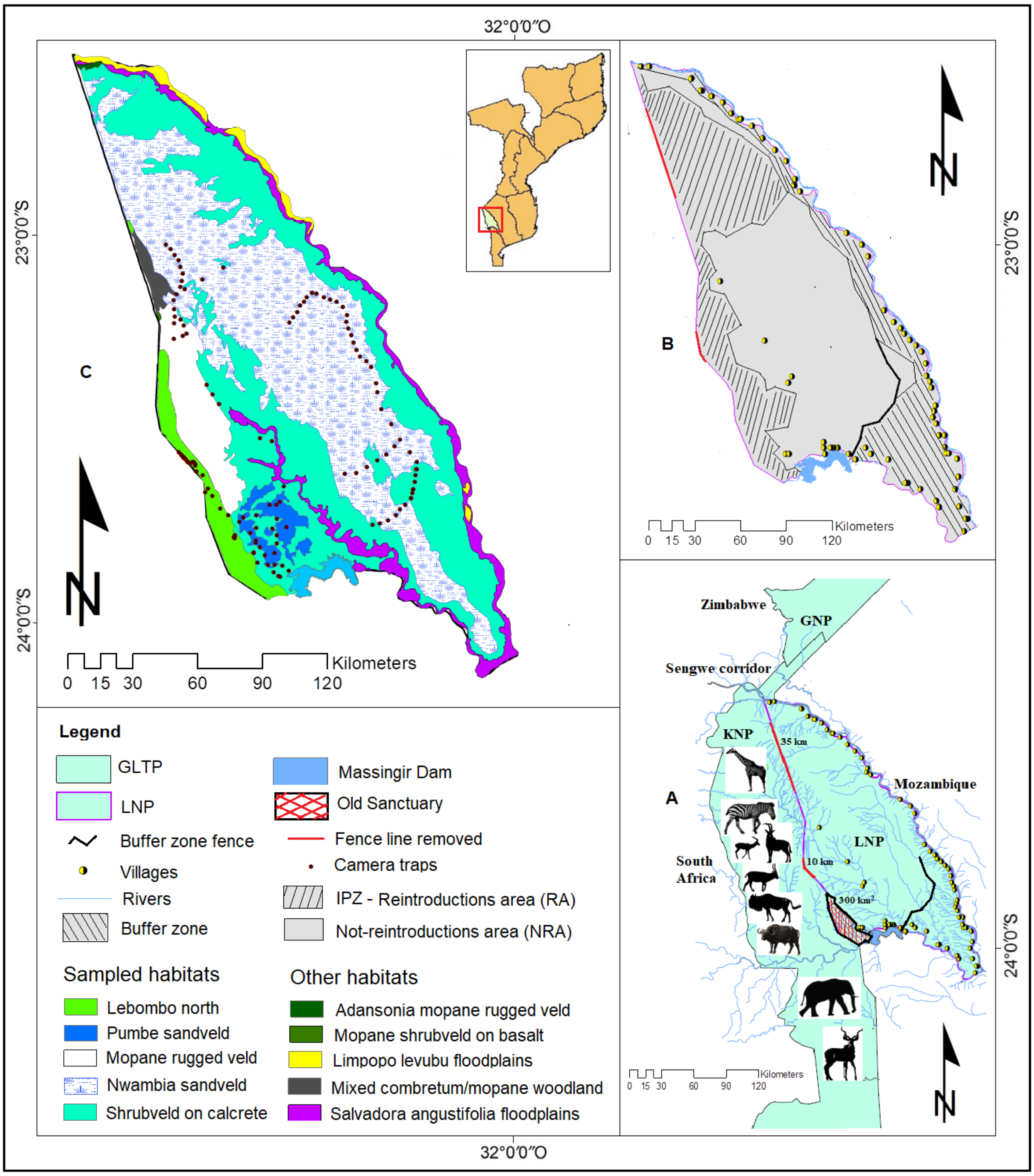

Figure 3.1. Overview of large herbivore reintroductions in the LNP and GLTP. (B) Reintroductions and not-reintroductions areas. (C) Sampling sites in five habitat types (Stalmans *et al.*, 2004). (GLTP – Great Limpopo Transfrontier Park, GNP – Gonarezhou National Park, IPZ – Intensive Protection Zone, KNP – Kruger National Park, LNP – Limpopo National Park).

3.2.4. Photo processing

We used the software "Camera Base – Adobe Bridge 2020 for Windows (Adobe systems)", an access database designed for managing camera trap surveys (Tobler *et al.*, 2009; Rovero *et al.*, 2010). We sorted all photographs by (1) species (Walker, 1997; Stuart and Stuart, 2001), (2) habitat type, (3) date and time, and we converted to camera-trap events, considered as the whole sequence of photos in which the same animal species appeared (Meek *et al.*, 2014). Independent event was defined as (i) consecutive photographs of individuals of different species; (ii) consecutive photographs of individuals of the same species taken more than 0.5 h apart; and (iii) nonconsecutive photos of individuals of the same species (O'Brien *et al.*, 2003; Tobler *et al.*, 2008). For species in herds, we chose the photograph with the highest number of individuals as the independent sample for that species (Bernard *et al.*, 2013). Detection was considered as one independent event of a species per camera and day (24h) (Garriga, 2012). Therefore, we counted photos with multiple individuals of the same species in the frame as single detection for that species (Palei *et al.*, 2016; Jędrzejewski *et al.*, 2017) to minimize bias in estimates of relative abundance (Evans and Rittenhouse, 2018).

3.2.5. Data analysis

Survey effort

The survey effort was the number of camera-trap days or nights, calculated by summing the days (24h period) each camera was operational (Bowkett *et al.*, 2008; Meek *et al.*, 2014; Oberosler *et al.*, 2017). The number of sampling units sampled in each habitat was: Lebombo North n = 40, Pumbe Sandveld n = 16, Shrubveld on Calcrete n = 30, Nwambia Sandveld n = 50; reintroductions area n = 76 and not-reintroductions area n = 70. The average length of camera deployment at each sampling unit was 69.5 days (SD = 31.2; min = 28; max = 122). To validate the sufficiency of the study period, we constructed an observed species accumulation curve (SAC) using the cumulative number of independent events with 95% confidence intervals using EstimateS 9.1.0 Software (Colwell and Elsensohn, 2014). SACs plot the cumulative number of species detected against the survey effort (number of camera trap days or number of individuals captured) and reach an asymptote when all species have been recorded (Willott, 2001; Ugland *et al.*, 2003; Meyer *et al.*, 2015). Additionally, we used the mean of the four commonly used nonparametric abundance-based richness estimators [ACE (Abundance coverage-based estimator), Chao1, Jackknife1 and Bootstrap] to assess the sampling completeness ratio (i.e., observed species number/estimated species number). In this case, we assumed sampling saturation when the ratio approached one (Edwards *et al*., 2009; Bernard *et al*., 2013).

Species diversity indices and relative capture frequency (RAI)

To understand how LH community composition changes among habitat types and from reintroductions to not-reintroductions areas, we estimated the following parameters: (1) species richness (S) as the total number of species captured in each habitat type, reintroductions area and the not-reintroductions area. The species richness in each habitat type, reintroductions and not-reintroductinos areas were compared in 100 trap nights; (2) diversity was estimated using the Shannon Diversity Index [$H' = \sum pi \ x \ \ln (pi)$], where pi represents the proportion of individuals from species i and ln represents Natural logarithm. To investigate differences in the Shannon diversity index among habitat types and between reintroductions areas and not-reintroductions areas, we performed a Diversity T-test. To compare abundance-activity indices, a measure of relative abundance index (RAI) (Jenks *et al*., 2011; Fiderer *et al*., 2019) among habitat types and between reintroductions and not-reintroductions areas were calculated for each camera trap. We calculated RAI at the species level and the level of total wildlife by using the number of detections divided by the total number of trap nights and converting this value as per 100 trap nights to facilitate comparisons. By using a Shapiro-Wilk Test and homogeneity of variance (Levene’s Test), we detected that RAI means and residuals were not normally distributed ($p < 0.05$). Thus, medians of RAI and inter-quartile range (IQR) were calculated for each species (Rottstock *et al*., 2020) in each habitat type in the reintroductions and not-reintroductions areas. Kruskal-Wallis with Dunn's post hoc test for multiple comparisons at a 95% probability level was used to compare RAI medians at the species and the total wildlife levels. We assumed that for most species, the number of events that the cameras recorded is proportional to the local density of the species, i.e., cameras will record a species more often where it is more abundant (O’Brien *et al*., 2003; Rovero and Marshall, 2009).

The composition of wildlife communities (browser-grazer-mixed feeder ratio and ungulate-potential predators’ ratio) was compared among habitat types and between reintroductions and not-reintroductions areas. These ratios show the percentage of independent events of a particular group of species concerning all independent events associated with wildlife (Liu *et al*., 2013; Rottstock *et al*., 2020). The relationship between ecological parameters (total RAI, grazer-browser-mixed feeder ratio and richness) was assessed by plotting the values of these parameters for each habitat type using Microsoft Excel 2010 (Starik *et al*., 2020). One-way ANOVA or Kruskal-Wallis test, depending on the types of data distribution, was used to compare the grazer-browser-mixed feeder ratio within and among habitat types and between reintroductions and not-reintroductions areas. The ungulate-potential predator ratio and ungulate-total wildlife ratio were used to assess the influence of predators on the distribution of ungulates. We consider those carnivore species as potential predators that have a body mass of ≥ 13 kg [lion (*Panthera leo*), leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*), spotted hyena (*Crocuta crocuta*), caracal (*Caracal caracal*), wild dog (*Lycaon pictus*) and black-backed jackal (*Canis mesomelas*)]. This was based on the assumption that the occurrence of those carnivore species can affect the occurrence, behaviour and distribution patterns of our target species (LH ≥ 10kg, including their offspring). Thus, we used a Kruskal-Wallis test to compare ungulates events (detection) concerning total wildlife events in the absence of potential predators and ungulates events when potential predators were present. We conducted the comparisons within habitat types and between reintroductions and not-reintroductions areas. We performed all analyses in Past 4.03 Software (Hammer *et al*., 2001).

Occurrence frequency/Naïve occupancy

The occurrence frequency of species in each habitat type, in reintroductions and not-reintroductions areas, was calculated as the proportion of sampling units a species was detected divided by the total number of camera-trap units placed in each habitat type and reintroductions and not-reintroductions areas (Rovero *et al*., 2014; Oberosler *et al*., 2017; Hedwig *et al*., 2018) and was considered as an index to compare LH distribution responses to habitat types and distance from sampling sites to reintroductions and not-reintroductions areas. Habitat use (LH distributional ranges) by each species was defined as the number of sampling units occupied by the species (Moore *et al*., 2019) in each habitat and reintroductions and not-reintroductions areas. Based on this, we calculated the naïve occupancy mean of each species in each habitat type, in reintroductions and not-reintroductions areas. We considered widely distributed species, those occupying all habitat types or reintroductions and not-reintroductions areas with naïve occupancy mean ≥ 0.4, and narrowly distributed species occurring in less than three habitat types or one or two areas (reintroductions and not-reintroductions areas) with naïve occupancy mean ≤ 0.39. To understand the effect of habitat type and distance from LH reintroductions area, we computed binomial confidence intervals for proportions at a 95% probability level only for those species with naïve occupancy ≥ 0.4. The confidence intervals that do not overlap indicate significant differences in the naïve occupancy.

3.3. Results

3.3.1. Trapping effort

Camera traps produced 21,553 successful photographs in 9,533 camera-trap days (Lebombo North = 1,999; Pumbe Sandveld = 1,062; Rugged Veld = 582; Shrubveld on Calcrete = 2,178; Nwambia Sandveld = 3,712/ reintroductions area = 4,164; not-reintroductions area = 5,369) (Table 3.S1). The observed species accumulation curve approached an asymptote at ~ 49 species. The sampling completeness ratio was 0.95 (ACE = 50.78; Chao1 = 49.6; Jack1 = 53.96; Bootstrap = 52.14; mean average = 51.62). The SAC suggests that a full inventory in the study area was almost done (Figure 3.2).

3.3.2. Species diversity index and relative capture frequency (RAI)

We collected a total of 5,138 animal-triggered events, of which 4,235 events (82.4%) represent our 15 target species (herbivores > 10kg), and 3,909 events (76%) represent 14 ungulates species. A total of 903 events (17.6% of all events) were associated with 34 no-target species, of which 237 events (4.6%) were caused by one out of seven potential predators’ species. We identified a total of 8,584 individuals belonging to 13 taxonomic orders and 25 families. The Order Artiodactyla was the most represented, with 17 species (Table 3.S2). While species richness (S) is highest in Lebombo North (LN) and a reintroductions area (RA) ($S_{LN} = S_{RA} = 15$) and similar among the other habitat types and in a not-reintroductions area (NRA) ($S_{PS=NS=NRA} = 12$ and $S_{SC=RV} = 11$), Shannon Diversity Index and evenness did not change (Table 3.S3). Total RAI was significantly higher in Lebombo North and Rugged Veld (RV) than in Pumbe Sandveld (PS), Shrubveld on Calcrete (SC), and Nwambia Sandveld (NS), and it was not significantly different between reintroductions and not-reintroductions areas (Figure 3.3, Table 3.2). There was an effect of habitat type in the mixed feeder ratio and browser ratio along the distance gradient of

LH reintroductions. However, the grazer-browser-mixed feeder ratio values oscillated among habitat types. (Figure 3.4, Table 3.S4). Only the grazer's ratio was significantly higher in reintroductions area than in not-reintroductions area, and the browser ratio was significantly higher in not-reintroductions area than reintroductions area (Table 3.S4). At the species-specific RAI level, there are some significant differences among habitat types (Kruskal–Wallis: 15.23, df = 4; *p* = 0.004) and between RA and NRA (Kruskal-Wallis: 4.4, df = 1; *p* = 0.03): while waterbuck, plains zebra, greater kudu, giraffe, impala and nyala showed a significantly higher RAI in Lebombo North; common duiker (*Sylvicapra grimmia*) and steenbok (*Raphicerus campestris*) showed a significantly higher RAI in Rugged Veld and Nwambia Sandveld and blue wildebeest in Pumbe Sandveld (Table 3.2, Figure 3.S1). Unlike common duiker and steenbok, warthog, waterbuck, plains zebra, giraffe, and impala showed a significantly higher RAI in the reintroductions area (Table 3.2, Table 3.S5). There were no significant differences in ungulates events (detection) in both the presence and absence of potential predators within habitat types (Kruskal-Wallis: 19.6, df = 4; *p* = 0.5) and between reintroductions area and not-reintroductions area (Kruskal-Wallis: 4.74, df = 1; *p* = 0.12) (Table 3.2).

Furthermore, the relationship between the ecological parameters [relative capture index (RAI), grazer-browser-mixed feeder ratio and species richness (S)] pointed towards different patterns of LH community responses to habitat type and increasing distance between sampling sites and the origin of LH reintroductions. The change of habitat type from Lebombo North to Pumbe Sandveld leads to a significant decrease in species richness and RAI. The changes from Pumbe Sandveld to Rugged Veld lead to an increase in RAI and browsers ratio and a decrease in grazers' ratio. The changes from Rugged Veld to Shrubveld on Calcrete led to significant decrease in RAI and browsers ratio. Finally, the changes from Shrubveld on Calcrete to Nwambia Sandveld led to a significant increase in the browsers ratio and a significant decrease in the mixed feeder ratio (Figure 3.4 and Table 3.2). Regarding the LH reintroductions origin, the increasing distance from reintroductions to not-reintroductions areas led to a significant decrease only in species richness, grazers' ratio, and a significant increase in browsers ratio (Tables 3.2 and 3.S4).

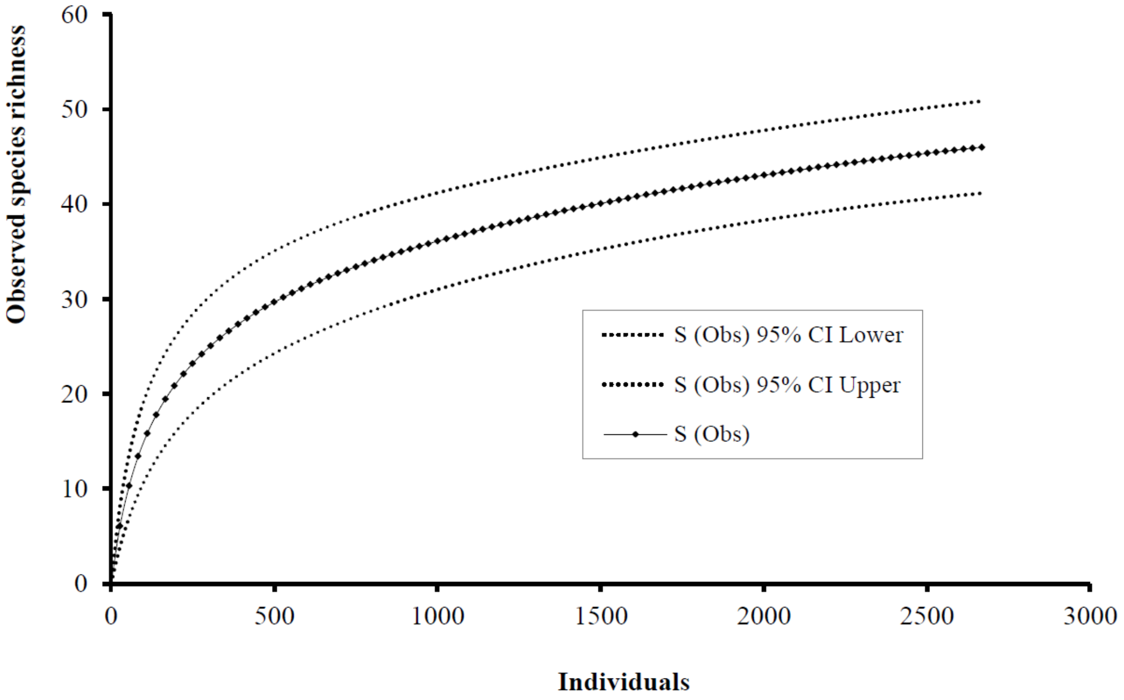

Figure 3.2. The observed species accumulation curves for all species captured in LNP. The curves were constructed using sample-based rarefaction approach with 1000 randomization runs in EstimateS 9.1.0 (Colwell and Elsensohn, 2014).

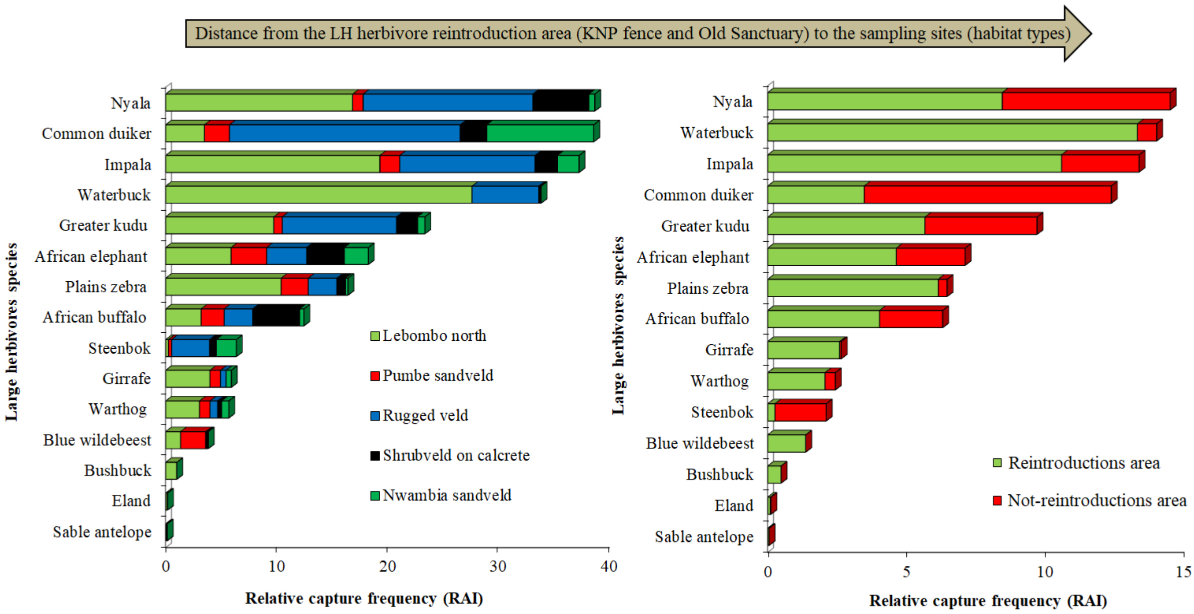

Figure 3.3. Species composition and capture frequency (RAI – detections/100 trap nights) among habitat types and between the reintroductions and not-reintroductions areas. KNP – Kruger National Park, LH – Large herbivores

Table 3.2. Comparison of relative abundance index (RAI) at the species level and total wildlife RAI, ungulates ratio with presence and absence of potential predators among habitat types and between reintroductions area and not-reintroductions area in the Limpopo National Park

Common name	**Habitat Type**							**Area type regarding wildlife reintroductions**			
	Median (IQR)							Median (IQR)			
	L. North *n* = 38	P. Sandveld *n* = 15	R. Veld *n* = 10	S. Calcrete *n* = 28	N. Sandveld *n* = 47	KW-Value	*p*-Value	RA *n* = 76	NRA area *n* = 70	KW-Value	*p*-Value
Warthog	0.0 (2.09)	0.0 (1.8)	0.0 (0.82)	0.0 (0.0)	0.0 (0.0)	1.99	0.43	0.0 (1.79)^{a}	0.0 (0.0)^{b}	4.6	< 0.01
Waterbuck	11.6 (38.2)^{a}	–	0.0 (2.01)^{b}	0.0 (0.0)^{b}	0.0 (0.0)^{b}	46.37	0.01	0.0 (12.9)^{a}	0.0(0.0)^{b}	15.03	< 0.01
Blue wildebeest	0.0 (0.0)	0.0 (1.7)^{a}	–	0.0 (0.0)^{b}	–	3.62	0.02	0.0 (0.0)	–	–	–
Plains zebra	5.1 (9.6)^{a}	1.8 (3.4)	0.0 (2.06)	0.0 (0.0)^{b}	0.0 (0.0)^{b}	37.55	< 0.01	2.2 (7.2)^{a}	0.0 (0.0)^{b}	30.2	< 0.01
African buffalo	0.0 (2.08)	0.0 (5.3)	0.0 (4.2)	1.5 (3.3)	0.0 (2.45)	2.62	0.5	0.0 (3.4)	0.0 (2.5)	1.24	0.2
Common duiker	0.0 (3.8)^{a}	0.0 (1.8)^{a}	16.7 (32.3)^{b}	0.0 (0.82)^{a}	5.6 (17.1)^{b}	32.44	< 0.01	0.0 (3.3)^{a}	4.1 (14.9)^{b}	12.9	< 0.01
Bushbuck	2.4 (0.0)	–	–	–	–	–	–	0.0 (0.0)	–	–	–
Greater kudu	6.2 (16.7)^{a}	0.0 (1.1)^{b}	6.25 (17.7)	0.0 (2.27)^{b}	2.08 (5.6)	16.01	0.01	0.84 (8.29)	1.14 (5.27)	0.008	0.9
Giraffe	0.0 (4.0)^{a}	0.0 (1.7)	0.0 (2.1)	–	0.0 (0.0)^{b}	8.21	< 0.01	0.0 (3.28)^{a}	0.0 (0.0)^{b}	12.05	< 0.01
Steenbok	0.0 (0.0)a	0.0 (0.0)	2.08 (6.1)^{b}	0.0 (0.0)	0.0 (2.45)^{b}	13.51	< 0.01	0.0 (0.0)^{a}	0.0 (2.5)^{b}	14.4	< 0.01
Impala	10.9 (27.3)^{a}	0.0 (1.1)^{b}	2.08 (14.5)	0.0 (1.5)^{b}	0.0 (2.5)^{b}	39.51	< 0.01	2.5 (18.6)^{a}	0.0 (2.6)^{b}	9.9	< 0.01
Nyala	4.8 (28.8)^{a}	0.0 (1.1)^{b}	6.3 (33.3)	1.7 (3.3)	1.1 (2.5)	11.2	0.01	0.0 (7.1)	1.7 (6.1)	1.4	0.22
Sable antelope	0.0 (0.0)	0.0 (0.0)	–	–	–	0.43	0.51	0.0 (0.0)	–	–	–
Eland	0.0 (0.0)	–	–	–	0.0 (0.0)	0.06	0.43	0.0 (0.0)	0.0 (0.0)	0.07	0.37
African elephant	0.0 (3.7)	1.09 (1.79)	2.08 (10.4)	1.81 (8.1)	0.0 (3.3)	5.34	0.17	0.0 (3.5)	0.0 (4.1)	0.07	0.76
TW RAI	66.6 (116)^{a}	8.79 (26.4)^{b}	58.3 (97.2)^{a}	18.5 (26.6)^{b}	27.4 (27.5)^{b}	36.58	< 0.01	3.5 (5.7)	0.7 (2.8)	3.4	0.06
U/TW ratio (%)	94.5/5.5	82.2/17.8	95.4/4.6	84/16	92/8	19.6	0.5	92.6/7.4	91.5/8.5	4.74	0.12
U/PP ratio (%)	95/5	98.7/1.3	97.3/2.7	90/10	92.5/7.5			95.6/4.4	92/8		
U/TC ratio (%)	92.4/7.6	97/3	94/6	88/12	88.3/11.7	–	–	93.2/6.8	88/12	–	–

IQR – Interquartile ranges, KW – Kruskal–Wallis, LH – Large herbivores, *n* – Sampling units, NRA – Not-reintroductions area, PP – Potential predators, RA – Reintroductions area, TC – Total carnivorous, TW – Total wildlife, U – Ungulates. Different letters (a, b) show significant differences ($p < 0.05$) in the comparisons of the specie-specific RAI medians and in the total wildlife RAI medians among habitat type and between the reintroductions and not-reintroductions areas.

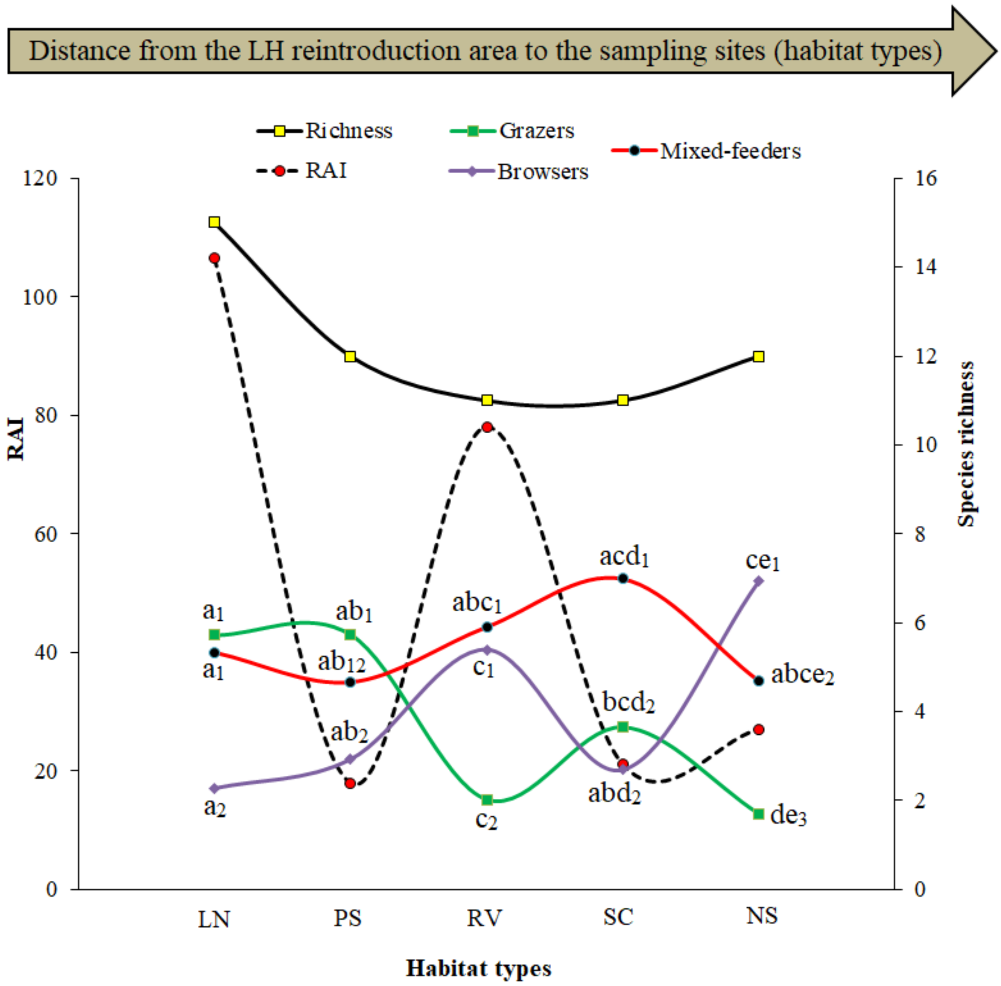

Figure 3.4. Relationship between ecological parameters (Total RAI, grazer-browser-mixed feeder-ratio). Different letters (a,b,c,d,e) and numbers (1,2,3) show significant differences ($p < 0.05$) in the comparisons of grazers-browsers-mixed feeders ratio among and within habitat types, respectively. LN – Lebombo North, PS – Pumbe Sandveld, RV – Rugged Veld, SC – Shrubveld on Calcrete, and NS – Nwambia Sandveld.

3.3.3. Occurrence frequency/Naïve occupancy

While African elephant, African buffalo, plains zebra, greater kudu, nyala, impala and common duiker showed a wide distribution range, blue wildebeest, eland, sable antelope, and bushbuck showed a narrow distribution range among habitat types and the reintroductions to not-reintroductions areas (Figure 3.S2). As the habitat type changes, the results pointed towards different patterns of LH responses: the occupancy range of impala and plains zebra was significantly wider in Lebombo North, the occupancy range of common duiker was significantly wider in Rugged Veld and Nwambia Sandveld, and the occupancy range of greater kudu was significantly wider in Nwambia sandveld (Figure

3.5A). However, as the distance between sampling sites and the origin of LH reintroductions increases, only the occupancy range of plains zebra was significantly wider in the reintroductions area, while common duiker showed the opposite behaviour (Figure 3.5B).

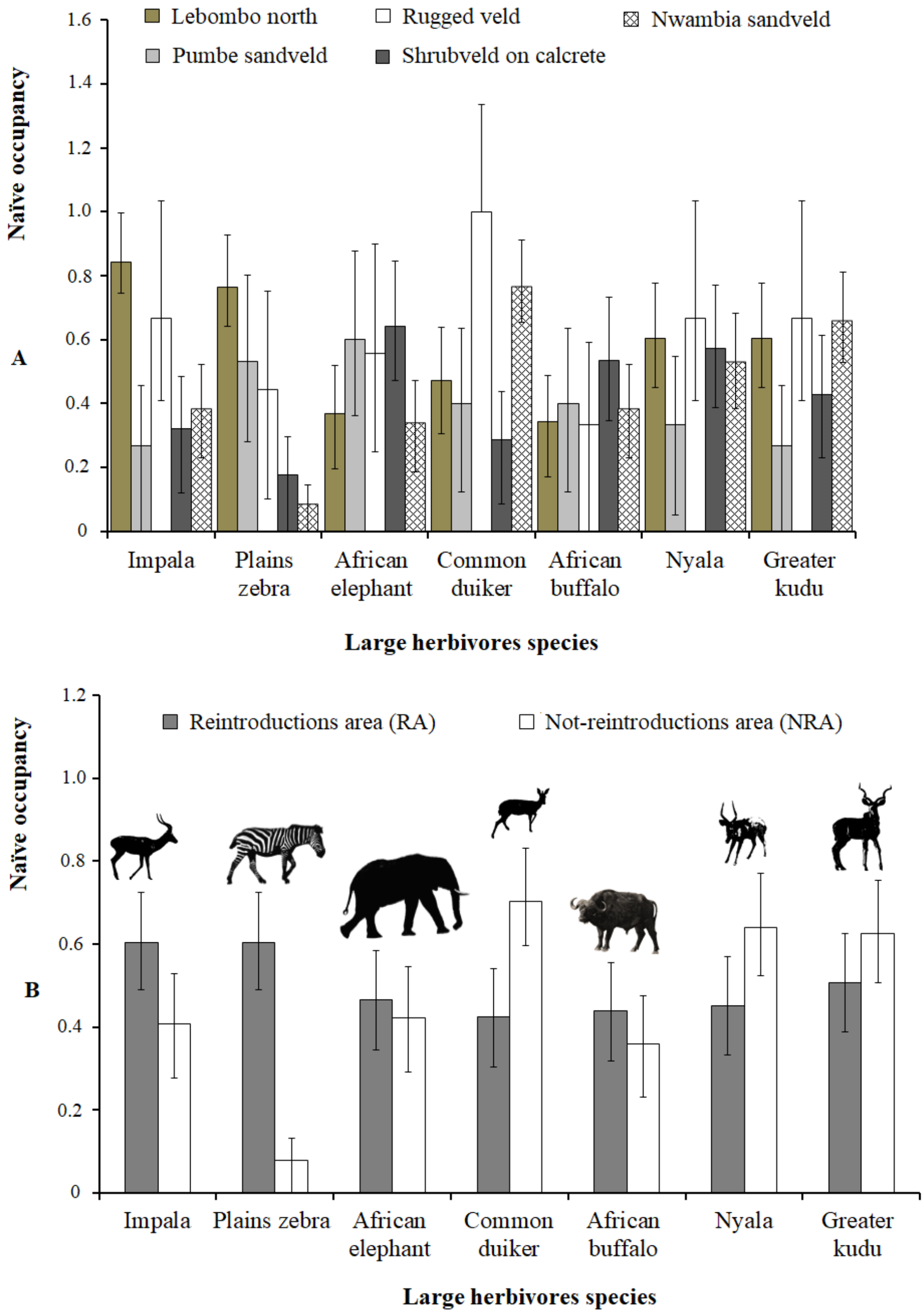

Figure 3.5. Species-specific naive occupancy (mean > 0.4) comparison among habitat types (A), between reintroductions and not-reintroductions areas (B). Vertical bars indicate binomial confidence intervals (α = 0.05) for proportions. The vertical bars that do not overlap indicate species significant differences in the naïve occupancy.

3.4. Discussion

This study is the first systematic assessment of large herbivore (LH) communities in Limpopo National Park (LNP), an area where most LH species were extinct until the early 2000s. We investigate whether the parameters of the LH community in LNP are linked with the availability of habitat types or the distance between the sampling site and the "origin of LH resettlement". Previously, 26 species had been reported in the LNP (Stephenson, 2010, 2013; Grossman *et al.*, 2014). In this study, 23 more species were recorded, accounting for 49 species in total. However, three actively reintroduced species (Lichtenstein's hartebeest, white rhinoceros, and roan antelope) could not be recorded, neither with camera traps nor via opportunistic observations.

We found that species richness, relative abundance index and grazer-browser ratio changed concerning habitat types. From reintroductions to not-reintroductions areas, only species richness and grazers-browsers ratio changed. The highest number of species recorded in Lebombo North and the reintroductions area corresponds with the fact that these areas are close to the Kruger National Park (KNP) border and benefit directly from LH entering from sections of dropped fence. Apart from these officially broken sections, there are many other "scape sites" into LNP along the fence due to lack of maintenance. Furthermore, the entire length of the transects in Lebombo North and reintroductions area are within the Intensive Protection Zone (IPZ) with many anti-poaching control posts (Grossman *et al*., 2014), providing LH security from poaching in this habitat.

Although Lebombo North and part of the reintroductions area are hilly, they are crossed by seasonal rivers (Machampane, Sambalala, and Guazi) (DINAC, 2003) and are made up of rocky soils (Jones *et al*., 1990), which promote water retention in the rainy season, creating diverse pools that extend into the late dry season. This can attract water-dependent grazers and mixed-feeders from the neighboring KNP and other habitats around Lebombo North. Similar to our findings, Whyte and Swanepoel (2006) found that the richness and distribution patterns of LH species were highest in Lebombo North and along the KNP border, and they recorded about 252 natural waterholes despite a rather poor rainfall season. These patterns (water-rich and safe area) not only explain the high species richness in Lebombo North and reintroductions area but also may explain the highest RAI and grazer ratio found in these two sites. However, the grazers' ratio decreased significantly from Pumbe Sandveld to Nwambia Sandveld, probably due to the lack of water and the prevalence of human settlements in Nwambia Sandveld. As the distance increases from Lebombo North towards Nwambia Sandveld, the area between the Shingwedzi Valley and the Limpopo River becomes waterless except for the small pans, which retain water only during the wet season (DINAC, 2003).

The Lebombo North and reintroductions area are part of the Intensive Protection Zone and therefore are ecologically preserved (Hofmeyr, 2004) because there are fewer human settlements and other disturbances when compared to Rugged Veld, Shrubveld on Calcrete and Nwambia Sandveld (Stephenson, 2013; Bazin *et al.*, 2016). Because agriculture, livestock grazing and resource extraction by humans are not allowed within the IPZ, and poaching is more controlled than in other parts of the LNP (Grossman *et al.*, 2014), the IPZ represents a relatively undisturbed savanna ecosystem in LNP. This can probably lead to an increase in species richness and RAI due to the lack of anthropogenic barriers that prevent the LH dispersal and colonization of new areas. This finding is supported by observations in Uganda, Tanzania, Indonesia, Brazil, and Costa Rica (Ahumada *et al.*, 2011) and Singapore (Turner, 1996), where different researchers documented higher species richness in intact than in fragmented habitats. However, the significant reduction in total RAI from Rugged Veld to Nwambia Sandveld can be explained by the opposite patterns to those presented above: from Rugged Veld to Shrubveld on Calcrete and Nwambia Sandveld (West-East gradient), the intensity of land use and forest resources exploitation increases due to the human settlements and livestock (grazing areas) (Grossman *et al.*, 2014). This leads to increased habitat degradation, which can lead to reduced total wildlife RAI. Likewise, studies conducted in Gabon (Hedwig *et al.*, 2018), Namibia and Tanzania (Rottstock *et al.*, 2020) confirm a decline in total wildlife RAI of small, medium and large herbivores mammal communities resulting from increasing grazing pressure and poaching.

There was a significant increase in RAI in Rugged Veld owing to individual RAI contributions of two mixed feeders (impala and nyala) and two browsers (common duiker and great kudu) (Table 3.S5). This increase in RAI can be explained by the fact that Rugged Veld is a heterogeneous mixture of tall woodland, tall shrub land and short woodland forest (Stalmans *et al.*, 2004), which are preferred habitat types of browsers, providing their main food resources (Owen-Smith and Cooper, 1989). Rugged Veld also has a rich grass component, including palatable and nutritious species such as *Panicum* *maximum* and *Urochloa mossambicensis* (Stalmans *et al*., 2004), which are crucial food resources for grazers and mixed feeders (Stuart and Stuart, 2001). The highest values of common duiker and kudu events (Table 3.S5) also lead to a significant increase in the browsers ratio in Nwambia Sandveld (Figure 4.2) and not-reintroductios area (Table 3.S5). Nwambia Sandveld and not-reintroductions area are low thicket forest areas with the shrubby condition of *Colophospermum mopane* (Stalmans *et al*., 2004), providing food resources for browsers (McNaughton and Georgiadis, 1986).

Our results give reason to assume that the different species of potential predators in LNP did not yet reach population sizes that might have a significant impact or cause a measurable effect on the distribution pattern of ungulates in the five habitat types, the reintroductions and not-reintroductions areas. There is scientific evidence of the presence of a viable population of cheetahs (*Acinonyx jubatus*) in LNP and the corridors of neighboring Banhine National Park (Andresen *et al*., 2012). However, given the size of the respective area, it is not surprising that these cheetahs do not origin a measurable effect on the LH communities in LNP. The spatial avoidance in agro-pastoralist human settlements areas and harassment of domestic dogs during illegal poaching by predators can also be the other reason for our findings. Similarly, different researchers (Andresen *et al*., 2014; Andresen, 2015) documented a low occurrence of predators (cheetahs) in the core area of the LNP (Shingwedzi Valley) that contains villages and near agro-pastoralist communities along the not-reintroductions area. Furthermore, the authors found high levels of livestock and bush meat poaching without predators and their signals in an abandoned village related to the undergoing voluntary resettlement of communities from the core area. Regarding species-specific distribution (naïve occupancy) of the 15 large herbivores target species, seven (African elephant, African buffalo, plains zebra, greater kudu, nyala, impala and common duiker) were widely distributed among habitat types and from reintroductions to not-reintroductions areas, and four (blue wildebeest, sable antelope, eland and bushbuck), were narrowly distributed. In the seven widely distributed species, there was strong support for the effects of habitat type on naïve occupancy because the occupancy range of five of them was significantly wider. However, there was little support for the effects of increasing distance from reintroductions to not-reintroductions areas on naïve occupancy because the occupancy range of only two of those seven species was significantly wider (Figure 3.5A-B). This showed that a natural colonization process of different LH species has already started in the LNP. This natural colonization process appears to be more linked with the availability of habitat features than the distance between the sampling sites and the origin of LH species reintroductions. Our results are corroborated by park census data (2006-2014) (Whyte and Swanepoel, 2006; Stephenson, 2010, 2013; Grossman *et al.*, 2014). We found that blue wildebeest, sable antelope and bushbuck had not expanded their range too far to the East from Lebombo North, possibly due to organismic limitations caused by these species' ecological adaptations and their inability to invade habitats disturbed by human settlements in the Shingwedzi Valley. This is consistent with findings by Limpopo Aerial Censuses that recorded the above-mentioned species to occur only in the "Old Sanctuary" and surroundings (Whyte and Swanepoel, 2006; Grossman *et al.*, 2014). Although no sable was actively introduced to the LNP from KNP, their numbers could probably be experiencing declines because it is currently the case in the KNP. Furthermore, sable antelopes are low-density herbivores (Owen-Smith and Mills, 2008) with a restricted distribution throughout the landscape.

3.5. Conclusions

Our results, particularly the association of most LH community parameters with habitat types rather than distance to initial release/recolonization, together with the species-specific and guild-specific response patterns of large herbivores, suggest Limpopo National Park is already in an early-intermediate stage of restoration. Areas with human settlements were avoided by reintroduced animals. The park will likely reach an advanced restoration stage when the ongoing process of resettlement of communities from some habitat types (Shrubveld on calcrete and *Salvadora angustifolia* floodplains) in the Shingwedzi Valley ends. Our results highlight the importance of post-release monitoring of reintroduced wildlife as a tool to assess the success of ecological restoration initiatives in transboundary conservation areas. Moreover, our study shows that LNP has an intrinsic conservation value to contribute to the development of the Great Limpopo Transfrontier Park. Besides the regional significance, our results represent arguments for the conservation of various large herbivore species, their habitats and the potential to create the basis for management and policy-making for further development of the Great Limpopo Transfrontier Park. Our study also provides a better understanding and contributing to the current knowledge of LH species conservation in an unfenced/fenced (LNP/KNP) landscape mixture that also is impacted by agro-pastoralist and human settlements. Because many protected areas in Sub-Saharan Africa are also human-dominated landscapes, our results can therefore be applied across these areas for conservation planning and management.

Acknowledgments

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3.6. Supplementary material

Table 3.S1. Camera trap survey effort and detailed information about camera trap performance in five habitat types, reintroductions and not-reintroductions areas in the Limpopo National Park

Measure	**Habitat type**						**Reintroductions of LH**		
	LN	PS	RV	SC	NS	Total	RA	NRA	Total
Sampling units (*n*)	40	16	10	30	50	146	76	70	146
Survey effort (trap days/nights)	1999	1062	582	2178	3712	9533	4164	5369	9533
Independent events (IE)	2528	205	511	569	1325	5138	2881	2257	5138
Successful images	12819	663	1832	2156	4083	21553	14069	7484	21553
Successful cameras	38	13	9	28	45	133	70	63	133
Mean trapping days/camera	52.6	70.8	64.6	77.8	78.9	69.5	57.04	83.9	69.5
Stolen cameras	1	0	1	1	2	5	1	4	5
Non-functional cameras	1	1	0	1	1	4	2	2	4
Blank cameras	0	2	0	0	2	4	3	1	4
Overall species/target species	35/15	19/12	22/11	24/11	42/12	49/15	37/15	43/12	49/15

Total does not mean the sum of numbers from different habitats and reintroductions and not-reintroductions areas: 69.5 – is the overall average for 146 sampling units, and 49/15 – is the total species (overall/target) photographed in the Limpopo National Park. LN – Lebombo North, PS – Pumbe Sandveld, RV – Rugged Veld, SC – Shrubveld on Calcrete; NS – Nwambia Sandveld, LH – Large herbivores, RA – Reintroductions area, NRA – Not-reintroductions area

Table 3.S2. Checklist of overall species recorded by camera traps grouped by taxonomic order and family in the Limpopo National Park

Taxonomic order	Family	Species	Common name	Habitat type														
				Lebombo North			**Nwambia Sandveld**			**Shruveld Calcrete**			**Pumbe Sandveld**			**Rugged Veld**		
				IE	**I**	**P**	**IE**	**I**	**P**	**IE**	**I**	**P**	**IE**	**I**	**P**	**IE**	**I**	**P**
Artiodactyla	Bovidae	*Aepyceros melampus*	Impala	386	1277	1933	71	136	255	44	167	194	19	33	45	71	123	306
		Connochaetes taurinus	Blue weldebeest	27	63	281				5	11	12	24	25	54			
		Hippotragus niger	Sable antelope										1	1	1			
		Kobus ellipsiprymnus	Waterbuck	552	955	3207	1	1	2	4	9	8				35	36	106
		Neotragus moschatus	Suni	1	2	3	2	2	6									
		Oreotragus oreotragus	Klipspringer	19	27	85												
		Raphicerus campestris	Steenbok	5	9	18	67	73	159	12	12	26	3	3	4	20	20	73
		Raphicerus sharpei	Sharpe's Grysbok	23	23	84	2	3	4									
		Sylvicapra grimmia	Common duiker	70	76	229	358	381	917	55	56	129	24	24	33	121	126	312
		Syncerus caffer	Buffalo	65	136	364	96	176	517	92	404	663	22	52	229	15	15	37
		Taurotragus oryx	Eland	3	3	15	1	2	3									
		Tragelaphus angasii	Nyala	337	478	1444	133	171	331	110	143	422	10	13	19	89	116	324
		Tragelapus scriptus	Bushbuck	20	25	68												
		Tragelaphus strepsiceros	Greater kudu	195	320	1266	147	197	484	41	43	98	8	8	15	60	75	302
	Giraffidae	*Giraffa camaleopardalis*	Giraffe	80	111	471	17	19	54				10	13	20	3	3	9
	Hippopotamidae	*Hippopotamusamphibius*	Hippoptamus	2	3	4												
	Suidae	*Phacochoerus africanus*	Warthog	61	108	242	24	43	150	8	10	11	10	10	11	4	7	15
		Potamochoerus porcus	Bushpig				12	15	67	1	1	2						
Bucerotiformes	Bucerotidae	*Tockus flavirostris*	Hornbills				5	5	12									
Carnivora	Canidae	*Canis adustus*	Side-striped jackal	4	4	9	1	1	2				1	1	1			
		Canis mesomelas	Black-backed jackal	2	2	3	57	59	129	7	7	12				8	8	19
		Lycaon pictus	Wild dog	5	7	32	1	1	3	2	3	3						
	Felidae	*Acinonyx jubatus*	Cheetah				11	11	30									
		Felis sylvestris lybica	African Wild Cat	3	3	5	12	12	23									
		Caracal caracal	Caracal				1	1	2	2	2	3						
		Panthera pardus	Leopard	13	13	35	1	1	3	1	1	1				1	1	2
		Panthera leo	Lion	1	1	2												
		Leptailurus serval	Serval				6	6	12	2	2	4				2	2	4
	Herpestidae	*Herpestes ichneumon*	Large g. mangoose				2	2	4									
		Mungos mungo	Banded Mongoose				3	3	6									
	Hyaenidae	*Crocuta crocuta*	Spotted Hyaena	5	5	10	3	3	4	31	35	64	2	2	3	3	3	6
	Mustelidae	*Mellivora capensis*	Honey badger	6	6	17	8	8	19	2	2	2				3	3	8
	Protelidae	*Proteles cristatus*	Aardwolf	2	2	6	7	7	14									

	Viverridae	*Civettictis civetta*	Civet	40	41	99	9	9	21	1	1	1	2	2	4	10	10	30
		Genetta genetta	Small-spotted genet	11	11	33	9	9	21	6	6	18				4	4	12
Crocodylia	Crocodylidae	*Crocodylus niloticus*	Crocodylus	1	1	2												
Galliformes	Numididae	*Numida meleagris*	H. Guineafowl				24	88	66									
	Phasianidae	*Perdix perdix*	Grey partridge				22	35	46									
Lagomorpha	Leporidae	*Lepus saxatilis*	Scrub hare	12	12	34	21	21	37	39	40	114				17	17	81
Primate	Cercopithecidae	*Chlorocebus aethiops*	Vervet monkey	32	61	163	4	8	10	1	1	2	1	1	1			
		Papio ursinus	Chacma baboon	123	339	779	21	82	209	14	18	27	1	6	2	5	15	31
Perissodactyla	Equidae	*Equus quagga*	Plain zebra	208	345	1011	8	12	33	17	35	113	26	43	112	15	23	65
Proboscidea	Elephantidae	*Loxodonta africana*	African elephant	117	157	619	80	115	239	72	101	227	34	51	68	21	24	80
Rodentia	Hystricidae	*Hystrix africaeaustralis*	Cape porcupine	16	19	49	17	26	39				2	3	4	2	2	4
	Pedetidae	*Pedetes capensis*	Springhare				12	15	42									
	Muridae	*Saccostomus campestris*	Pouched Mouse				5	5	12									
Struthioniformes	Struthionidae	*Struthio camelus*	Ostrich				2	2	3									
Testudines	Testudinidae	*Kinixys belliana belliana*	Bell's hinge-back tortoise				1	1	2									
Tubulidentata	Orycteropodida.	*Orycteropus afer*	Aardvark				41	41	91				5	5	7	2	2	6
TOTAL 13	25	49		**2528**	**4734**	**12819**	**1325**	**1808**	**4083**	**569**	**1110**	**2156**	**205**	**297**	**633**	**511**	**635**	**1832**

IE – Independent events, I – Number of individuals recorded, P – Number of photographs

Table 3.S3. Comparison of Shannon – diversity index using diversity t test among habitat types; between reintroductions and not-reintroductions area in Limpopo National Park. LN – Lebombo North; PS – Pumbe Sandveld; RV – Rugged Veld; SC – Shrubveld on Calcrete; NS – Nwambia Sandveld

<table>
<tr><th colspan="12">Habitat type</th><th colspan="2">Reintroductions of large herbivores</th></tr>
<tr><td colspan="14">Richness (S)/100 trap nights</td></tr>
<tr><td>LN</td><td colspan="2">PS</td><td colspan="3">RV</td><td colspan="3">SC</td><td colspan="3">NS</td><td>Reintroductions area</td><td>Not-reintroductions area</td></tr>
<tr><td>15</td><td colspan="2">12</td><td colspan="3">11</td><td colspan="3">11</td><td colspan="3">12</td><td>15</td><td>12</td></tr>
<tr><td colspan="14">Shannon’s equitability ($E_{H'}$)</td></tr>
<tr><td>0.74</td><td colspan="2">0.88</td><td colspan="3">0.83</td><td colspan="3">0.75</td><td colspan="3">0.81</td><td>0.78</td><td>0.81</td></tr>
<tr><td colspan="14">Shannon – Wiener diversity index (H')</td></tr>
<tr><td rowspan="2">LN
PS</td><td rowspan="2">1.99
2.18</td><td rowspan="2">t = 1.185
df = 36.9
p = 0.24</td><td rowspan="2">LN
RV</td><td rowspan="2">1.99
1.99</td><td rowspan="2">t = 0.004
df = 232.2
p = 0.99</td><td rowspan="2">LN
SC</td><td rowspan="2">1.99
1.78</td><td rowspan="2">t = 1.24
df = 65.04
p = 0.21</td><td rowspan="2">LN
NS</td><td rowspan="2">1.99
2</td><td rowspan="2">t = 0.12
df = 55.1
p = 0.9</td><td>2.12</td><td>2.02</td></tr>
<tr><td colspan="2" rowspan="2">t = 0.68
df = 73.5
p = 0.49</td></tr>
<tr><td>PS
RV</td><td>2.18
1.99</td><td>t = 1.14
df = 40.9
p = 0.25</td><td>PS
SC</td><td>2.18
1.78</td><td>t = 1.87
df = 65.5
p = 0.06</td><td>PS
NS</td><td>2.18
2</td><td>t = 0.88
df = 57.1
p = 0.38</td><td>RV
SC</td><td>1.99
1.78</td><td>t = 1.21
df = 71.5
p = 0.23</td></tr>
</table>

RV NS	1.99 2.0	t = 0.11 df = 61.6 *p* = 0.9	SC NS	1.78 2	t = 1.1 df = 81.2 *p* = 0.27

Table 3.S4. Pairwise comparison of grazer-browser-mixed feeder ratio within and among habitat types and between reintroductions and not-reintroductions area. Significant differences between group means/medians (p < 0.05) were obtained using One-Way ANOVA or Kruskal-Wallis test

	LN_GZ	LN_BW	LN_MF	PS_GZ	PS_BW	PS_MF	RV_GZ	RV_BW	RV_MF	SC_GZ	SC_BW	SC_MF	NS_GZ	NS_BW	NS_MF
LN_GZ		**F(1.74)= 29.83; p=0.0006**		F(1,.51) = 0.02; p = 0.9			**F(1.45)= 23.51; p=0.0001**			**KW = 7.38; p=0.006**			**F(1.83)= 48.87; p=0.006**		
LN_BW			**KW = 22.74; p=0.001**		KW = 0.02; p=0.9			**F(1,45)= 17.9; p=0.001**			KW = 3.37; p=0.06			**KW = 23.08; p=0.0001**	
LN_MF	F(1,74)= 29.83; p=0.9					F(1,51)= 3.44; p=0.06			F(1,45)= 0.78; p=0.38			KW = 3.47; p=0.06			KW = 3.51; p=0.06
PS_GZ					**F(1,28)= 4.55; p=0.04**	F(1,28)= 1.03; p=0.31	**F(1,22)= 8.03; p=0.009**			KW = 2.0; p=0.14			**KW = 8.13; p=0.002**		
PS_BW						F(1,28)= 1.4; p=0.24		**KW = 5.98; p=0.01**			KW = 1.03; p=0.28			**KW = 12.43; p=0.0004**	
PS_MF									F(1,22)= 3.57; p=0.07			**KW = 5.98; p=0.01**			KW = 0.42; p=0.51
RV_GZ								**KW = 10.67; p=0.001**	**F(1,16)= 26.3; p=0.0001**	KW = 1.17; p=0.26			KW = 0.05; p=0.8		
RV_BW									F(1,16)= 0.1; p=0.75		**KW = 9.16; p=0.001**			KW = 0.73; p=0.38	
RV_MF												KW = 0.61; p=0.43			KW = 3.23; p=0.07
SC_GZ											KW = 1.03; p=0.28	**KW = 12.1; p=0.0004**	KW = 2.99; p=0.07		
SC_BW												**KW = 21.2; p=0.0002**		**KW = 21.3; p=0.0001**	

SC_MF															**KW = 9.17; p=0.002**
NS_GZ														**KW = 33.7; p=0.0003**	**KW = 24.2; p=0.0005**
NS_BW															**KW = 7.68; p=0.006**

Comparison between LH reintroductions area and not-reintroductions area

RA_GZ vs RA_BW	RA_GZ vs RA_MF	RA_BW vs RA_MF	RA_GZ vs NRA_GZ	RA_MFvs NRA_MF	NRA_GZ vs NRA_MF	NRA_BW vs NRA_MF	RA_BW vs NRA_BW
KW = 19.6; p=0.0008	KW = 0.49; p=0.48	**KW = 14.7; p=0.0001**	**KW = 42.5; p=0.0003**	KW = 3.74; p=0.053	**KW = 56.8; p=0.002**	KW = 0.71; p=0.39	**KW = 17.1; p=0.0003**

NRA_GZvs NRA_BW
KW = 35.7; p=0.0009

LN – Lebombo North, PS – Pumbe Sandveld, RV – Rugged Veld, SC – Shrubveld on Calcrete, NS – Nwambia Sandveld, GZ – grazers, BW – browsers, MF – mixed feeders, RA – reintroductions area, NRA – not-reintroductions area, KW – Kruskal-Wallis value

Figure 3S1. Species colonization in different habitat types and between reintroductions area (RA) and not-reintroductions area (NRA) from “Old Sanctuary. Pies show capture frequency (RAI) – detections/100 trap nights, the size of the pie charts relates to differences in the species RAI among habitat types and between reintroducntions and not-reintroductios areas

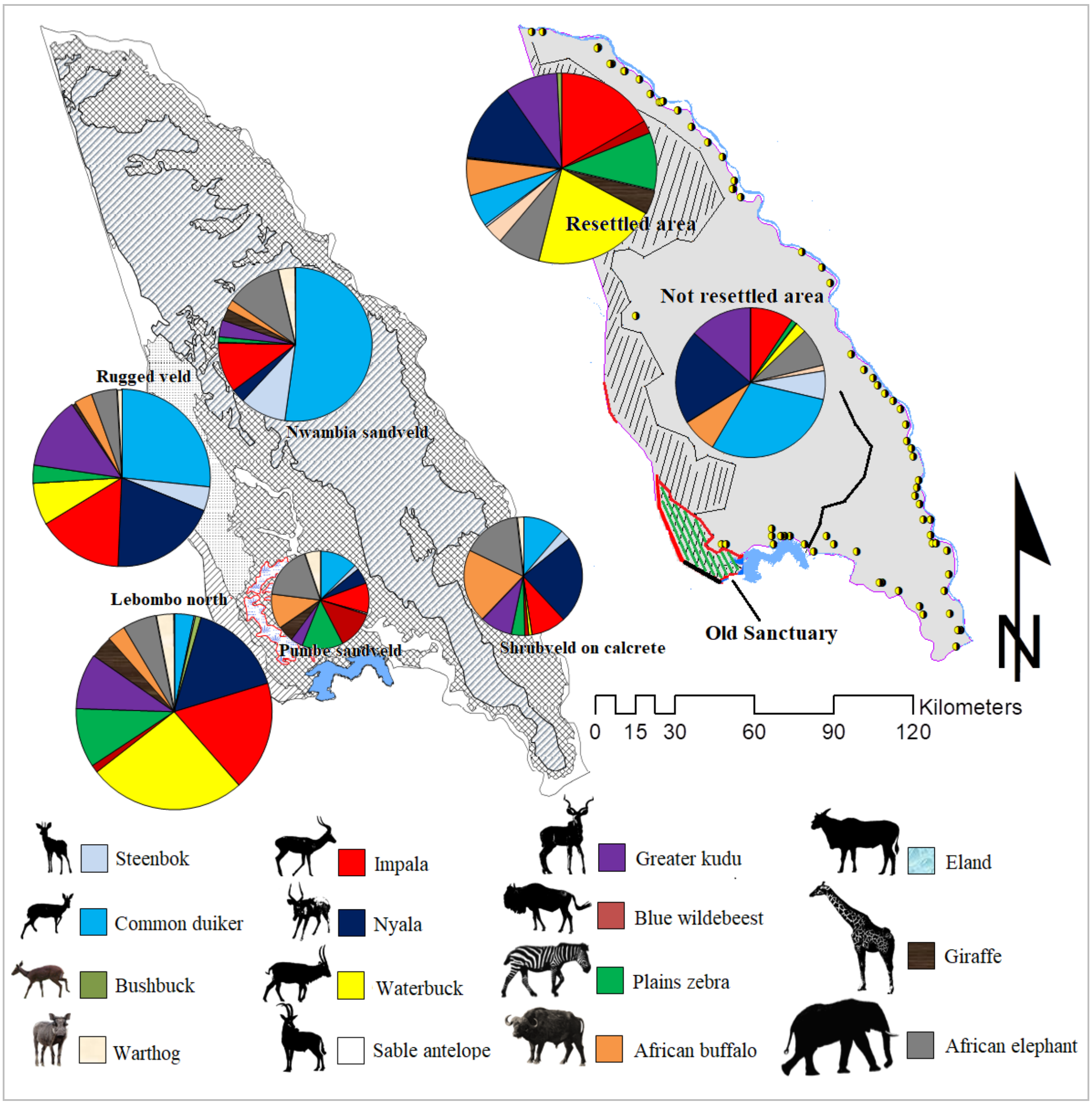

Figure 3.S2. Species-specific naive occupancy of reintroduced large herbivores among habitat types in the Limpopo National Park. LN – Lebombo North, PS – Pumbe Sandveld, RV – Rugged Veld, SC – Shrubveld on Calcrete, NS – Nwambia Sandveld, KNP – Kruger National Park, LH – large herbivores

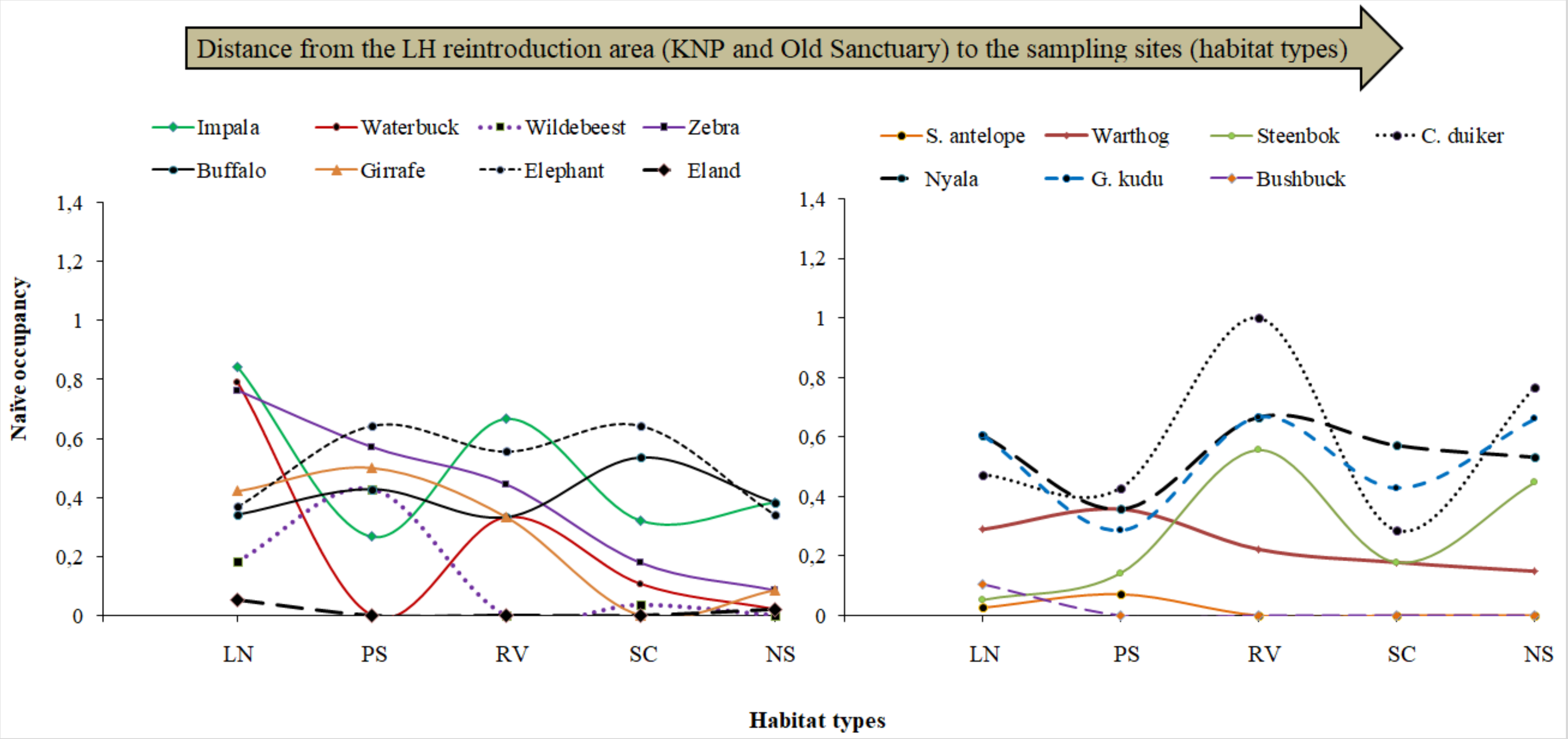

Table 3.S5. Large herbivores species recorded by habitat type and reintroductions/not-reintroductions areas in Limpopo National Park; RAI – relative abundance based on detected individuals per species per 100 trap nights IE – independents events; n – nr of sample units (camera traps), RA-NRA – reintroductions/not-reintroductions areas

Species	**Habitat type**										**Reintroductions of large herbivores**			
	Lebombo North *n* = 38		Pumbe Sandveld *n* =15		Rugged Veld *n* = 10		Shrubveld on Calcrete *n* = 28		Nwambia Sandveld *n* = 47		RA *n* = 76		NRA *n* = 70	
	IE	RAI	IE	RAI	IE	RAI	IE	RAI	IE	RAI	IE	RAI	IE	RAI
Warthog	61	3.05	10	0.94	4	0.69	8	0.37	24	0.65	86	2.07	20	0.37
Waterbuck	552	27.6	–	–	35	6.01	4	0.18	1	0.03	555	13.3	37	0.69
Blue wildebeest	27	1.35	24	2.26	–	–	5	0.23	–	–	57	1.37	–	–
Plains zebra	208	10.4	26	2.45	15	2.58	17	0.78	8	0.22	256	6.15	17	0.32
African buffalo	64	3.2	22	2.07	15	2.58	92	4.22	96	2.59	168	4.03	122	2.27
Common duiker	70	3.5	24	2.26	121	20.8	52	2.39	358	9.64	145	3.48	478	8.9
Bushbuck	20	1.0	–	–	–	–	–	–	–	–	20	0.48	–	–
Greater kudu	195	9.76	8	0.75	60	10.31	41	1.88	147	3.96	236	5.67	217	4.04
Giraffe	80	4.0	10	0.94	3	0.52	–	–	17	0.45	108	2.6	3	0.06
Steenbok	5	0.25	3	0.28	20	3.44	13	0.6	67	1.8	11	0.26	99	1.84
Impala	386	19.3	19	1.79	71	12.2	44	2.02	72	1.94	441	10.6	150	2.8
Nyala	337	16.9	10	0.94	89	15.3	110	5.05	133	3.58	352	8.45	325	6.05
Sable antelope	1	0.05	1	0.09	–	–	–	–	–	–	2	0.05	–	–
Eland	3	0.15	–		–	–	–	–	1	0.03	4	0.09	1	0.02
African elephant	118	5.9	34	3.2	21	3.61	74	3.4	80	2.16	193	4.63	133	2.48
Total Wildlife RAI	106.4		17.9		78.04		21.12		27.05		63.23		29.84	
Grazer’s ratio (%)	42.9		43		15.2		27.4		12.8		42.6		12.2	
Browsers ratio (%)	17.1		22		40.5		20.2		52		19.3		43.6	
Mixed feeder ratio (%)	40		35		44.3		52.4		35.2		38.1		44.2	

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CHAPTER FOUR

4. Ecological and anthropogenic determinants of the landscape distribution of large herbivores species in the Limpopo National Park, Mozambique

Abstract

African savanna ecosystems are home to the world’s richest large herbivore (LH) assemblages. However, its landscapes are changing faster than any other region on Earth due to human activities and natural events. Understanding the factors influencing the distribution of LH in human-dominated environments is crucial for wildlife management decision-making. The study aimed to assess how ecological (habitat types, perennial rivers, and rainfall) and anthropogenic (human settlements and cattle grazing areas) factors influence the distribution of large herbivore (LH) species in Limpopo National Park (LNP) surveyed over 21 years through a generalized linear model (GLM). Based on logistic regression models, I used park-aerial censuses (2001-2018), camera trap surveys, and dung count transects (2019-2021) to distinguish 25 km^2 cells occupied by African elephants, African buffalos, plains zebras, greater kudu, nyala, and impalas from unoccupied regions in the LNP as a function of distances to rivers, settlements, and cattle grazing areas, habitat types, and rainfall. Habitat types and rainfall were the most influential factors shaping positively the pattern of LH distribution in the LNP, except the elephants, whose prevalence was not associated with rainfall. The prevalence of zebras was positively associated with the proximity to perennial rivers, while kudus avoided these areas. While some species (zebras, kudus, and impalas) tended to avoid settlements, others (elephants, buffalos, and nyala) seemed attracted to settlements. Cattle grazing areas were the worst predictors of the distribution of all study species. The results disclosed the role of ecological factors for the distribution of LH and showed that anthropogenic disturbances seemed to either (partially) prevent the occurrence of LH or show the potential for human-wildlife conflict risk in the study area. Therefore, the results highlight the need to investigate/quantify the potential human-wildlife conflict risk at finer spatial scales to improve future management in the Limpopo National Park.

Keywords: African savanna ecosystems, anthropogenic factors, ecological factors, distribution of species, human-dominated landscapes, large herbivores, Limpopo National Park.

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4.1. Introduction

Understanding the factors influencing the distribution of large herbivores (LH) is crucial for decision-making on wildlife and habitat management (Gordon *et al*., 2004, Murwendo *et al*., 2020). Management of LH in African savannas is essential because the population of some species are critically low, and others are endangered due to habitats loss, fragmentation, encroachment by humans (Newmark, 2008; Sawyer *et al*., 2018), and illegal overhunting (Gordon *et al*., 2004). Furthermore, besides LH having great economic value through sport hunting (van der Waal and Dekker, 2000) and ecotourism (Ogutu, 2002), they drive the structure, composition, and functioning of sub-Saharan African savannas ecosystems (Pickup *et al*., 1998; Naiman *et al*., 2003; Shorrocks and Bates, 2015). Therefore, any decision to manage LH in these ecosystems implies landscape and habitat management.

Surface-water availability is a primary determinant of herbivores' distribution because most strictly water-dependent species require drinking water to complement forage consumption (Western, 1975; Gordon *et al*., 2004; Cain *et al*., 2012). Water sources promote the development of resource utilization gradients (Chamaille-James *et al*., 2007a). The regular need to access drinking water restrains the ability of animals to range far from water, leading to the decrease of water-dependent species distribution and abundance with increasing distance to water (Western, 1975; Redfern *et al*., 2003). Nevertheless, the extent to which LH may use the proportion of the habitats within a certain distance of water will depend upon their water requirements, physiology and mobility (Western, 1975). Unlike browsers, which are less strictly water-dependent, grazers are most strictly water-dependent (Skinner and Chimimba, 2005; Estes, 2012). Therefore, their spatial distribution and abundance are higher in areas closer to water (Western, 1975; Redfern *et al*., 2003). In arid and semi-arid savannas, changes in water availability during the dry season might cause changes in the distribution of LH because, in areas without water, forage will not be used by animals (Chamaillé-Jammes *et al*., 2007b).

Many wildlife populations in African protected areas are isolated from one another due to anthropogenic disturbances (Newmark, 2008). LH species with a lower body mass are highly mobile and very sensitive to anthropogenic disturbances because they require well-connected patches (Di Minin *et al*., 2013) and explore large home ranges (Shannon *et al*., 2006; Göttert *et al*., 2010; Owen-Smith and Martin, 2015). In some protected areas, LH species avoid areas with human settlements, livestock keeping, agriculture, harvesting of flora resources, and illegal hunting (Leblond *et al*., 2013; Muposhi *et al*., 2016a). However, LH can also persist in some human-dominated areas, often causing human-wildlife conflicts (Virtanen *et al*., 2021). LH species adapt their foraging behaviour by using a 'refuge' habitat or feeding on alternative food resources in the presence of cattle competing for forage resources (Stephens *et al*., 2001; Young *et al*., 2005; Hibert *et al*., 2010).

Different habitat types for LH determine differences in resources and conditions (Owen-Smith, 2002; Tews *et al*., 2004). Habitat selection by LH is an adaptive process that increases fitness (Martin, 1998). It is related to the suitability of that habitat (Thornton *et al*., 2013), which in turn depends on plant species composition and distribution, microclimatic features, surface-water availability (Chamaille-James *et al*., 2007a), competition (Fritz *et al*., 1996), predation risk and disturbances (Valeix *et al*., 2009; Muposhi *et al*., 2016b). Herbivores with smaller body sizes require habitats with relatively less forage but of higher nutritional quality, whereas larger herbivores tolerate habitats with low-quality food, provided that it is of sufficient quantity (Bell, 1971; Jarman, 1974; Hopcraft *et al*., 2012; le Roux *et al*., 2020). As a result, larger species exploit a higher diversity of habitat and, as such, may utilize a higher proportion of the landscape compared to medium or smaller herbivore species (Olff *et al*., 2002; Cromsigt *et al*., 2009). However, larger grazers will avoid some habitats with few resources (e.g. forests or thickets) and concentrate only on habitats with abundant grass (Olff *et al*., 2002; Cromsigt *et al*., 2009).

Rainfall is a crucial factor that shapes vegetation dynamics (Castillioni *et al*., 2022). It controls vegetation growth, quantity and quality (Deshmukh, 1984). Rainfall received during a wet season strongly affects vegetation growth, the composition of the herbaceous layer, and hence the capacity to produce forage of a suitable quality

(Rutherford, 1980; Owen-Smith and Ogutu, 2003), while rainfall falling during the dry season promotes the retention of green foliage improving the nutritional quality (Mduma *et al*., 1999). Rainfall determines the surface water availability across the landscape (Redfern *et al*., 2005) and vegetation resource utilization (Chamaille-James *et al*., 2007a) and, therefore, influences the distribution of animals in the landscape.

The LNP was established in 2001. It is one of five core protected areas in the Great Limpopo Transfrontier Park and Conservation Area (GLTFCA). LNP in Mozambique, Gonarezhou National Park (GNP) in Zimbabwe, and the Kruger National Park (KNP) in South Africa form the Great Limpopo Transfrontier Park (GLTP). These three parks, together with Banhine National Park (BNP), Zinave National Park (ZNP), and the interstitial zone between these parks in Mozambique, form the GLTFCA (Milgroom and Spierenburg, 2008; ANAC, 2022). Before 2001, LNP was a trophy-hunting concession (DINAC, 2003; Mavhunga and Spierenburg, 2009; Massé, 2016). In 2001, wildlife populations were nearly extirpated due to Mozambique's civil war (1976-1992) and decades of poaching (Hatton *et al*., 2001; Lunstrum, 2016). However, the LNP is in the early-intermediate stage of restoration of wildlife populations (Roque *et al*., 2021, 2022) due to a restoration program carried out from 2001 to 2008 through active wildlife translocation from KNP of 4,725 LH individuals (African elephant, white rhino, African buffalo, giraffe, blue wildebeest, plains zebra, waterbuck, roan antelope, Lichtenstein hartebeest, and impala) to a 300 km^2 fenced area so-called "Old Sanctuary" (Hofmeyr, 2004; Mabunda *et al*., 2012), and passive wildlife reintroductions through three sections of KNP-LNP fence removed (Figure 3.1A, Chapter 3) to allow wildlife cross border movements from KNP into LNP (Mabunda *et al*., 2003).

Although some park management decisions, such as resettling people from Shingwedzi Valley to the buffer zone (ANAC, 2022), establishing an Intensive Protection Zone (IPZ) and increase of anti-poaching control posts (PNL, 2012; Grossman *et al*., 2014), there are still 1,380 households, living in four villages, including about 9,600 head of cattle inside the core area of the park. Settlements and unsustainable resource harvesting in the core area prevent wildlife numbers from growing and restrict their distribution (Bazin *et al*., 2016; ANAC, 2022). The villages in the core area are being resettled in the buffer zone as part of a Resettlement Programme started in 2005. As the number of people increases in the buffer zone, the use of land for agriculture in the eastern LNP expands and intensifies (Andresen *et al.*, 2014; Bazin *et al.*, 2016), preventing LH access to riparian resources along the Limpopo River in the dry season (Macandza and Ruiz, 2012; ANAC, 2022). The livestock stocking levels are increasing in the LNP (Grossman *et al.*, 2014; ANAC, 2018; 2022), and cattle still share grazing areas with wildlife. Despite evidence of slight LH recovery in the LNP (Roque *et al.*, 2021, 2022), to my knowledge, no study has attempted to understand how ecological and anthropogenic factors shape their distribution at landscape and habitat scales. This study will provide a scientific basis for decision-making concerning habitats or locations to prioritize when conserving target species, human resettlements, and human-wildlife conflict mitigation in the LNP. Furthermore, as many protected areas in Sub-Saharan Africa are also human-dominated landscapes, the study can be applied as a tool for conservation planning and management beyond the LNP. The study aimed to assess how ecological (perennial rivers, habitat types, and rainfall) and anthropogenic (human settlements and cattle grazing areas) factors influence the distribution of LH in the LNP landscape. I hypothesized that:

1. While grazers will concentrate on short-low woodland savanna and short-to-tall grassland savannas, mixed feeders and browsers will concentrate on all savanna types (short-low woodland savanna, short-to-tall grassland savannas, dense woodland savanna, thicket savanna and tall shrubland savanna;
2. Since grass production is positively affected by rainfall, grazers and mixed feeders will concentrate in high-rainfall areas, while browsers will be less affected by rainfall;
3. Unlike browsers, grazers and mixed feeders will concentrate their distribution near perennial water sources;
4. All study guilds (grazers, mixed feeders, and browsers) will avoid human settlements and cattle grazing areas.

4.2. Material and methods

4.2.1. Study area

I conducted this study in LNP (22°25'S – 24°10'S, 31°18'E – 32°39'E), a protected area in Gaza province in Mozambique. This park, together with KNP in South Africa, GNP in Zimbabwe, BNP, ZNP as well as several communities and private concession areas in

Mozambique, form the GLTFCA. The LNP and its buffer zone cover about 10,980 km^2, and the western perimeter of the LNP shares the border with South Africa and stretches in a North-South direction for nearly 200 km. The Zimbabwean boundary touches on the most northerly tip of the area and then extends to the North-East. A line 5 km from the right bank of the Limpopo River floodplain forms the Eastern boundary, whilst a 5 km line from the left bank of the Olifants (Elefantes) River forms the southern boundary below the Massingir Dam wall. Upstream of the dam wall, the park boundary follows the dam basin property boundary up to the South African (ANAC, 2022). The climate of the LNP is warm dry tropical, with two seasons, the wet season (November to April) and the dry season (May to October). Temperatures increase from South to North, with maximum temperatures above 40°C being common from November to February. The average annual temperature fluctuates between 24°C and 30°C. Rainfall is low, ranging from 360 mm/year in the North to 530 mm/year in the South. Rainfall is also markedly seasonal, with 95% of the yearly rainfall occurring in the wet season. The altitude in the park varies between 260 and 840 m above sea level (Brito and Julaia, 2007, ANAC, 2022).

Geologically, LNP is dominated by rhyolite volcanic rock in the southern region, while the North consists of the red sand mantle, whereas alluvium and clay sediments characterize the Limpopo floodplains. Hydrologically, the study area is dominated by three river systems (ANAC, 2022): (1) the Limpopo is the largest perennial river, although water becomes restricted to pools along the river bed at the end of the dry season during dry cycles, (2) the Olifants remain perennial throughout the season, and (3) the Shingwedzi is a much smaller non-perennial river, although it retains water for long periods and attracts wildlife from the dry waterless Sandveld interior. These river systems have an overwhelming impact on the land use of the study area by influencing the distribution of people and wildlife.

Subsistence farming, free livestock grazing and poaching bush meat are the main activities linked to people's settlements (Andresen *et al.*, 2014). About 30,000 people live in the LNP, of which 51 communities live in the buffer zone, consisting of 5,155 households – approximately 22,748 people with 38,280 heads of cattle (Bazin *et al.*, 2016; ANAC, 2022). The remaining inhabitants awaiting resettlement in the buffer zone (Massé, 2016) live in seven villages in the central area (Shingwedzi Valley) of the park (Milgroom and Spierenburg, 2008), with 9,600 heads of cattle sharing grazing and natural water sources with wildlife (ANAC, 2022). Ecologically, the most significant part of the buffer zone is the section along the Limpopo River, consisting of floodplains, permanent water sources, and pans that provide water and productive alluvial soils. This area is suitable habitat for the productivity, diversity, and reliance of the LNP ecosystems and their species, especially the large mammals. However, it is also heavily settled and farmed (DINAC, 2003; ANAC, 2022) and acts as a barrier to wildlife distribution and movements in the GLTFCA and access to the Limpopo River resources.

Based on woody vegetation, species composition, and physiognomy, Stalmans *et al*. (2004) described ten landscape/habitat types with 15 plant communities combination covering the study area: (i) Nwambia Sandveld, (ii) Pumbe Sandveld, (iii) Rugged Veld, (iv) Lebombo North, (v) Shrubveld on Calcrete, (vi) Shrubveld on Basalt, (vii) Woodland, (viii) Limpopo Levubu Floodplains, (ix) Rugged Veld, and (x) *Salvadora angustifolia* floodplains. Five of them, Nwambia Sandveld, Pumbe Sandveld, Rugged Veld, Lebombo North, and Shrubveld on Calcrete, cover more than 90% of the park surface (Figures 4.S1-S3). These habitat types represent resources (food and water), condition (safety and shelter), and social interaction places for reproduction:

(i) Lebombo North (LN): covers 398.78 km^2 (3.5% of LNP) and corresponds to short and low woodland savanna and short grassland savanna (Stalmans *et al*., 2004). Although LN has high grass species composition (44 species), the grass biomass average (2,076.5 ± 569.83 kg/ha) and shrub resources are lowest than Nwambia and Shrubveld. The main species in the grass layer are *Panicum maximum*, *Urochloa mossambicensis*, and *Schmidittia pappaphoroides*. *Setaria incrassate is* the tall short grassland component of LN. The ecologically important trees are *Colophospermum mopane* and *Combretum apiculatum*. The tree’s average height is 2.9 m (Ribeiro *et al*., 2019). The main rivers crossing LN are Machampanhe, Shingwedzi and their tributaries (ANAC, 2022).

(ii) Pumbe Sandveld (PS): covers 256.08 km^2 (2.3% of LNP) and corresponds to short and low woodland savanna with high grass and shrub resources and low tree resources. It is dominated by *Combretum apiculatum*, *Acacia nigrescens*, and *Terminalia sericea*. The main species in the grass layer are *Panicum maximum*, *Urochloa mossambicensis*, *Schmidittia pappaphoroides*, and *Eragrostis pallens*. The main rivers in PS are Machampanhe and Shingwedzi.

(iii) Rugged Veld (RV): covers 699.11 km^2 (6.21% of LNP). RV is a mixture of short and tall woodland savanna and tall shrubland savanna with reasonable grass, shrub and tree food resources. The main species in the grass layer are *P. maximum*, *Urochloa mossambicensis*, *Heteropogon contortus*, and *Schmidittia pappaphoroides*. The most ecologically important trees are *C. mopane*, *Acacia nigrescens*, *Sclerocarya birrea* and *Combretum imberbe*. The main river in RV is Shingwedzi and its tributaries.

(iv) Shrubveld on Calcrete (SC): covers 4,158.9 km^2 (38.8% of LNP). SC is a mixture of short woodland savanna, thicket shrubland, and tall grassland. Similarly to LN, SC has the highest richness in its grass composition (44 species) with, however, medium average biomass (2,968 ± 635.63 kg/ha). *Urochloa mossambicensis*, *Heteropogon contortus*, *Digitaria eriantha*, *Penisetum glaucum* and *P. maximum* are the dominant grass species (Ribeiro et al., 2019). *Setaria incrassate is* the tall grassland component of SC. Calcrete is homogeneous in species composition; shrubby *C. mopane* and *Grewia bicolo*r are the overwhelmingly dominating species. The tree's average height is lower (~2.25 m) than other habitats (Ribeiro *et al.*, 2019). Limpopo and Shingwedzi Rivers supply SC. This habitat is densely populated by humans because most of the villages are settled within this habitat.

(iv) Nwambia Sandveld (NS): is the most extensive habitat covering 4586.41 km^2 (41.1% of LNP) and corresponds to low woodland and thicket savanna. Although the grass composition is relatively low (35 species), NS has the highest grass biomass (3,630.5 ± 298.62 kg/ha) than other habitats, higher shrub food resources, and the tallest tree, with ~4.25 m. *P. maximum*, *Digitaria eriantha* and *Urochloa mosambicensis* are the dominant grass. The most ecologically important trees are *Combretum apiculatum*, *Sclerocarya birrea* and *Xeroderris stuhlmannii* (Ribeiro *et al.*, 2019). NS is waterless throughout its extension.

Although wildlife populations were almost decimated due to Mozambique's civil war (1976-1992) and decades of poaching (Hatton *et al.*, 2001; Hofmeyr, 2004; Lunstrum, 2016), currently, populations of LH are increasing in the LNP (Grossman *et al.*, 2014; ANAC, 2018), even though it is still a lower abundance compared to the period before the civil war (Roque *et al.*, 2022). About 43 species of mammals were reported to occur in the LNP (Stephenson, 2010, 2013; Grossman *et al.*, 2014; ANAC, 2018; Roque *et al.*, 2021). However, roan antelope and hartebeest have never been recorded since 2007 to date. White rhinos were recorded for the last time in 2013. These three species were also actively reintroduced into the park (Hofmeyr, 2004; Lunstrum, 2016). Some of these species (roan and hartebeest) seem not to have adapted better (Whyte and Swanepoel, 2006), while white rhino was heavily impacted by poaching between 2010 and 2014 (Lunstrum, 2016).

4.2.2. Study period and selection of species

I selected the period from 2001 to 2021 due to data availability: LH occurrence data from aerial wildlife censuses covered the period from 2001 to 2018, while camera trap surveys and dung count covered the period from 2019 to 2021. Based on the data availability, I selected six LH species (Table 4.1), representing different feeding guilds and water dependency. These six species were recorded at least ten times in each habitat type during the study period, which is the minimum required to perform the logistic regression.

Table 4.1. Large herbivores species selected for the study in the Limpopo National Park and their functional grouping by water dependency and feeding guild

Common name	**Scientific name**	**Water dependency** (Skinner and Chimimba, 2005; Estes, 2012)	**Feeding guild** (Skinner and Chimimba, 2005; Estes, 2012)
Plains zebra	*Equus quagga*	Strictly dependent	Grazer
African buffalo	*Syncerus caffer*	Strictly dependent	Grazer
Greater kudu	*Tragelaphus strepsiceros*	Not strictly dependent	Browser
Impala	*Aepyceros melampus*	Dependent	Mixed feeder
Nyala	*Tragelaphus angasii*	Dependent	Mixed feeder
African elephant	*Loxodonta Africana*	Strictly dependent	Mixed feeder

4.2.3. Data collection

Census data

Ecological aerial surveys were conducted in LNP in 2006, 2007, 2008, 2010, 2013, 2014, and 2018 between September and October when visibility was considered best (Redfern *et al.*, 2002; Stephenson, 2013). Census transects were 800 m apart, and four observers, two on each side of a fixed-wing aircraft, recorded the geographical locations of species and the number of animals. The aircraft was calibrated for each observer and flew at a mean altitude of 90 m above ground level. All data were recorded on a laptop computer linked to a Garmin Geographic Positioning System (GPS). Therefore, positional accuracies would be uncertain within 0.8 km (Viljoen and Retief, 1994). At each sighting number of individuals, time, date, latitude, longitude, speed, and altitude were recorded. Human activity, farming, and livestock grazing areas also were recorded.

Camera trap and dung count data

From November 2019 to June 2021, I randomly deployed in ~2 km x 2 km grid cells (Woog *et al*., 2010; Rovero *et al*., 2013), 24 infrared wildlife camera traps (Foxelli Outdoor Gear Oak's Eye Trail Cam® -14 MP 1080 Full HD) in a 60 x 108 km^2 grid cells surveyed. I deployed one camera trap in each grid (Rovero *et al*., 2014; Debata and Swain, 2018) at 0.50 to 1.5 meters in height on trees and shrubs. The cameras were active 24 hours a day and took bursts of two successively high-resolution photos, 14 MP (4426 x 3312P), with a delay of 60 seconds between trigger activations. Each camera trap location/station constituted the sampling units (Mena *et al*., 2020). I moved the cameras from one station to another six times and collected LH data on 146 sampling units. The average length of camera deployment at each sampling unit was 69.5 days (SD = 31.2; min = 28; max = 122). I also recorded each camera trap station using a handheld GPS. I covered 6,000 km^2 (60%) out of 9,260 km^2 of the park with the camera traps. During the camera trap surveys, I also walked 70 dung counts transects of 2 km established from 140 random points 5 km apart. I counted and recorded the dung presence of study species within one meter on each side of the transect using a handheld GPS. I walked each transect six times with a mean interval between the walks of 80 days.

4.2.4. Data analysis

Spatial and temporal scales

I used the period from 2001 to 2021 to assess how ecological and anthropogenic factors influence the distribution of LHs (≥ 70 kg) from aerial wildlife censuses, camera trap surveys, and dung count data in the LNP. I selected the period from 2001 to 2021 because the aerial wildlife censuses since the establishment of the LNP covered that period, while camera trap surveys and dung count along transects covered the period from 2019 to 2021. I divided the LNP into 5 km x 5 km grid cells in Arc Map (version 10.8.1), a

Geographical Information System software (GIS). I chose the 25 km^2 scale to form the basis for these analyses because it approximates the mean home range size estimates for the study species in the neighboring KNP (Chirima *et al*., 2013; Robson and van Aarde, 2018). Furthermore, this spatial scale is most appropriate for highly mobile herbivores because it reflects the smallest and largest daily area (Young *et al*., 2009) the selected species may use. I did not include in the analysis grids along the park boundary covering less than half (i.e. less than 12.5 km^2) of which the centroid was outside the park boundary. I considered a total of 462 grids with a minimum occupation by studied species of 15% (69 grids). This percentage is the minimum necessary to have more than ten observations of the least frequent species in the data used so that the assumptions of the logistic regression could not be violated (Manly *et a*l., 2002). I overlaid the grid shape file on a map of LNP that showed the geographical positions of each study species and classified each grid as showing the presence/absence of an animal or herd record. For aerial census data, I considered each species present if a grid had at least two records of the same species during the study period. I did this to exclude the occasional presence of the species in the grids due to potential predation that was not included in the study.

I excluded all wet season camera trap and dung count data from the analyses because all wildlife censuses in the LNP were conducted in the dry season (Whyte and Swanepoel, 2006; Stephenson, 2010, 2013; Grossman *et al*., 2014; ANAC, 2018). Thus, I considered camera trap and dung count data from April to September 2020 and 2021, respectively. I sorted all photographs by species, date, and time in each grid using the software “Camera Base-Adobe Bridge 2020 for Windows (Adobe Systems),” an access database designed for managing camera trap data (Tobler *et al*., 2009; Rovero *et al*., 2010). I converted them to camera-independent observation/detection (independent events). Independent events were defined as (i) consecutive photographs of individuals of different species; (ii) consecutive photographs of individuals of the same species taken more than 0.5 h apart; and (iii) non-consecutive photos of individuals of the same species (O’Brien *et al*., 2003; Tobler *et al*., 2008). I considered as independent events dung piles 50 m apart along the transects. I assumed an animal was present if a grid presented at least two independent events for camera trap and dung count transects. I treated grids with multiple individuals of the same species as a single “presence”. By doing so, I controlled spatial autocorrelation in LH observation within the grid without removing duplicated occurrence to avoid underestimation of the contribution of suitable areas where the high density of records reflects the real ecological value for the species (Fourcade *et al*., 2014). One approach to overcome the imperfect detection issue (i.e., the species was present but undetected) without explicitly incorporating detection probability in the analysis is to assume that sufficient surveying effort has been expended such that the false absence probability is negligible (Mackenzie and Royle 2005). I calculated the probability of false absence based on the number of favourable detections and the total number of possible detections in 462 grids, following Mackenzie and Royle (2005): $P = (1 - k)^n$ where, P = probability of false absence, k = probability of detecting the species in a survey, and n = number of surveys conducted. Assuming that six of eight surveys carried out covered the total study area, the probability of not detecting the study species was: African elephant = 0.05, African buffalo = 0.18, plains zebra = 0.32, greater kudu = 0.04, nyala = 0.028 and impala = 0.12. Thus, I assumed that the chance of not detecting LH species (probability of false absence) over the 20 years spanned by my analysis, even when present, is vanishingly reduced. Furthermore, the data collection has involved multiple surveys (eighth surveys) using various observers and different methods of LH detection (aerial census, camera trap surveys, and dung count transects). Therefore, the survey effort at surveyed sites increased enough so that detection can be assumed precise enough and suitable for modelling.

Explanatory variables selection

I selected five predictor variables, three ecological (perennial water sources, rainfall and habitat types) and two anthropogenic (human settlements and cattle grazing areas), expected to affect LH occurrence in the Limpopo National Park. I did not include predation as a predictor in the analyses because there is not yet a significant impact of potential predators on ungulates in the Limpopo National Park (Roque *et al*., 2021). As LNP is in the early restoration stage (Roque *et al*., 2021), the local species abundance and density are still low (Stephenson, 2010, 2013; Grossman *et al*., 2014; ANAC, 2018). Thus, I did not include direct competition as a predictor in the analysis. I did not directly include fire frequency as a predictor in the analysis because, according to Ribeiro *et al*. (2019), human activities are the main causes of fires in LNP. The two most important activities, agriculture and livestock, which are related to settlements and cattle grazing areas, respectively, were included as predictor variables in the study. Before extracting the predictor variables, all rasters were resampled in ArcGIS10.8.1 to 25 km^2 (5 km x 5 km) usind Data Management Tools to match the scale of the analyses on the defined 5 km x 5 km grids.

Distance to water sources

I downloaded free shape files of rivers from Mozambique, South Africa and Zimbabwe at https://data.amerigeoss.org/dataset/gis-osm-water-a-free-1. I projected all rivers in GLTP shape files, and using clip extension on the Data Management Tools, I clipped the perennial rivers corresponding to the study area. I created a 5 km x 5 km grid shape file, and I calculated the nearest distance in kilometers from the centre of each grid to permanent rivers using the nearest-features extension on the Analysis Tools in ArcGIS 10.8.1. This approach avoided spatial autocorrelation in LH occurrence between grids because the average distance among neighbouring grid centroids is exactly 5 km. Although I recognize that the occurrence records do not necessarily count as if the species were observed exactly at the central pixel of the corresponding grid cell, the predictor's influence at that pixel may not be far from those at the place where the species were actually observed within the cell (Sillero and Barbosa 2021). I created three categories: 0-5 km, 5.1-10 km, and > 10 km, based on the percentiles (Borkowf *et al*., 2003, Chirima *et al*., 2013) because it is useful to model non-linear effects into linear models and allow the treatment of all factors similarly. It allowed capturing the impact variations in the values of predictors (intermediate distances, or only above or below some threshold distance levels) have on LH prevalence. I used these distances as the explanatory variables.

Habitat types

I used the shape file of LNP Landscape (Stalmans *et al*., 2004), representing different habitat types. I preferred the map of Stalmans *et al*. (2004) to the recent maps of Lötter *et al*. (2023) and Stalmans and Lötter (2021) because the habitat types described in the Stalmans map better represent different resources (food and water) and conditions (safety and shelter) than the other maps. Additionally, the Stalman map was produced using a combination of fieldwork at a finer spatial scale and analysis of Landsat satellite imagery. I selected five habitat types (Lebombo North, Pumbe Sandveld, Rugged Veld, Shrubveld on Calcrete, and Nwambia Sandveld) representing more than 90% of the park surface. I created a 5 km x 5 km grid shape file and extracted the habitat type present in each grid as an explanatory variable. In cases where more than one habitat occurred on the grid, I considered the most predominant habitat types. I classified each habitat type according to vegetation structure and composition, representing different food resources and conditions (shelter and safety).

Rainfall

I download rainfall data (https://crudata.uea.ac.uk/cru/data/hrg/cru_ts_4.06/) from "Climatic Research Unit Gridded Time Series (CRU TS version 4.06) from 2001 to 2021. These data are a widely used climate dataset on a 0.5° latitude by 0.5° longitude grid over all land domains of the world except Antarctica. It is derived by the interpolation of monthly climate anomalies from extensive networks of weather station observations (Harris *et al*., 2020). I used the extension Make NetCDF Raster Layer in the Multi Dimension Tools in Arc Map 10.8.1 to project the rainfall data to the LNP shape file. Using the Raster Calculator extension in the Spatial Analyst Tools, I computed the annual rainfall mean by summing all 21 years of monthly rainfall data divided by the number of months in the same period. From Conversion Tools, I created Raster Data. I used Spatial Analyst Tools to perform interpolation using ordinary kriging techniques on the Raster Data. I masked the raster data using the LNP shape file in the Process Extent and finally created a categorical variable with three levels: low (0-450 mm), medium (> 450-500 mm), and high (> 500 mm). I created a 5 km x 5 km grid shape file and extracted the rainfall category present in each grid as an explanatory variable. In cases where more than one rainfall category occurred on the grid, I considered the most predominant.

Distance to human settlements

Human settlements in LNP consist of villages and farming fields along the Limpopo, Olifants, and Shingwedzi Rivers (Milgroom and Spierenburg, 2008; Bazin *et al*., 2016). I considered villages and farming activities as human settlements. I downloaded free shape files of Mozambique human settlements at https://data.humdata.org/dataset/mozambique-settlement-shapefiles and clipped the villages corresponding to the LNP. The farming fields were recorded during aerial wildlife censuses in the LNP (Stephenson, 2010, 2013; Grossman *et al*., 2014; ANAC, 2018). I created a 5 km x 5 km grid shape file, and I calculated the nearest distance in kilometers from the centre of each grid to human settlements using the nearest-features extension on the Analysis Tools, yielding three categories: 0-5 km, 5.1-10 km, and > 10 km. I used the distance from each human settlement site as the explanatory variable.

Distance to cattle grazing areas

I considered cattle, goats and sheep as livestock species that can compete with LH (Hibert *et al*., 2010) for grazing areas. Cattle, goats, and sheep grazing areas were recorded during aerial wildlife censuses (Whyte and Swanepoel, 2006; Stephenson, 2010, 2013; Grossman *et al*., 2014; ANAC, 2018). I also created a 5 km x 5 km grid shape file, and I calculated the nearest distance in kilometers from the centre of each grid to cattle grazing areas using the nearest-features extension on the Analysis Tools in ArcGIS, yielding three categories: 0-5 km, 5.1-10 km, and > 10 km. I used the distance from each cattle grazing area site as the explanatory variable.

Statistical analysis and model selection

To establish the factors that determine LH distribution, I fitted logistic regression models because the technique is considered suitable for modelling dichotomous outcomes (Hosmer and Lemeshow, 2000; Manly *et al*., 2002). I modelled dichotomous outcomes (i.e. presence = 1/absence = 0) of LH in the LNP using five variables: (i) distance to the nearest perennial rivers, (ii) distance to the nearest human settlements, and (iii) distance to the nearest cattle grazing areas, each of them with three categories (0-5 km, 5.1-10 km, and > 10 km), (iv) habitat types with five categories (Nwambia Sandveld, Shrubveld on Calcrete, Rugged Veld, Pumbe Sandveld, and Pumbe Sandveld), and (v) rainfall with three categories (0-450 mm, > 450-500 mm, and > 500 mm). The full or saturated model for each LH species was: Rivers (3 levels) + Settlements (3 levels) + Cattle grazing areas (3 levels) + Habitat types (5 levels) + Rainfall (3 levels). Before fitting the models, I verified whether the data met all the logistic regression assumptions (Peng and So, 2002; Peng *et al*., 2002; Park, 2013): (i) the dependent variable is dichotomous, and the desired outcome, was coded to be 1 (species detected or present = 1, not detected or present = 0), (ii) the observation of a species was independent of others, and I considered at least more than ten observation for the least frequent species, (iii) the standardized residuals revealed no influential outliers (standardized residual values < 3, Figure 4.1), (iv) the Variance Inflation Factor (VIF) revealed a very low correlation among variables (VIF_{Rivers} = 4.39, df

= 2; $VIF_{Settlements}$ = 1.83, df = 2; $VIF_{Cattle\ grazing\ areas}$ = 3.72, df = 2; $VIF_{Habitat\ types}$ = 2.58, df = 4, and $VIF_{Rainfall}$ = 1.25, df = 2). The smallest possible value for VIF is 1 (i.e., a complete absence of collinearity), and a VIF value that exceeds 10 indicates a problematic amount of multicollinearity.

I fitted models using all possible subsets regression approach (exhaustive searches for the best subsets of explanatory variables) (Thompson, 1989, 1995; Pedhazur, 1997; Manly *et al*., 2002; Lewis, 2007) to assess the distribution of selected species as a function of (i) distance to perennial water sources, (ii) distances to settlements, (iii) distances to cattle grazing areas, (iv) habitat types, and (v) rainfall. I preferred all possible subsets regression fashion to stepwise and hierarchical regressions because it is a relatively straightforward approach that explores the variance explained by each predictor individually and then in all possible combinations up to the complete set of predictors (Pedhazur, 1997). Furthermore, the purpose of this study was exploratory, not predictive modelling. Although widely applied in species distribution modelling (Thompson, 1989; Araújo and Guisan, 2006; Smith *et al*., 2009), stepwise regression is often discouraged due to biases and inconsistencies in parameter estimation, model selection algorithms, selection of the single best magic model (Whittingham *et al*., 2006; Nathans *et al*., 2012), and very often, it depends on the first predictor entering the model, which determines the variance of other predictors in the model, posing serious Type I errors associated with inflated F-values (Thompson, 1995; Nimon *et al*., 2008; Nathans *et al*., 2012).

Although representing an improvement over stepwise regression, hierarchical regression (Thompson, 1995; Lewis, 2007) ignores the relative importance of certain predictor variables and fails to address multicollinearity (Petrocelli, 2003; Ray-Mukherjee *et al*., 2014). However, as the focus of all possible subsets regression is on the total effect rather than the particular contribution of variables that make up that effect, the multicollinearity concept became less relevant (Kraha *et al*., 2012). Therefore, to address the multicollinearity issue (Seibold and Mcphee, 1979; Nimon *et al*., 2010), evaluates the contribution of each predictor in the models in addition to measures of shared variance for all combinations of predictors (Rowell, 1991; Pedhazur, 1997; Zientek and Thompson, 2010; Nimon and Reio, 2011), and identify the most parsimonious model (Kraha *et al*., 2012), I combined all possible subsets regression procedures with regression commonality analysis (CA).

For model selection, I applied Akaike's Information Criterion (AIC) and Likelihood Ratio Test (LRT) procedures to compare the relative support weight for each model. The model with the lowest value of AIC is the best-supported model. If the *p*-value of the likelihood ratio test is greater than 0.05, the model with the fewest predictors is the best model due to its parsimony/simplicity (Burnham and Anderson, 2002; Manly *et al*., 2002), i.e. the model that best explains the distribution of each species of LH. I computed delta AIC (ΔAIC) as the difference in AIC values between each candidate model and the best model. I used the difference as follows to determine the level of support for each candidate model (Burnham and Anderson, 2002; Fabozzi *et al*., 2014): If (i) ΔAIC < 2, this indicates there is substantial evidence to support the candidate model (i.e., the candidate model is almost as good as the best model), however, in the event of several models presenting ΔAIC values of < 2, the model with the fewest parameters (i.e. the most parsimony) is the best, (ii) ΔAIC between 4 and 7 units of the best model, this indicates that the model has substantial support that should be considered candidates for the best model, and (iii) ΔAIC > 10, there is essentially no support for the candidate model (i.e., it is unlikely to be the best model). Because the magnitude of the ΔAIC is not meaningful in itself (Fabozzi *et al*., 2014), I calculated the Akaike weight (W_m) as the relative likelihood of the model, which is just exp(-0.5*ΔAIC score for that model) divided by the sum of these values across all models, to measure the strength of evidence for a candidate model. The Akaike weights are the probability that the candidate model is the best among a set of candidate models (Burnham and Anderson, 2002; Manly *et al*., 2002; Fabozzi *et al*., 2014). No model showed an over-dispersion much greater than one that required adjustment of model statistics. I assessed the overall fit of the models using the Hosmer-Lemeshow (H-L) goodness of fit test (Hosmer and Lemeshow 2000). I built a confusion matrix and computed predicted accuracy to validate the models. Accuracy is an evaluation metric used for classification tasks. It represents the percentage of accurate predictions. I calculate it as a ratio of the total number of correct predictions to the total number of predictions generated by the model (Hilbe, 2015). I performed all analyses in R software (R Core Team, 2018). To complement the assessment of the presence of LH species as a function of each category in each factor, I computed 95% binomial confidence limits for proportions. I calculated the proportion of each species as the number of grids occupied by the species divided by the number of grids in each category of each factor. Because the presence of the species corresponds to 25 km^2 grids, the greater the number of grids occupied, the wider the species distribution.

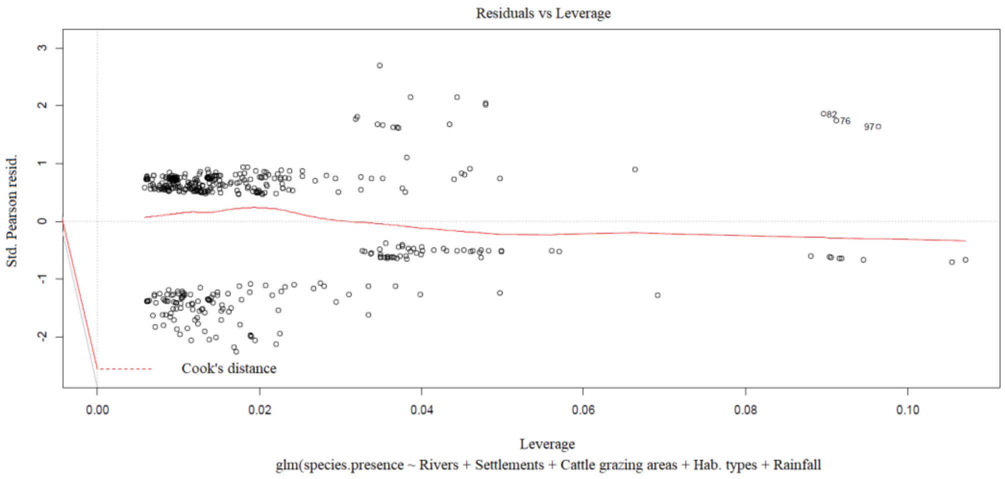

Figure 4.1. Standardized residual values (outliers/leverage points output) plotted from the satured model (Rivers + Settlements + Cattle grazing areas + Habitat types + Rainfall)

4.3. Results

Elephants and buffalos

Elephants were recorded on 177 (38.3%), while buffalos on 117 (25.3%) of the 462 grids. The models yielded a modestly accurate prediction (69.7% and 74.6%) for elephants and buffalos, respectively, which suggests the models' substantial positive and negative discrimination power. Among single predictors separately, habitat types had the most influence on the presence of elephants (79.2%), followed by settlements (11.4%). For buffalos, habitat types were the most influential predictor (73.7%), followed by rainfall (10.4%) and settlements (7.5%). Cattle grazing areas received the worst statistical support from the data in explaining the presence of both species (3.8% and 0.27%, respectively) (Tables 4.2 and 4.3). Lebombo North (LN), Pumbe Sandeveld (LN), and Rugged Veld (RV) were the habitat types positively associated with the prevalence of elephants and buffalos, while Nwambia Sandveld (NS) ($\beta = -2.5$, SE = 0.5, $p = 0.002$ and $\beta = -1.7$, SE = 0.43, $p < 0.001$, respectively) and Shrubveld on Calcrete (SC) ($\beta = -2.0$, SE = 0.5, $p < 0.001$ and $\beta = -1.9$, SE = 0.44, $p < 0.001$, respectively) were negatively associated with the prevalence of both species. The presence of elephants and buffalos was significantly and positively associated with 0 to 5 km ($\beta = 0.9$, SE = 0.46, $p = 0.03$ and $\beta = 1.7$, SE = 0.74, p

= 0.01, respectively) and 5.1 to 10 km (β = 1.2, SE = 0.49, $p = 0.01$ and β = 1.6, SE = 0.78, $p = 0.04$, respectively) from the settlements (Figures 4.2A-C and 4.3A-C). While buffalos were more prevalent in > 450-500 mm areas of average rainfall (β = 0.8, SE = 0.36, $p = 0.03$), the prevalence of elephants was not affected by rainfall (Figures 4.2A-C and 4.3A-C). Nevertheless, the best-fitting model (H-L statistic = 0.14098, df = 3, $p = 0.9865$) for elephants included the additive effects of distance to settlements and habitat types, while for buffalos (H-L statistic = 5.414, df = 6, $p = 0.4919$) included the additive effects of distance to settlements, habitat types, and rainfall (Tables 4.2 and 4.3).

Plains zebras

Zebra occurred on 77 (17%) of the 462 grids. The model yielded a good accurate prediction (93.7%), which suggests a good power of positive and negative discrimination. Amongst the effects of single predictors separately, habitat types received better statistical support from the data in explaining the occurrence of zebra, while settlements and cattle grazing areas were the worst influential predictors of the presence of zebras (Table 4.4). The distribution of zebra was positively and significantly associated with the proximity to rivers: 0 to 5 km and 5.1 to 10 km from the rivers (β = 1.2, SE = 0.37, $p < 0.001$ and β = 1.0, SE = 0.42, $p < 0.01$, respectively), while the distance > 10 km from the rivers was avoided by zebras. Similar to elephants and buffalos, LN, PS, and RV were the habitat types positively associated with the prevalence of zebras, while NS (β = - 5.1, SE = 0.6, $p < 0.001$) and SC (β = - 5.2, SE = 0.7, $p < 0.001$) were avoided by zebras. The presence of zebras was also positively and significantly associated with > 450-500 mm areas of average rainfall (β = 1.8, SE = 0.6, $p = 0.01$). However, 0-450 mm areas of average rainfall were avoided by zebras (Figure 4.4A-C). Nevertheless, the best-fitting model (H-L statistic = 0.0001, df = 5, $p = 1$) was the interaction between habitat types and rainfall (Table 4.4).

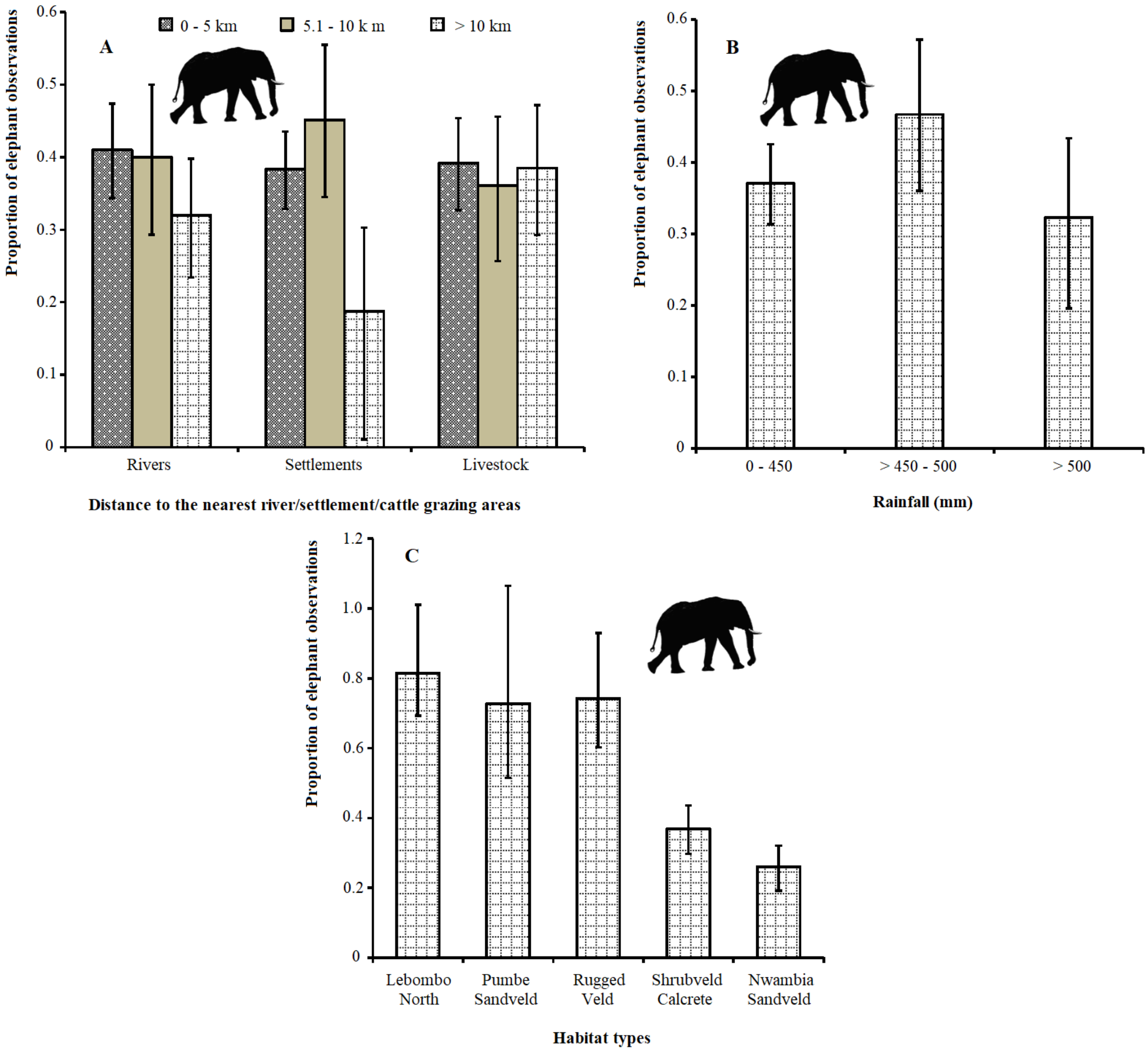

Figure 4.2A-C. Proportion of elephant's presence as a function of distance to rivers, settlements, and cattle grazing areas, habitat types and rainfall. Bars denote 95% binomial confidence intervals.

Greater kudu

Kudus were recorded on 195 (42.2%) of the 462 grids. The model yielded a modest accurate prediction (64%), which suggests the model's substantial positive and negative discrimination power. Amongst single predictors separately, habitat types had the most influence on the presence of kudus (53.2%), followed by rainfall (14.9%), while settlements and cattle grazing areas were the worst influential predictors on the presence of kudus (Table 5.5). The prevalence of kudus was positively associated with the PS, RV, LN, and NS and negatively associated with SC (β = - 1.1, SE = 0.427, *p* = 0.008). The presence of kudus was also positively and significantly associated with 0-450 mm and >

450-500 mm areas of average rainfall ($\beta = 1.8$, SE = 0.39, $p < 0.001$ and $\beta = 1.9$, SE = 0.43, $p < 0.001$, respectively). The distance of 0 to 5 km from the rivers and cattle grazing areas was avoided by kudus ($\beta = - 0.49$, SE = 0.22, $p = 0.02$ and $\beta = - 0.4$, SE = 0.23, $p = 0.07$, respectively) (Figure 4.5A-C). Nevertheless, the best-fitting model (H-L statistic = 1.2165, df = 5, $p = 0.9433$) was the additive effects of habitat types and rainfall (Table 4.5).

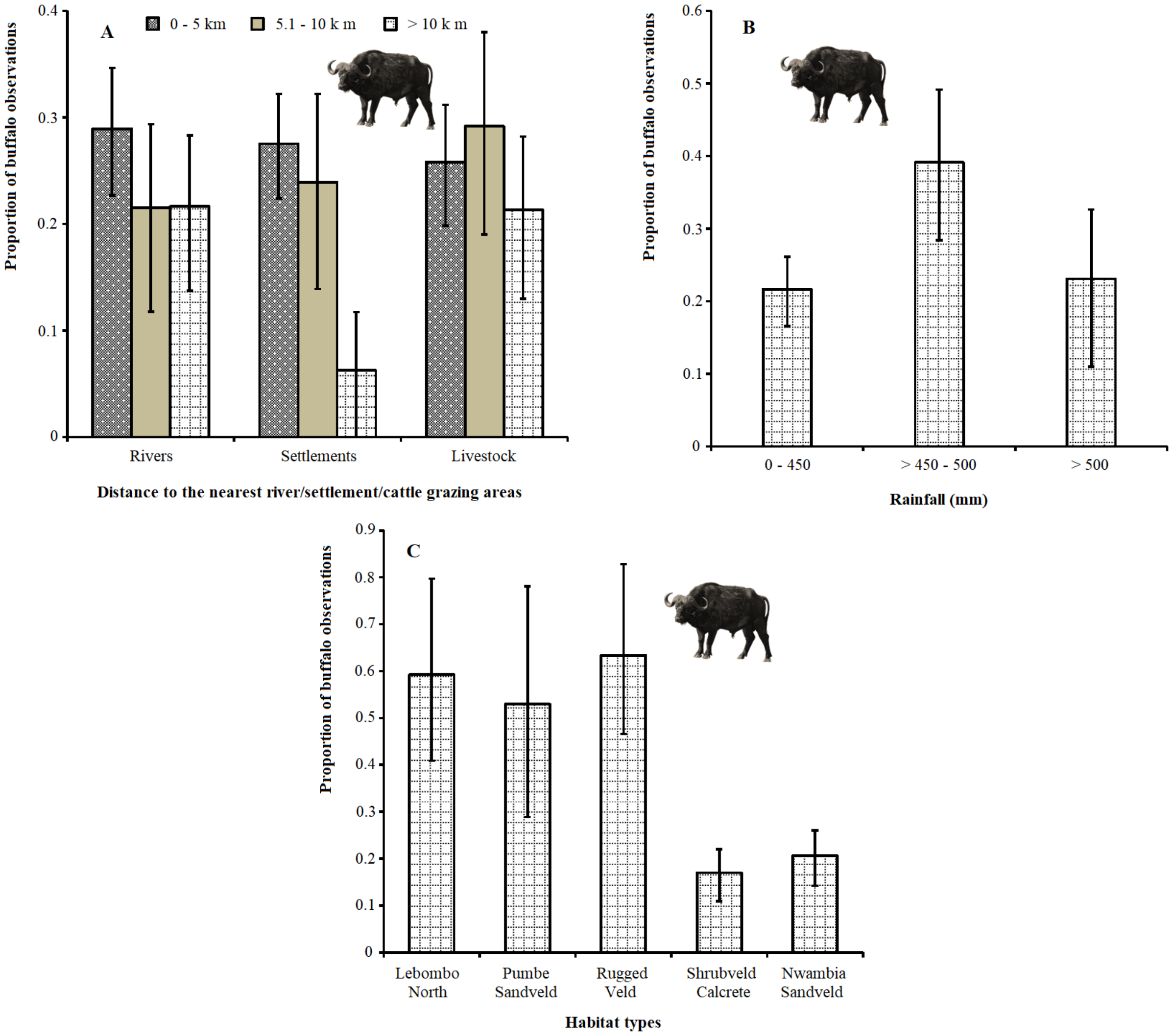

Figure 4.3A-C. Proportion of buffalo's presence as a function of distance to rivers, settlements, and cattle grazing areas, habitat type and rainfall. Bars denote 95% binomial confidence intervals.

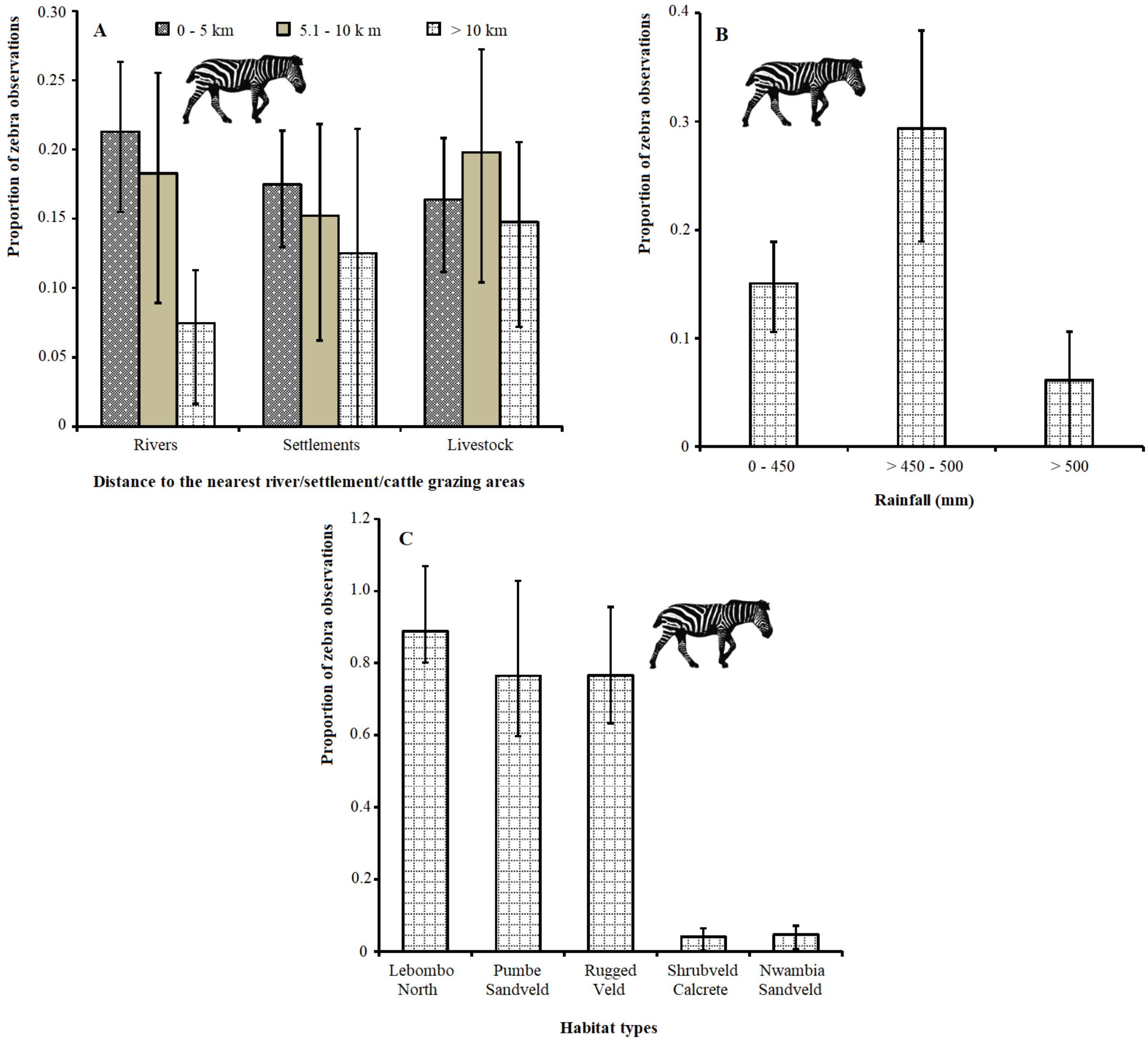

Figure 4.4.A-C. Proportion of zebra's presence as a function of distance to rivers, settlements, and cattle grazing areas, habitat types and rainfall. Bars denote 95% binomial confidence intervals.

Nyala

Nyala was recorded on 209 (45.2%) of the 462 grids. The model yielded a modest accurate prediction (58%), which suggests a substantial power of positive and negative discrimination. Amongst single predictors separately, rainfall received relatively better statistical support from the data in explaining the distribution of nyala (40%), followed by habitat types (34.8) and settlements (12%), while rivers and cattle grazing areas were the worst influential predictors on the presence of nyala (2% and 2.4%, respectively, Table 4.6). The prevalence of nyala was positively associated with PS and RV and negatively associated with SC and NS (β = -0.004 and β = - 0.19, respectively), as also positively associated with 0-450 mm ($\beta = 1.5$, SE = 0.34, $p < 0.001$) and > 450-500 mm ($\beta = 1.5$, SE = 0.38, $p < 0.001$) areas of average rainfall. The presence of nyala was also positively associated with 0 to 5 km from the settlement (Figure 4.6A-C). Nevertheless, the best-fitting model (H-L statistic = 3.3737, df = 7, $p = 0.8484$) included the additive effects of settlements, habitat types, and rainfall (Table 4.6).

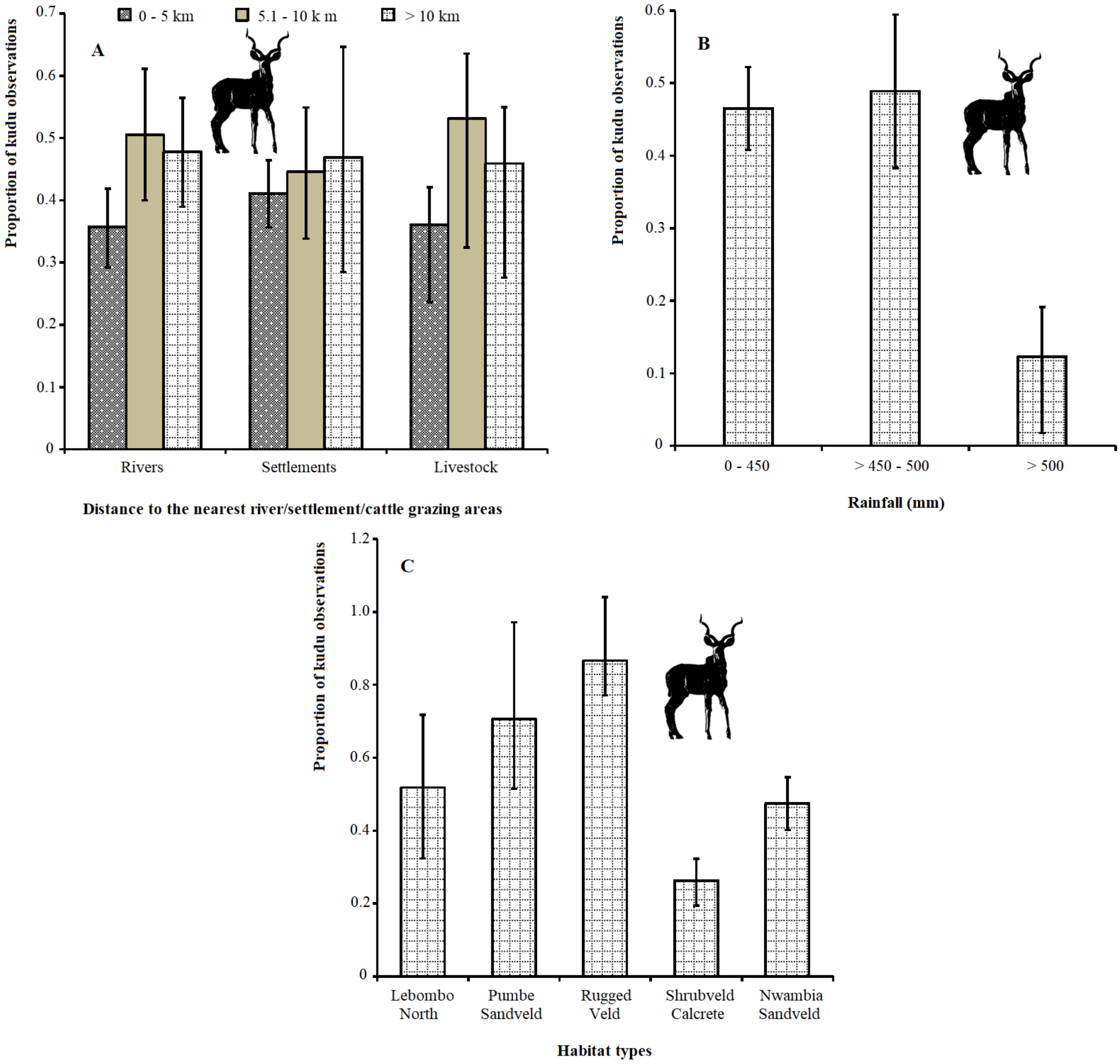

Figure 4.5A-C. Proportion of kudu's presence as a function of distance to rivers, settlements, and cattle grazing areas, habitat types and rainfall. Bars denote 95% binomial confidence intervals.

Impala

Impalas were recorded on 138 (29.8%) of the 462 grids. The model yielded a modest accurate prediction (76.6%), which suggests a substantial power of positive and negative discrimination. Amongst single predictors separately, habitat types had the most influence on the presence of impalas (68.7%), followed by rainfall (10.5%), while settlements (1.27%) and cattle grazing areas (0.14%) were the worst influential predictors on the distribution of impalas (Table 4.7). Similar to elephants, buffalos, and zebras, LN, PS, and RV were the habitat types significantly and positively associated with the prevalence of impalas, while NS ($\beta = -1.2$, SE = 0.42, $p = 0.003$) and SC ($\beta = -1.4$, SE = 0.42, $p = 0.007$) were avoided by impalas. Similar to nyala and kudus, the presence of impalas was also positively and significantly associated with 0-450 mm ($\beta = 1.2$, SE = 0.42, $p = 0.003$) and > 450-500 mm ($\beta = 1.9$, SE = 0.45, $p < 0.001$) areas of average rainfall (Figure 4.7A-C). Nevertheless, the best-fitting model (H-L statistic = 1.7326, df = 5, $p = 0.8848$) included the additive effects of habitat types and rainfall (Table 4.7).

4.4. Discussion

In this study, overall, I predicted that ecological factors (habitat types, rainfall, and perennial rivers) are positively associated with LH distribution, and anthropogenic factors (settlements and cattle grazing areas) have the opposite effect. Habitat types and rainfall were the most influential factors shaping the pattern of LH distribution in the LNP. Indeed, Roque *et al.* (2021) reported strong associations of LH community parameters (species richness, relative abundance index, grazers-browsers-mixed feeder ratio, and naïve occupancy) with habitat types. I found that grazers (buffalos and zebras) and mixed feeders (elephants and impala) were concentrated in the LN, PS, and RV and avoided NS and SC. While nyalas were prevalent in PS and RV and avoided SC, browsers (kudus) were the most widely distributed species occupying LN, PS, RV, and NS and avoided SC. The highest prevalence of almost all species in LN, PS, and RV and avoidance for NS and SC reveal that LHs prefer and select these habitats in the park. LN, PS, and RV cover smaller park surfaces (3.5%, 2.3% and 6.2%, respectively) than SC and NS, which covers 38.8% and 41% of the park surfaces, respectively (Figures 4.S1-S3). According to Krausman (1999), habitat preference occurs when animals spend a high proportion of time in habitats that are not very abundant in the landscape. LN is open-low, short woodland and short grassland savanna, PS is short-low woodland savanna (Stalmans *et al*., 2004) suitable for grazers (buffalos and zebras) and mixed feeders (elephants, nyala, and impalas) (Lamprey, 1963). RV is tall woodland and shrubland savanna suitable for mixed feeders and browsers (kudus) (Lamprey, 1963; Averbeck, 2001).

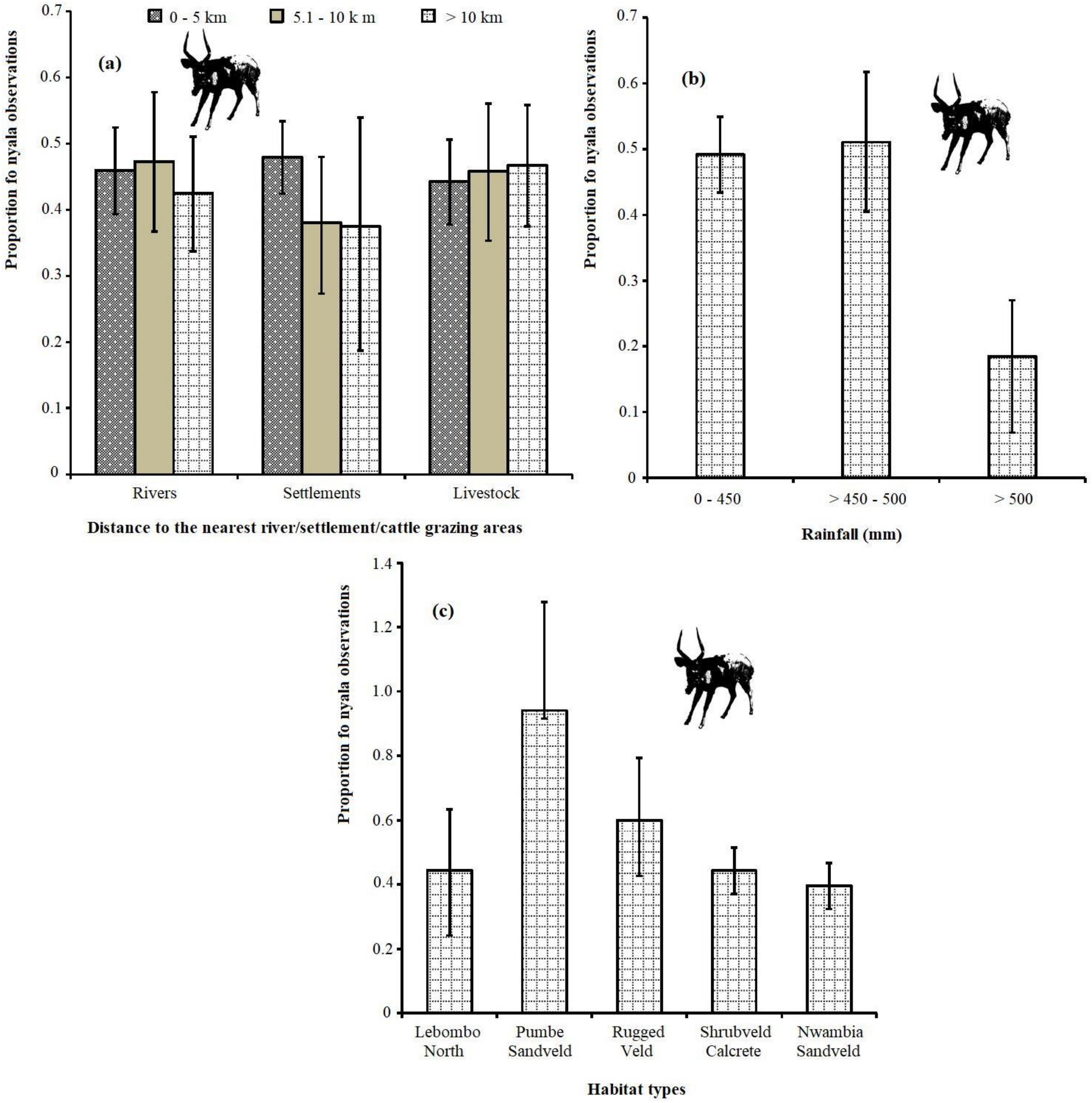

Figure 4.6A-C. Proportion of nyala's presence as a function of distance from rivers, settlements, and cattle grazing areas, habitat types and rainfall. Bars denote 95% binomial confidence intervals.

The preference of LH for LN, PS, and RV can be due to the availability of resources (higher-quality food, water) and conditions (shelter, shade, and safety) that meet the need of these species. Food resources in LN, PS, and RV include average grass biomass of 2,076.5 ± 569.83 kg/ha (Ribeiro *et al*., 2019) of highly nutritious and palatable short to medium grass species, such as *Panicum maximum* and *Urochloa mossambicensis* (Stalmans *et al*., 2004; Mandinyenya *et al*., 2020). *Panicum maximum* provides palatable forage for the buffalos, zebras, nyalas, and impalas until the late dry season (Ryan *et al*., 2006). *Urochloa mosambicensis* provide high nitrogen and phosphorus content and persist under intense utilization (Treydte *et al*., 2013). These habitats also consist of short to medium shrub cover of *Grewia* sp, *Euclea undulata*, and *Commiphora* sp, trees of *Colophospermum mopane*, *Acacia* sp *Sclerocarya birrea*, *Combretum apiculatum*, *Terminalia sericea*, and *Combretum imberbe* with 2 to 3 m height (Stalmans *et al*., 2004; Ribeiro *et al*., 2019) that provide food resources, protection, shade and shelter for LH and are habitat features suitable for mixed-feeder (elephants, nyala, and impalas) and kudus (Lamprey, 1963; Averbeck, 2001). The leaves of *Colophospermum mopane* are feeding alternative sources for elephants and kudus due to their high protein content in young leaves (Ben-Shahar, 1998; Smallie and O'Connor, 2000; Styles and Skinner (2001). Furthermore, LN, PS, and RV are less disturbed habitats because they have fewer human settlements when compared to RV and NS, are inside the Intensive Protection Zone (Dunham, 2004), and are adjacent or crossed by permanent rivers, such as the Shingwedzi and its tributaries, Olifants, and Machampanhe (ANAC, 2022) that may further attract strictly water-dependent species, such as elephants, buffalos, zebras, nyala and impalas. The lack of water in NS and SC (ANAC, 2022) could be a reason that all study species, except kudu, avoided these habitats despite having the highest surface cover, grass biomass (3630.5 ± 298.62 kg/ha and 2968 kg/ha ± 635.63, respectively), and tree height (~4.25 m and ~2.25 m, respectively) (Ribeiro *et al*., 2019). These findings concerning habitat types features concur with Melletti *et al*. (2007); Mandinyenya *et al*. (2020), who reported buffalos' preferences for mixed grassland and open woodland habitat in Zambezi National Park and Central Africa, respectively. Ryan *et al*. (2006) stated that buffalo preferentially select higher-quality food in South Africa. Roque *et al*. (2021, 2022) reported zebra's abundance in LN, PS, and RV instead of NS, and SC. Valls-Fox *et al*. (2018) reported zebras avoiding closed woodland habitats and preferring short or open woodland and open grassland habitats instead in Hwange National. Viljoen *et al*. (2013) reported elephant's preference for *Sclerocarya birrea*, *Vachellia nigrescens*, *Terminalia sericea* and *Combretum apiculatum* in different habitat types (Lebombo bushveld, Mixed bushwillow woodlands, Pretoriuskop sourveld, Delagoa and Sabie thickets) in KNP. Averbeck (2001); Skinner and Chimimba (2005) documented that abundant shade, cover for predators' scape, and nutritious grass and browse in shrubland and woodland savanna are essential for impalas and nyalas.

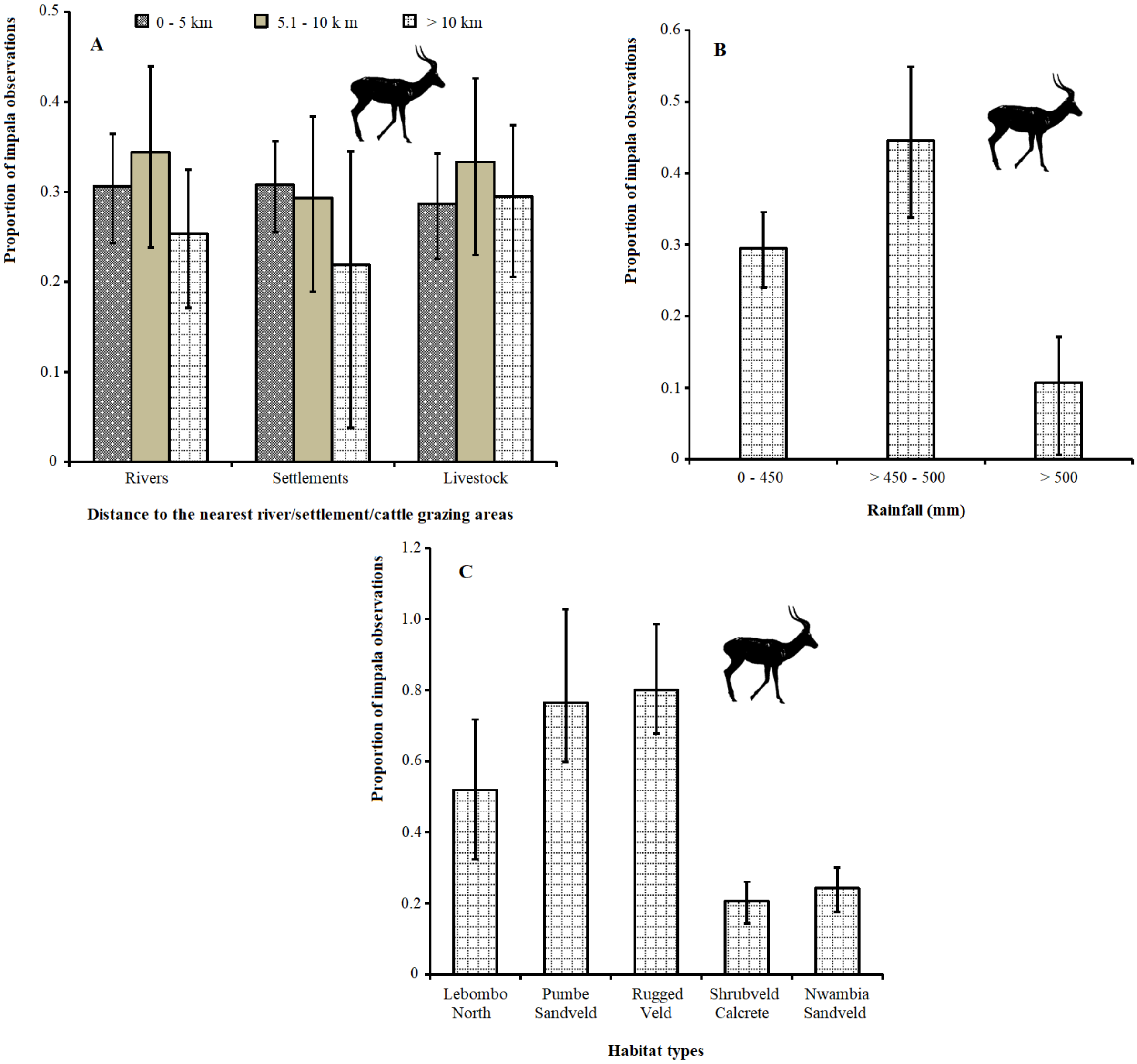

Figure 4.7 A-C. Proportion of impala's presence as a function of distance to rivers, settlements, and cattle grazing areas, habitat types and rainfall. Bars denote 95% binomial confidence intervals.

As predicted, greater kudu was the most widely distributed species in the park. Although kudus prefer dense woodland savanna (Lamprey, 1963), they could be found browsing in open woodland and tall and wooded grassland savanna. Furthermore, according to wildlife censuses by Grossman *et al*. (2014); ANAC (2018), kudu is one of the most abundant wildlife species widely distributed in almost the entire LNP landscape.

Likewise, van Eeden (2006) reported a kudu preference for open and closed woodland in Tembe Elephant Park, South Africa. Fetene *et al*. (2011) documented wider distribution of kudu in open woodland, tall grassland, and wooded grassland in Ethiopia.

Rainfall is also influential in the distribution of all study species in the LNP, except for elephants that were prevalent in low, medium and high areas of average rainfall (0-450 mm, > 450-500 mm, and > 500 mm, respectively). As larger biomass herbivores, elephants are less affected by rainfall because they can cover great distances and manage to use simultaneously high-quality diets in high-quality habitats and tolerate low-quality habitats given that they consume sufficient amounts of biomass (Bell, 1971; Jarman, 1974; le Roux *et al*., 2020).

As predicted, buffalos and zebras avoided low rainfall areas (0-450 mm) because these are of low grass biomass production (Gandiwa *et al*., 2016), preventing larger grazers to obtain enough food. Low rainfall decreases the retention of surface water, which is a key resource for strictly water-dependent grazers (Owen-Smith and Ogutu, 2003). Likewise, Mills *et al*. (1995) reported a negative response of buffalo to low rainfall in the African savanna. As expected, grazers (buffalos and zebras) and mixed feeders (nyala and impala) preferred medium (> 450-500 mm) areas of average rainfall because these areas stimulate high grass biomass production with medium and tall grasses (Gandiwa *et al*., 2016). Furthermore, the medium rainfall areas coincide with the most suitable habitats in the park (LN and PS) with high-quality resources (food and water) and conditions (cover for protection, shelter and shade). These habitats are also the most ecologically preserved without human settlements (Hofmeyr, 2004) and have many anti-poaching control posts (Grossman *et al*., 2014), providing undisturbed habitat patches that can be viewed as high-quality habitats. Similarly, Roque *et al*. (2021) reported high impalas, nyalas, buffalos, and zebras proportion and significantly higher capture frequency in LN and PS than in NS and SC, which coincide with medium rainfall areas. Macandza *et al*. (2004); Musiega *et al*. (2006) reported zebra and buffalos preferred to graze in habitats with medium and tall grasses, respectively. Contrary to expectation, mixed feeders (impalas and nyalas) were prevalent in low (0-450 mm) areas of average rainfall, possibly due to the availability of some shrub leaves and twigs for some time in the dry season. As expected, browsers (kudus) were prevalent in low and medium rainfall areas (0-450 mm and > 450-500 mm, respectively). Browsers and mixed feeders appeared to be least affected by low and medium rainfall (Owen-Smith and Ogutu, 2003), possibly due to the availability of some browsing resources for some time in the dry season (Owen-Smith and Ogutu, 2003; Gandiwa *et al*., 2016). Similarly, Owen-Smith and Ogutu (2003) reported mixed feeders being less affected by rainfall fluctuation in the KNP. Shrader *et al*. (2010); Gandiwa *et al*. (2016) reported browsers being less affected by the lowest rainfall than grazers in the African savanna. Except for elephants, the rest of the species do not have access to the area of high rainfall mean (> 500 mm) because it is fenced to avoid human-wildlife conflicts. Elephants break through the fence, enter the area, and create gaps that serve as an entrance for other species in the buffer zone, increasing human-wildlife conflict risks.

As predicted, I found zebra distribution close to perennial water sources (0-5 km and 5.1-10 km) because zebras are strictly water-dependent species (Western, 1975; Estes, 2012). However, the occurrence of zebras declined with increasing distance from the river (> 10 km) as the distance from the most suitable habitats (LN, PS, and RV) increased, revealing a common effect between habitat types and water sources in the prevalence of zebras. Similarly, Redfern *et al*. (2003) reported zebras closer to surface water than would be expected in KNP, a savanna ecosystem similar to LNP. Cain *et al*. (2012) reported zebras' water source visits to drink at 1-2 days intervals in the KNP. As predicted, browsers (kudus) avoided areas close to perennial water sources (0-5 km), possibly because they are browsers less strictly water-dependent (Skinner and Chimimba, 2005; Estes, 2012). Furthermore, they may have felt unsafe in these areas due to potential predation risk and human pressure along Shingwedzi Valley. The prevalence of kudus was not affected at 5.1-10 and > 10 km to rivers. These findings concur with other studies where kudu distribution patterns were characterized by a weak relationship with distance close to water (Redfern *et al*., 2003). However, the findings are contrary to de Leeuw *et al*. (2001); Smit *et al*. (2007); Muposhi et al. (2016b), who documented the prevalence of kudus declining with increasing distance from the river.

The influence of settlements in the LNP showed interesting patterns. It seems that some species (zebras, kudus, and impalas) tended to avoid settlements, while others (elephants, buffalos and nyala) seemed to be attracted to settlements. This is contrary to previous studies (Hoare and du Toit, 1999; Harris *et al*., 2008; Jackson *et al*., 2008; Graham *et al*., 2009; Atickem and Loe, 2013; Selier *et al*., 2015; Muposhi *et al*., 2016b) that reported elephants, buffalos, and nyala avoiding areas close to human settlements.

However, looking more closely (Figures 4.S1-S3), it appears that these species are not attracted to settlements as a whole but to some settlements along the Shingwedzi Valley. The reasons behind this behaviour could be:

(i) The proximity of Shingwedzi Valley villages to the most suitable habitats and Intensive Protection Zone (IPZ) in the LNP: the high-quality habitats in the park (LN, PS, and RV) for grazers and mixed feeders are around Shingwedzi Valley. All Lebombo North extension and part of the Pumbe and Rugged Veld area are inside IPZ with many anti-poaching control posts (Grossman *et al.*, 2014) and where people movements, flora resources extraction, poaching, and cattle grazing are forbidden (PNL, 2012). This provides security for wildlife, including species with a lower body mass, such as nyala.

(ii) Competition for resources (food, water) and space: most of the villages in the LNP are along major river systems (Limpopo, Shingwedzi and Olifants Rivers) (ANAC, 2022). As the people and wildlife increase, they share the same landscape and compete for the same resources and space in the peak of dry seasons (Dunham *et al*., 2010), when food and water resources are depleted and scarcity (Owen-Smith *et al.*, 2010; Cornélis *et al.*, 2011), leading to increased human-wildlife conflict risks. This is more likely to occur in the villages of the Shingwedzi Valley (western border) than on the Limpopo River (eastern side), where human settlement and activities prevent LH species access to seasonally valuable resources. Likewise, Stoldt *et al*. (2020) reported an increase in elephants and buffalos in the Kavango-Zambezi Transfrontier Conservation Area (Namibia) over the previous decades that caused increases in crop damage.

(iii) Crops as alternative resources for wildlife: the Shingwedzi and Olifants Rivers areas are fertile and allow communities to grow crops (Milgroom and Spierenburg, 2008; Bazin *et al*., 2016) even at the peak of the dry season. This may attract LH because crops may represent alternative food resources at the end of the dry season (September to October). Coincidentally, the wildlife censuses recorded elephants, buffalos and nyala around Swingwedzi villages at the peak of the dry season. Likewise, Cook *et al*. (2015) reported the highest proportion of elephants close to settlements in the dry season in the same study area. Milgroom and Spierenburg (2008); Witter (2013) reported crop raiding by elephants and buffalos around villages in the Shingwedzi Valley.

(iv) The balance between population density and wildlife pressure along Shingwedzi Valley and Limpopo River: About 22,748 people with 38,280 heads of cattle live in the buffer zone, and the remaining 7,252 people with 9,600 heads of cattle live in the central area (Shingwedzi Valley) of the park sharing grazing and natural water sources with wildlife (ANAC, 2022). Wildlife pressure through fragmentation of the natural areas and bush meat poaching (illegal hunting of wildlife for local consumption) in Shingwedzi Valey (western boundary) is relatively controlled compared to the Limpopo River area (eastern boundary) (Lunstrum, 2014). Furthermore, there is a lack of access to the Limpopo River for wildlife. Thus, elephants, buffalos, and nyala appeared to maintain coexistence with people in Shingwedzi Valley because this area (western boundary) is secure while the Limpopo River and linkages of the parks to the East and North are not (ANAC, 2022). Probably, these species maintain coexistence with people adopting different daytime and night-time behaviour, increasing their rate of movement at night (Douglas-Hamilton *et al*., 2005) and leaving areas entirely when human presence reaches a certain threshold during daytime (Hoare and du Toit, 1999). These species may overlap with people in space but not in time (Cook *et a*l., 2015). It allows these species to invade smallholder farmland to raid crops. The findings of Graham *et al*. (2009), in which elephants facultatively alter their behaviour to avoid risk in human-dominated landscapes in Kenya, corroborate this result. Studies conducted by Harris *et al*. (2008) in Maputo Elephant Reserve (Mozambique) reported distances from human settlements as the best predictor for elephants. Harris' results highlighted that bulls were more attracted to settlements. Cook *et al*. (2015) reported a higher proportion of elephants in the 0-2 and 2-4 km from settlements in the LNP during the evening-midnight period than in the other periods in the dry season.

Unfortunately, in human-dominated landscapes wildlife and people do not always coexist peacefully. According to Dunham *et al*. (2010), six elephants were shot within the LNP between 2006 and 2008 as a consequence of human-wildlife conflict. Conflicts with buffalos were reported mainly from central or southern Mozambique, with a high incidence in districts adjacent to KNP. Many studies revealed that the way elephants use the areas surrounding villages depends on their spatial and temporal knowledge of human activities, such as when crops represent alternative food sources, humans are least active or how humans react to their presence (Hoare and du Toit, 1999; Douglas-Hamilton *et al*., 2005; Graham *et al*., 2009; Cook *et al*., 2015). Although people resettlement in the LNP buffer zone is in progress, there are still reports of human-wildlife conflicts. Indeed, the results of the present study clearly showed an occurrence of species such as elephants and buffalo likely to create more severe human-wildlife conflicts near human resettlements. Therefore, there is a need to improve the future management of elephants and other wildlife and their interactions with humans and the ecosystem in the LNP.

I acknowledge that there could be a scale effect in the patterns of results shown in this study. Certain relationships or patterns of LH distribution may fail to be seen at a coarse spatial scale because they would occur at finer spatial scales. Foraging behaviour within the patches influences the distribution of LH at broader scales (Owen-Smith *et al*., 2010) because, at this scale, the LH decision is where to be within the landscape, while on the finer spatial scale, the decision is on how to utilize the local resources (Murwira and Skidmore, 2005). Non-food resources (water, shelter, salt licks) and protection from predators are highly localized on the landscapes, but forage resources are dispersed. Water is often concentrated at discrete locations, and selection for watering points occurs less frequently than the selection for dietary reasons or plant communities. The West LNP is hilly and crossed by seasonal rivers (ANAC, 2022). Because water and nutrients accumulate at a finer scale, i.e. in valley slopes and small depressions, these areas can serve as nutrient hotspots attracting a variety of herbivores due to the higher biomass and forage quality availability (Bergman *et al*., 2001, Grant and Scholes 2006).

The study findings reveal that, although with the selection of some categories within the predictors, ecological factors (rivers, habitat types, and rainfall) seem to play a crucial role in the occurrence of LH in the LNP. Large herbivores with lower body mass avoided settlements, except nyala. Habitats without or with few anthropogenic disturbances, such as Lebombo North, Pumbe Sandveld, and Rugged Veld, are also found to have suitable resources (food) and conditions (shelter, protection) that allow for a wider distribution of LH. These resources and conditions appear to be linked to low (0-450 mm) and medium (> 450-500 mm) average rainfall. The results highlight the importance of understanding the ecological and anthropogenic factors in African savanna ecosystems as tools for the adaptive management of species and their habitats because they showed how these factors influence the species occurrence. People resettlement issues to avoid human-wildlife conflicts and conservation of priority habitats for the most vulnerable species can be better managed. As this study generated distribution patterns of LH based on a likelihood of a species occurrence in a grid according to resources and conditions available, its results may be used to assess future species distribution changes in the landscape. Furthermore, the maps showing concentration areas of LH will allow making management decisions about locations or habitats to prioritize when conserving target species. The results can also serve as a conservation planning and management tool in LNP and other Protected Areas in Mozambique. As many Sub-Saharan savannas in Africa are also human-dominated landscapes, the relationship among the villages’ location, cattle grazing areas and the distribution of LH can be better understood to mitigate human-wildlife conflicts.

Table 4.2. All subset models comparison statistics for ecological (rivers, habitat types, and rainfall) and anthropogenic (settlements and cattle grazing areas) factors influencing the distribution of elephants

Model ranking	Models structure	CA (%)	LRT	K	AIC	ΔAIC	AIC weight (w_m)	Relative likelihood
01	Settlements + Habitat types	0.97	0.28	7	559.7	0	0.304	1.000
02	Rivers + Settlements + Habitat types	-1.71	0.38	9	560.4	0.7	0.214	0.705
03	Settlements + Cattle grazing areas + Habitat types	0.33	0.27	9	561.4	1.7	0.130	0.427
04	Rivers + Settlements + Cattle grazing areas + Habitat types	-0.30	0.47	11	561.8	2.1	0.106	0.350
05	Settlements + Habitat types + Rainfall	0.08	0.17	9	562.7	3	0.068	0.223
06	Rivers + Settlements + Habitat types + Rainfall	0.19	0.19	11	563.5	3.8	0.045	0.150
07	Settlements + Cattle grazing areas + Habitat types + Rainfall	0.19	0.15	11	564	4.3	0.035	0.116
08	Rivers + Settlements + Cattle grazing areas + Hab. types + Rainfall	-0.26	0.00	13	564.3	4.6	0.030	0.100
09	Rivers + Habitat types	3.81	0.04	7	565.1	5.4	0.020	0.067
10	Habitat types	73.92	0.03	5	565.1	5.4	0.020	0.067
11	Cattle grazing areas + Habitat types	0.63	0.01	7	567.7	8	0.006	0.018
12	Habitat types + Rainfall	3.38	0.01	7	567.7	8	0.006	0.018
13	Rivers + Habitat type + Rainfall	0.97	0.02	9	567.9	8.2	0.005	0.017
14	Rivers + Cattle grazing areas + Habitat types	-1.15	0.01	9	568	8.3	0.005	0.016
15	Habitat types x Rainfall	---	0.007	12	569.4	9.7	0.002	0.008
16	Cattle grazing areas + Habitat types + Rainfall	1.21	0.007	9	570.3	10.6	0.002	0.005
17	Rivers + Cattle grazing areas + Habitat types + Rainfall	-1.89	0.006	11	570.3	10.6	0.002	0.005
18	Rivers + Settlements + Rainfall	-0.10	0.00	7	609.3	49.6	0.000	0.000
19	Rivers + Settlements	0.14	0.00	5	609.3	49.6	0.000	0.000
20	Settlements	11.43	0.00	3	609.6	49.6	0.000	0.000
21	Rivers + Settlements + Cattle grazing areas	0.58	0.00	7	609.7	50	0.000	0.000
22	Rivers + Settlements + Cattle grazing areas + Rainfall	0.17	0.00	9	610	50.3	0.000	0.000
23	Settlements + Rainfall	0.13	0.00	5	610.1	50.4	0.000	0.000
24	Settlements + Cattle grazing areas + Rainfall	0.21	0.00	7	612.2	52.5	0.000	0.000
25	Settlements + Cattle grazing areas	-1.98	0.00	5	612.5	52.8	0.000	0.000
26	Rivers x Settlements	---	0.00	9	612.6	52.9	0.000	0.000
27	Rainfall	1.96	0.00	3	613.2	53.5	0.000	0.000

28	Rivers + Rainfall	-0.11	0.00	5	613.5	53.8	0.000	0.000
29	Rivers	4.53	0.00	3	613.9	54.2	0.000	0.000
30	Rivers x Settlements + Rivers x Cattle grazing areas	---	0.00	15	614.4	54.7	0.000	0.000
31	Settlements x Cattle grazing areas	-1.98	0.00	8	614.7	55	0.000	0.000
32	Rivers + Cattle grazing areas	-0.64	0.00	5	615.4	55.7	0.000	0.000
33	Rivers + Cattle grazing areas + Rainfall	0.35	0.00	7	615.5	55.8	0.000	0.000
34	Cattle grazing areas + Rainfall	-0.81	0.00	5	616.4	56.7	0.000	0.000
35	Cattle grazing areas	3.77	0.00	3	616.9	57.2	0.000	0.000
36	Rivers x Settlements x Cattle grazing areas	---	0.00	21	621.1	61.4	0.000	0.000
37	Rivers x Cattle grazing areas	---	0.00	9	621.3	61.6	0.000	0.000

CA – Commonality Analysis, LRT – Likelihood Ratio Test, K – Number of parameters, AIC – Akaike Information Criteria, ΔAIC – Delta AIC. The ranking of the models were based on AIC. Plus signs (+) imply additive terms in the model. Times signs (x) impiesy interactions among variables.

Table 4.3. All subset models comparison for ecological (rivers, habitat types, and rainfall) and anthropogenic (settlements and cattle grazing areas) factors influencing the distribution of buffalos

Model ranking	Models structure	CA (%)	LRT	K	AIC	ΔAIC	AIC weight (w_m)	Relative likelihood
01	Settlements + Habitat types + Rainfall	-0.93	0.81	9	472.6	0	0.565	1.000
02	Rivers + Settlements + Habitat types + Rainfall	0.50	0.86	11	475.3	2.7	0.147	0.259
03	Settlements + Cattle grazing areas + Habitat types + Rainfall	-0.41	0.53	11	476.2	3.6	0.093	0.165
04	Settlements + Habitat types	-2.12	0.12	7	476.9	4.3	0.066	0.116
05	Habitat types + Rainfall	2.43	0.11	7	477.4	4.8	0.051	0.091
06	Rivers + Settlements + Cattle grazing areas + Hab. types + Rainfall	0.28	0.00	13	478.9	6.3	0.024	0.043
07	Rivers + Settlements + Habitat types	1.46	0.06	9	479.9	7.3	0.015	0.026
08	Rivers + Habitat type + Rainfall	0.69	0.06	9	480.2	7.6	0.013	0.022
09	Settlements + Cattle grazing areas + Habitat types	-0.90	0.04	9	480.7	8.1	0.010	0.017
10	Cattle grazing areas + Habitat types + Rainfall	0.66	0.04	9	480.9	8.3	0.009	0.016
11	Rivers + Cattle grazing areas + Habitat types + Rainfall	-0.14	0.01	11	483.4	10.8	0.003	0.005
12	Rivers + Settlements + Cattle grazing areas + Habitat types	0.86	0.01	11	483.7	11.1	0.002	0.004

13	Habitat types	73.74	0.007	5	483.8	11.2	0.002	0.004
14	Rivers + Habitat types	-0.23	0.003	7	486.6	14	0.001	0.001
15	Rivers + Cattle grazing areas + Habitat types	-0.34	0.001	9	489.3	16.7	0.000	0.000
16	Settlements + Rainfall	2.20	0.00	5	514.7	42.1	0.000	0.000
17	Rivers + Settlements + Rainfall	0.16	0.00	7	517.8	45.2	0.000	0.000
18	Settlements + Cattle grazing areas + Rainfall	0.39	0.00	7	517.8	45.2	0.000	0.000
19	Rainfall	10.40	0.00	3	518	45.4	0.000	0.000
20	Rivers + Rainfall	-0.25	0.00	5	519.6	47	0.000	0.000
21	Settlements	7.52	0.00	3	519.9	47.3	0.000	0.000
22	Rivers + Settlements + Cattle grazing areas + Rainfall	0.21	0.00	9	520.7	48.1	0.000	0.000
23	Cattle grazing areas + Rainfall	-0.05	0.00	5	520.8	48.2	0.000	0.000
24	Rivers + Cattle grazing areas + Rainfall	-0.07	0.00	7	522.5	49.8	0.000	0.000
25	Settlements + Cattle grazing areas	0.96	0.00	5	522.7	50.1	0.000	0.000
26	Rivers + Settlements	0.14	0.00	5	522.9	50.3	0.000	0.000
27	Rivers + Settlements + Cattle grazing areas	-0.50	0.00	7	525.3	52.7	0.000	0.000
28	Rivers	1.77	0.00	3	525.6	53	0.000	0.000
29	Cattle grazing areas	0.27	0.00	3	527	54.4	0.000	0.000
30	Rivers + Cattle grazing areas	0.01	0.00	5	528	55.4	0.000	0.000
31	Habitat types x Rainfall	---	0.007	12	569.4	96.8	0.000	0.000
32	Cattle grazing areas + Habitat types	1.28	0.003	7	586.8	114.2	0.000	0.000
33	Rivers x Settlements	---	0.00	9	612.6	140	0.000	0.000
34	Rivers x Settlements + Rivers x Cattle grazing areas	---	0.00	15	614.4	141.8	0.000	0.000
35	Settlements x Cattle grazing areas	---	0.00	8	614.7	142.1	0.000	0.000
36	Rivers x Settlements x Cattle grazing areas	---	0.00	21	621.1	148.5	0.000	0.000
37	Rivers x Cattle grazing areas	---	0.00	9	621.3	148.7	0.000	0.000

CA – Commonality Analysis, LRT – Likelihood Ratio Test, K – Number of parameters, AIC – Akaike Information Criteria, ΔAIC – Delta AIC. The ranking of the models were based on AIC. Plus signs (+) imply additive terms in the model. Times signs (x) imply interactions among variables.

Table 4.4. All subset models comparison statistics for ecological (rivers, habitat types, and rainfall) and anthropogenic (settlements and cattle grazing areas) factors influencing the distribution of zebras

Model ranking	Models structure	CA (%)	LRT	K	AIC	ΔAIC	AIC weight (w_m)	Relative likelihood
01	Habitat types x Rainfall	---	0.4	12	217.4	0	0.537	1.000
02	Habitat types	87.34	0.43	5	219.5	2.1	0.188	0.350
03	Habitat types + Rainfall	5.62	0.54	7	220.5	3.1	0.114	0.212
04	Cattle grazing areas + Habitat types	0.33	0.4	7	221.7	4.3	0.063	0.116
05	Rivers + Habitat types	5.75	0.38	7	221.8	4.4	0.059	0.111
06	Settlements + Habitat types	-0.07	0.29	7	222.8	5.4	0.036	0.067
07	Rivers + Settlements + Cattle grazing areas + Hab. types + Rainfall	-0.25	0.38	13	227.5	10.1	0.003	0.006
08	Rivers + Rainfall	0.03	0.00	5	394.4	177	0.000	0.000
09	Rivers x Settlements	---	0.00	9	404.9	187.5	0.000	0.000
10	Rainfall	0.36	0.00	3	406.1	188.7	0.000	0.000
11	Rivers + Cattle grazing areas	-0.03	0.00	5	407.8	190.4	0.000	0.000
12	Rivers	0.37	0.00	3	408.9	191.5	0.000	0.000
13	Settlements + Rainfall	0.06	0.00	5	409.3	191.9	0.000	0.000
14	Cattle grazing areas + Rainfall	0.01	0.00	5	409.4	192	0.000	0.000
15	Rivers x Settlements + Rivers x Cattle grazing areas	---	---	15	410.9	193.5	0.000	0.000
16	Rivers + Settlements	-0.09	0.00	5	411.1	193.7	0.000	0.000
17	Rivers x Cattle grazing areas	---	0.00	9	412.6	195.2	0.000	0.000
18	Cattle grazing areas	0.38	0.00	3	421.3	203.9	0.000	0.000
19	Settlements	0.26	0.00	3	421.6	204.2	0.000	0.000
20	Rivers x Settlements x Cattle grazing areas	---	---	25	422.2	204.8	0.000	0.000
21	Settlements + Cattle grazing areas	-0.08	0.00	5	424.6	207.2	0.000	0.000
22	Settlements x Cattle grazing areas	---	0.00	9	425.8	208.4	0.000	0.000
23	Settlements + Habitat types + Rainfall	-0.07	0.81	9	472.6	255.2	0.000	0.000
24	Rivers + Settlements + Habitat types + Rainfall	0.12	0.86	11	475.3	257.9	0.000	0.000
25	Settlements + Cattle grazing areas + Habitat types + Rainfall	0.15	0.53	11	476.2	258.8	0.000	0.000
26	Rivers + Settlements + Habitat types	0.06	0.06	9	479.9	262.5	0.000	0.000
27	Rivers + Habitat type + Rainfall	-0.10	0.05	9	480.2	262.8	0.000	0.000

28	Settlements + Cattle grazing areas + Habitat types	0.32	0.04	9	480.7	263.3	0.000	0.000
29	Cattle grazing areas + Habitat types + Rainfall	0.95	0.04	9	480.9	263.5	0.000	0.000
30	Rivers + Cattle grazing areas + Habitat types + Rainfall	-0.75	0.01	11	483.4	266	0.000	0.000
31	Rivers + Settlements + Cattle grazing areas + Habitat types	-0.12	0.01	11	483.7	266.3	0.000	0.000
32	Rivers + Cattle grazing areas + Habitat types	-0.53	0.001	9	489.3	271.9	0.000	0.000
33	Rivers + Settlements + Rainfall	-0.02	0.00	7	517.8	300.4	0.000	0.000
34	Settlements + Cattle grazing areas + Rainfall	-0.02	0.00	7	517.8	300.4	0.000	0.000
35	Rivers + Settlements + Cattle grazing areas + Rainfall	-0.01	0.00	9	520.7	303.4	0.000	0.000
36	Rivers + Cattle grazing areas + Rainfall	0.02	0.00	7	522.5	305.1	0.000	0.000
37	Rivers + Settlements + Cattle grazing areas	0.00	0.00	7	525.3	307.9	0.000	0.000

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Table 4.5. All subset models comparison statistics for ecological (rivers, habitat types, and rainfall) and anthropogenic (settlements and cattle grazing areas) factors influencing the distribution of kudu

Model ranking	**Models structure**	**CA (%)**	**LRT**	**K**	**AIC**	**ΔAIC**	**AIC weight (w_m)**	**Relative likelihood**
01	Habitat types + Rainfall	12.19	0.35	7	568.3	0	0.340	1.000
02	Rivers + Habitat type + Rainfall	-0.23	0.46	9	569.3	1	0.206	0.607
03	Cattle grazing areas + Habitat types + Rainfall	2.74	0.34	9	570.2	1.9	0.132	0.387
04	Settlements + Habitat types + Rainfall	-0.12	0.23	9	571.3	3	0.076	0.223
05	Rivers + Settlements + Habitat types + Rainfall	0.16	0.41	11	571.4	3.1	0.072	0.212
06	Rivers + Cattle grazing areas + Habitat types + Rainfall	1.02	0.4	11	571.5	3.2	0.069	0.202
07	Habitat types x Rainfall	---	---	12	572.3	4	0.046	0.135
08	Settlements + Cattle grazing areas + Habitat types + Rainfall	0.08	0.19	11	572.9	4.6	0.034	0.100
09	Rivers + Settlements + Cattle grazing areas + Hab. types + Rainfall	1.62	0.00	13	573.7	5.4	0.023	0.067
10	Rivers + Habitat types	1.48	0.002	7	581.6	13.3	0.000	0.001
11	Rivers + Cattle grazing areas + Habitat types	0.21	0.002	9	581.9	13.6	0.000	0.001
12	Cattle grazing areas + Habitat types	0.34	0.002	7	582.1	13.8	0.000	0.001

13	Habitat types	53.15	0.001	5	583.5	15.2	0.000	0.001
14	Rivers + Settlements + Cattle grazing areas + Habitat types	0.11	0.0006	11	584.2	15.9	0.000	0.000
15	Rivers + Settlements + Habitat types	-0.04	0.0008	9	584.4	16.1	0.000	0.000
16	Settlements + Cattle grazing areas + Habitat types	-0.37	0.0005	9	585.3	17	0.000	0.000
17	Settlements + Habitat types	-0.68	0.0002	7	587.4	19.1	0.000	0.000
18	Rivers + Rainfall	1.79	0.00	5	602.9	34.6	0.000	0.000
19	Rainfall	14.85	0.00	3	603.4	35.1	0.000	0.000
20	Cattle grazing areas + Rainfall	2.82	0.00	5	605.2	36.9	0.000	0.000
21	Rivers + Cattle grazing areas + Rainfall	1.61	0.00	7	605.4	37.1	0.000	0.000
22	Rivers + Settlements + Rainfall	-0.32	0.00	7	606	37.7	0.000	0.000
23	Settlements + Rainfall	-0.11	0.00	5	607.2	38.9	0.000	0.000
24	Rivers + Settlements + Cattle grazing areas + Rainfall	0.03	0.00	9	608.2	39.9	0.000	0.000
25	Settlements + Cattle grazing areas + Rainfall	-0.63	0.00	7	608.6	40.3	0.000	0.000
26	Rivers + Cattle grazing areas	0.70	0.00	5	625.4	57.1	0.000	0.000
27	Cattle grazing areas	2.30	0.00	3	626.1	57.8	0.000	0.000
28	Rivers	4.14	0.00	3	626.8	58.5	0.000	0.000
29	Settlements x Cattle grazing areas	---	0.00	9	627.8	59.5	0.000	0.000
30	Rivers + Settlements + Cattle grazing areas	-0.19	0.00	7	628.4	60.1	0.000	0.000
31	Rivers x Settlements	---	0.00	9	629.8	61.5	0.000	0.000
32	Settlements + Cattle grazing areas	-0.08	0.00	5	629.8	61.5	0.000	0.000
33	Rivers + Settlements	-0.83	0.00	5	630.6	62.3	0.000	0.000
34	Rivers x Cattle grazing areas	---	0.00	9	632.5	64.2	0.000	0.000
35	Rivers x Settlements + Rivers x Cattle grazing areas	---	---	15	632.8	64.5	0.000	0.000
36	Rivers x Settlements x Cattle grazing areas	---	---	25	632.8	64.5	0.000	0.000
37	Settlements	2.25	0.00	3	634.5	66.2	0.000	0.000

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Table 4.6. All subset models comparison statistics for ecological (rivers, habitat types, and rainfall) and anthropogenic (settlements and cattle grazing areas) factors influencing the distribution of nyala

Model ranking	Models structure	CA (%)	LRT	K	AIC	ΔAIC	AIC weight (w_m)	Relative likelihood
01	Settlements + Habitat types + Rainfall	1.08	0.64	9	602.2	0	0.419	1.000
02	Habitat types + Rainfall	11.30	0.27	7	603.3	1.1	0.242	0.577
03	Settlements + Cattle grazing areas + Habitat types + Rainfall	-1.05	0.53	11	604.9	2.7	0.109	0.259
04	Rivers + Settlements + Habitat types + Rainfall	-0.49	0.51	11	605	2,8	0.103	0.247
05	Rivers + Habitat types + Rainfall	-2.74	0.14	9	606.6	4.4	0.046	0.111
06	Cattle grazing areas + Habitat types + Rainfall	0.07	0.12	9	606.9	4.7	0.040	0.095
07	Rivers + Settlements + Cattle grazing areas + Hab. types + Rainfall	-3.28	0.00	13	607.7	5.5	0.027	0.064
08	Rivers + Cattle grazing areas + Habitat types + Rainfall	-2.49	0.04	11	610.1	7.9	0.008	0.019
09	Habitat types x Rainfall	---	0.01	12	611.6	9.4	0.004	0.009
10	Settlements + Rainfall	-2.27	0.005	5	613.37	11.17	0.002	0.004
11	Rivers + Settlements + Rainfall	-1.48	0.001	7	616.8	14.6	0.000	0.001
12	Settlements + Cattle grazing areas + Rainfall	-1.84	0.001	7	617	14.8	0.000	0.001
13	Rivers + Rainfall	1.98	0.0008	5	618.4	16.2	0.000	0.000
14	Rainfall	40.07	0.0006	3	618.4	16.2	0.000	0.000
15	Rivers + Settlements + Cattle grazing areas + Rainfall	-1.34	0.0004	9	620.1	17.9	0.000	0.000
16	Cattle grazing areas + Rainfall	4.14	0.0003	5	620.7	18.5	0.000	0.000
17	Rivers + Cattle grazing areas + Rainfall	2.86	0.0001	7	621.9	19.7	0.000	0.000
18	Habitat types	34.81	0.0001	5	622.2	20	0.000	0.000
19	Settlements + Cattle grazing areas + Habitat types	1.02	0.00	9	623.8	21.6	0.000	0.000
20	Cattle grazing areas + Habitat types	-1.12	0.00	7	623.9	21.7	0.000	0.000
21	Rivers + Habitat types	-0.17	0.00	7	624.4	22.2	0.000	0.000
22	Settlements + Habitat types	-0.47	0.00	7	624.6	22.4	0.000	0.000
23	Rivers + Settlements + Habitat types	4.27	0.00	9	624.9	22.7	0.000	0.000
24	Rivers + Settlements + Cattle grazing areas + Habitat types	3.29	0.00	11	625.6	23.4	0.000	0.000
25	Rivers + Cattle grazing areas + Habitat types	-0.48	0.00	9	626.8	24.6	0.000	0.000
26	Settlements	12.10	0.00	3	638.6	36.4	0.000	0.000
27	Settlements + Cattle grazing areas	-1.44	0.00	5	639.9	37.7	0.000	0.000

28	Rivers	2.05	0.00	3	641.7	39.5	0.000	0.000
29	Rivers + Settlements	-0.49	0.00	5	642.1	39.9	0.000	0.000
30	Cattle grazing areas	2.37	0.00	3	642.1	39.9	0.000	0.000
31	Rivers + Settlements + Cattle grazing areas	-0.15	0.00	7	643.4	41.2	0.000	0.000
32	Settlements x Cattle grazing areas	---	0.00	9	644.5	42.3	0.000	0.000
33	Rivers + Cattle grazing areas	-0.12	0.00	5	644.6	42.4	0.000	0.000
34	Rivers x Settlements	---	0.00	9	647.5	45.3	0.000	0.000
35	Rivers x Cattle grazing areas	---	0.00	9	647.5	45.3	0.000	0.000
36	Rivers x Settlements + Rivers x Cattle grazing areas	---	---	15	649.1	46.9	0.000	0.000
37	Rivers x Settlements x Cattle grazing areas	---	---	25	656.1	53.9	0.000	0.000

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Table 4.7. All subset models comparison statistics for ecological (rivers, habitat types, and rainfall) and anthropogenic (settlements and cattle grazing areas) factors influencing the distribution of impalas

Model ranking	**Models structure**	**CA (%)**	**LRT**	**K**	**AIC**	**ΔAIC**	**AIC weight (w_m)**	**Relative likelihood**
01	Habitat types + Rainfall	14.25	0.8	7	500	0	0.502	1.000
02	Rivers + Habitat types + Rainfall	-0.94	0.85	9	502.3	2.3	0.159	0.317
03	Settlements + Habitat types + Rainfall	-0.09	0.69	9	503.2	3.2	0.101	0.202
04	Cattle grazing areas + Habitat types + Rainfall	1.75	0.55	9	503.9	3.9	0.071	0.142
05	Habitat types x Rainfall	---	---	12	504	4	0.068	0.135
06	Rivers + Settlements + Habitat types + Rainfall	0.13	0.92	11	505.1	5.1	0.039	0.078
07	Rivers + Cattle grazing areas + Habitat types + Rainfall	-1.32	0.52	11	506.3	6.3	0.022	0.043
08	Settlements + Cattle grazing areas + Habitat types + Rainfall	0.02	0.34	11	507.1	7.1	0.014	0.029
09	Habitat types	68.67	0.05	5	508.2	8.2	0.008	0.017
10	Rivers + Settlements + Cattle grazing areas + Hab. types + Rainfall	-0.70	0.00	13	508.9	8.9	0.006	0.012
11	Rivers + Habitat types	1.98	0.04	7	509.9	9.9	0.004	0.007
12	Cattle grazing areas + Habitat types	0.40	0.02	7	511.5	11.5	0.002	0.003

13	Settlements + Habitat types	-0.15	0.02	7	511.6	11.6	0.002	0.003
14	Rivers + Settlements + Habitat types	0.99	0.02	9	512.6	12.6	0.001	0.002
15	Rivers + Cattle grazing areas + Habitat types	-0.45	0.01	9	513.5	13.5	0.001	0.001
16	Settlements + Cattle grazing areas + Habitat types	-0.13	0.008	9	514.5	14.5	0.000	0.001
17	Rivers + Settlements + Cattle grazing areas + Habitat types	0.62	0.004	11	515.8	15.8	0.000	0.000
18	Rivers + Rainfall	0.56	0.00	5	546.9	46.9	0.000	0.000
19	Rainfall	10.46	0.00	3	546.9	46.9	0.000	0.000
20	Settlements + Rainfall	0.44	0.00	5	549.1	49.1	0.000	0.000
21	Rivers + Settlements + Rainfall	-0.19	0.00	5	550	50	0.000	0.000
22	Cattle grazing areas + Rainfall	0.68	0.00	5	550.5	50.5	0.000	0.000
23	Rivers + Cattle grazing areas + Rainfall	0.37	0.00	7	550.7	50.7	0.000	0.000
24	Settlements + Cattle grazing areas + Rainfall	-0.30	0.00	7	553.1	53.1	0.000	0.000
25	Rivers + Settlements + Cattle grazing areas + Rainfall	-0.08	0.00	9	553.6	53.6	0.000	0.000
26	Settlements x Cattle grazing areas	---	0.00	9	561.2	61.2	0.000	0.000
27	Rivers	2.16	0.00	3	567.1	67.1	0.000	0.000
28	Rivers x Settlements x Cattle grazing areas	---	---	25	568	68	0.000	0.000
29	Settlements	1.27	0.00	3	568.2	68.2	0.000	0.000
30	Rivers x Cattle grazing areas	---	0.00	9	568.6	68.6	0.000	0.000
31	Cattle grazing areas	0.14	0.00	3	568.7	68.7	0.000	0.000
32	Rivers + Cattle grazing areas	-0.05	0.00	5	569.1	69.1	0.000	0.000
33	Rivers + Settlements	-0.38	0.00	5	570.3	70.3	0.000	0.000
34	Settlements + Cattle grazing areas	-0.14	0.00	5	570.9	70.9	0.000	0.000
35	Rivers + Settlements + Cattle grazing areas	0.04	0.00	7	571.8	71.8	0.000	0.000
36	Rivers x Settlements	---	0.00	9	571.9	71.9	0.000	0.000
37	Rivers x Settlements + Rivers x Cattle grazing areas	---	---	15	574.6	74.6	0.000	0.000

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4.5. Supplementary material

Figure 4.S1. African elephants and African Buffalos sightings and explanatory variables in the Limpopo National Park

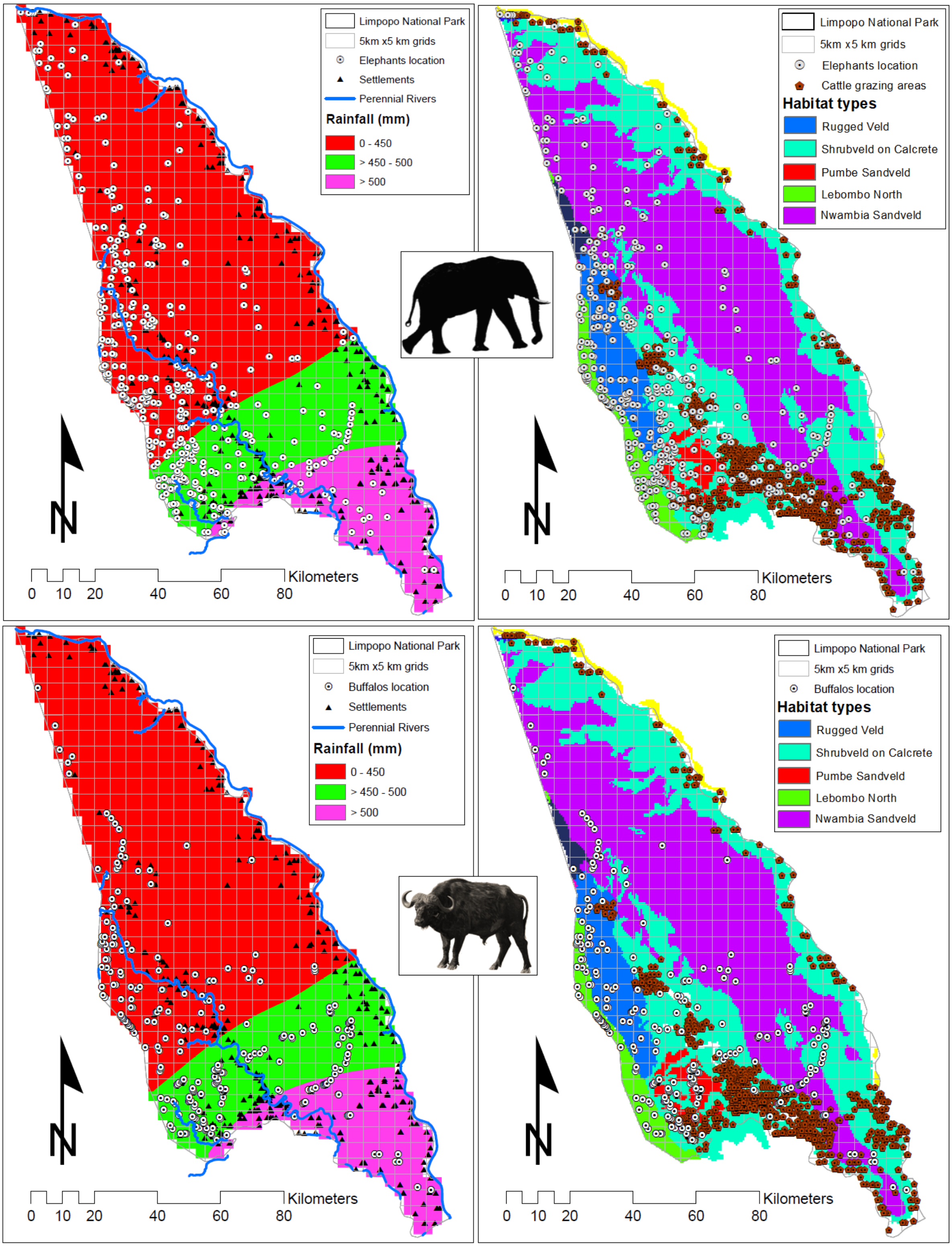


Figure 4.S2. Plains zebra and greater kudu sightings and explanatory variables in the Limpopo National Park

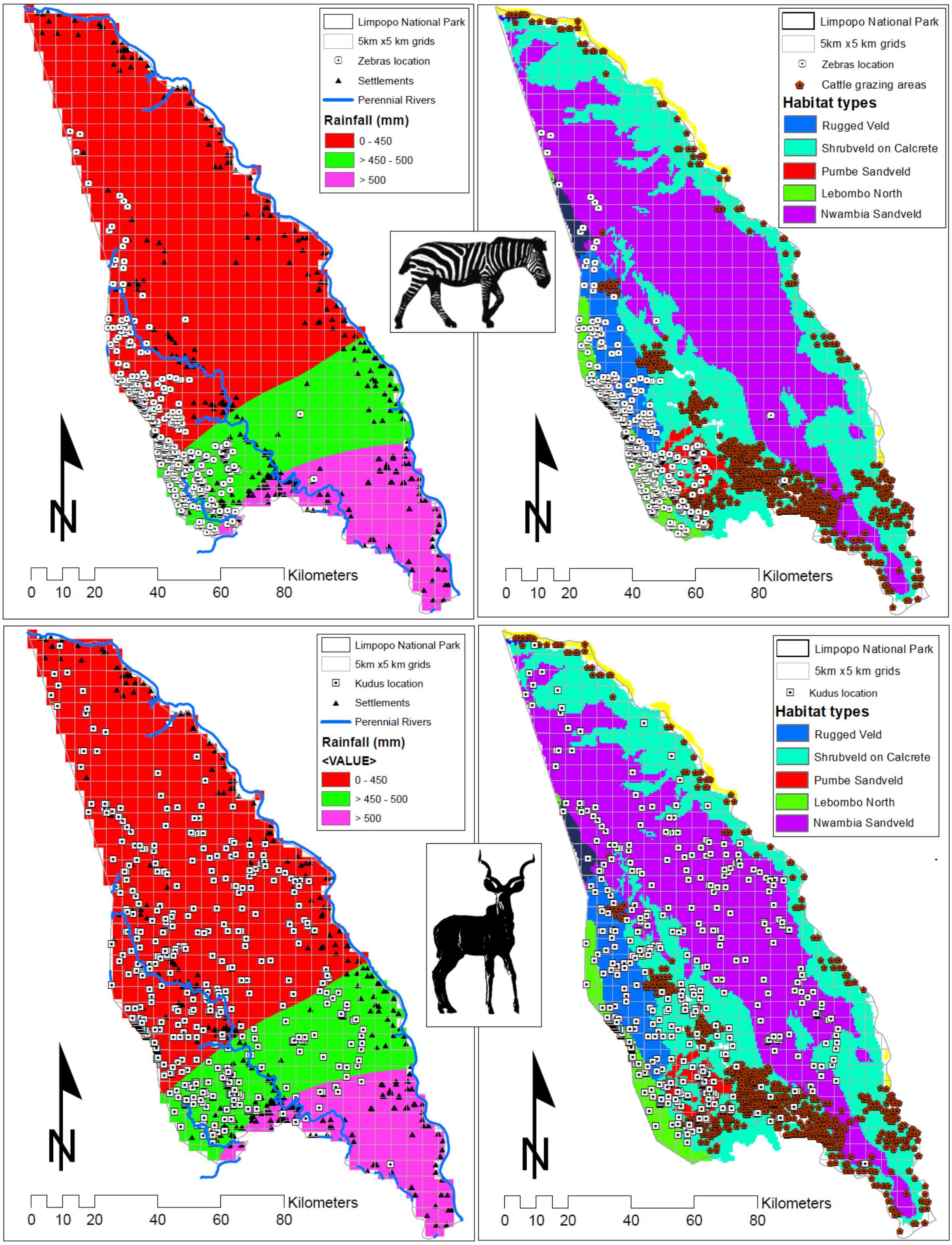
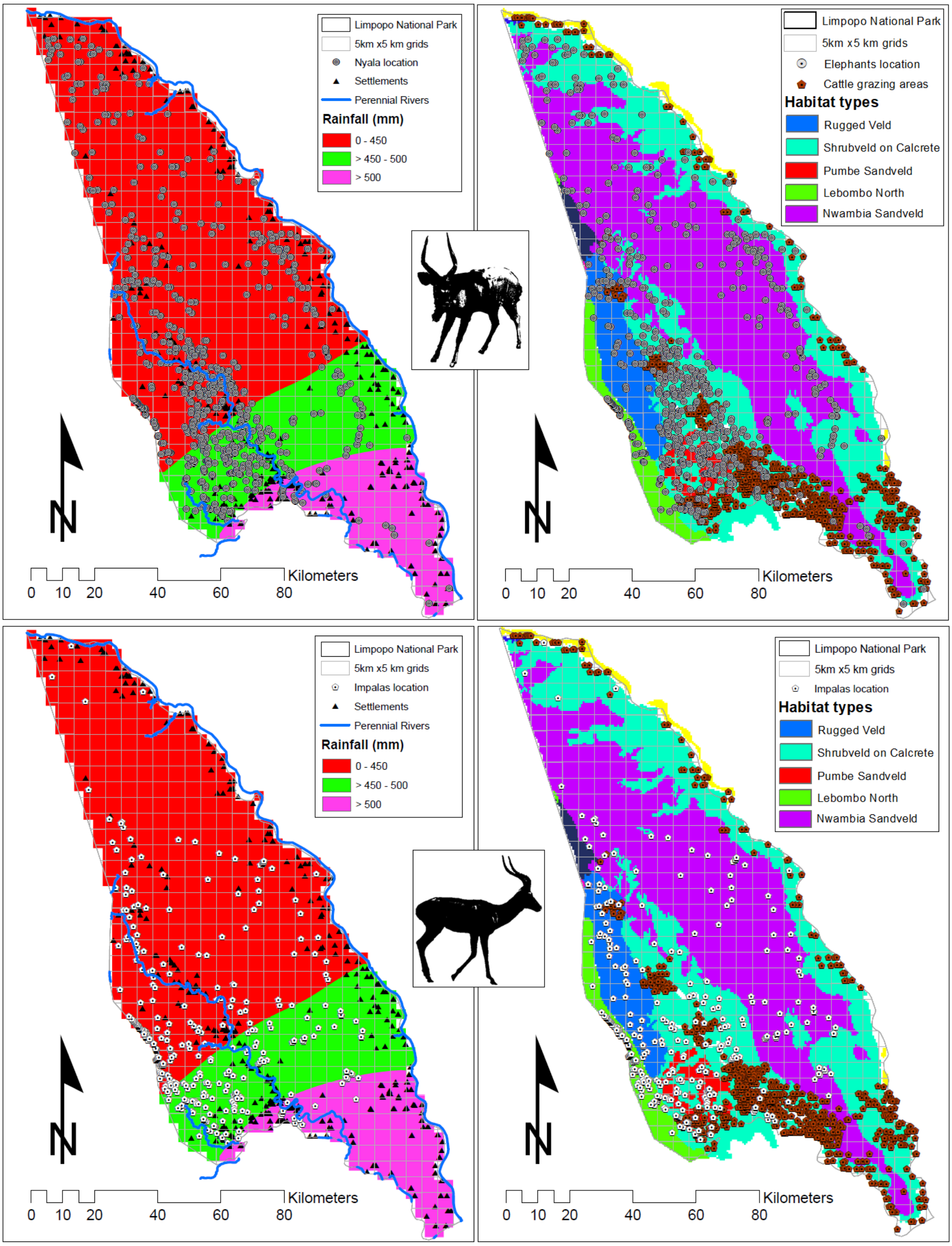


Figure 4.S3. Nyala and impala sightings and explanory variables in the Limpopo National Park



R code to support the models building

Code to support the models building on the ecological and anthropogenic determinants of the landscape distribution of selected species of large herbivores in the Limpopo National Park, Mozambique

This script can be used to fit the full large herbivore models with five predictors in "R 3.5.1"

R 3.5.1 is free software developed by R Core Team (2018) codenamed "Feather Spray"

The full model incorporates five categorical predictors:

(i) Distance to the nearest rivers with three categories

(ii) Distance to the nearest human settlements

(iii) Distance to the nearest cattle grazing areas

These three predictors above each one has three categories (0-5 km, 5.1-10 km, and > 10 km)

(iv) Habitat types ### with five categories (Lebombo North, Pumbe Sandveld, Rugged Veld, Shrubveld on Calcrete, and Nwambia Sandveld)

(v) Rainfall ### with three categories (0-450 mm, 450-500 mm, and > 500 mm)

File descriptions:

The occurrence data of large herbivores (present = 1, not present = 0) and predictors are packaged in one file named "Large herbivores distribution modelling" available on an Online Data Repository: Dionísio V. Roque, Thomas Göttert, Ulrich Zeller, & Valério A. Macandza. (2023). Large herbivores distribution modelling [Data set]. Zenodo. https://doi.org/10.5281/zenodo.8182156

Main files for modelling:

Buffalos.csv

Elephants.csv

Zebra.csv

Kudu.csv

Nyala.csv

Impala.csv

Within these files, the following data objects exist:

- The occurrence data of elephants, buffalos, zebra, kudu, nyala and impala are in separate .csv files. Each file consists of six columns with 1) grid number, 2) rivers categories in km, 3) settlements categories in km, 4) grazing areas categories in km, 5) habitat types, and 6) rainfall categories in mm;
- R script that can be used to fit the full large herbivore models with five predictors in “R 3.5.1 software”.

Dichotomous outcomes (Hosmer and Lemeshow 2000), i.e. presence = 1/absence = 0 of six large herbivores species (African elephant, African buffalo, plains zebra, greater kudu, nyala, and impala) were modelled through logistic regression in R 3.5.1 free software developed by R Core Team (2018) code-named "Feather Spray". The full model incorporates five categorical predictors: Rivers (3 levels) + Settlements (3 levels) + Cattle grazing areas (3 levels) + Habitat types (5 levels) + Rainfall (3 levels). The response variable is the presence of species. 1 = species present; 0 = species not present

Plus signs (+) imply additive terms in the model. Times signal (x) implies interactions among variables

```
##################################################################################
### Load required packages ####
library(yhat)
library(pscl)
library(generalhoslem)
##################################################################################
#### Loading data for modelling e.g. Buffalos. Observations: For Elephants, Zebra, Kudu, Nyala, and Impala, the procedure is the same as shown below step by step for buffalo’s model buildings
> mydata<-read.csv("Buffalos.csv",header=TRUE,
+ sep=",")
> str(mydata)
##################################################################################
#### Full/saturated model (all variables)
mod1<glm(Presence~factor(River)+factor(Settlement)+factor(Grazing)+factor(Habitat)+factor(Rainfall),
+ data=mydata,family="binomial")
```

```
> summary(mod1)
###############################################################################
#### Running Commonality Analysis (CA)
#### Required package
> library(yhat)
>CCmydata=commonalityCoefficients(mydata,"Presence",list("River","Settlement","Grazing","Habitat","Rainfall"),"F")
> print(CCmydata)
###############################################################################
#### Running all other models (one, two, three, four predictors and some interactions)
> mod2<-glm(Presence~factor(River),
+ data=mydata,family="binomial")
> summary(mod2)
> mod3<-glm(Presence~factor(Settlement),
+ data=mydata,family="binomial")
> summary(mod3)
> mod4<-glm(Presence~factor(Grazing),
+ data=mydata,family="binomial")
> summary(mod4)
> mod5<-glm(Presence~factor(Habitat),
+ data=mydata,family="binomial")
> summary(mod5)
> mod6<-glm(Presence~factor(Rainfall),
+ data=mydata,family="binomial")
> summary(mod6)
> mod7<-glm(Presence~factor(River)+factor(Settlement),
+ data=mydata,family="binomial")
> summary(mod7)
> mod8<-glm(Presence~factor(River)+factor(grazing),
+ data=mydata,family="binomial")
> summary(mod8)
> mod9<-glm(Presence~factor(River)+factor(Habitat),
```

```
+ data=mydata,family="binomial")
> summary(mod9)
> mod10<-glm(Presence~factor(River)+factor(Rainfall),
+ data=mydata,family="binomial")
> summary(mod10)
> mod11<-glm(Presence~factor(Settlement)+factor(Grazing),
+ data=mydata,family="binomial")
> summary(mod11)
> mod12<-glm(Presence~factor(Settlement)+factor(Habitat),
+ data=mydata,family="binomial")
> summary(mod12)
> mod13<-glm(Presence~factor(Settlement)+factor(Rainfall),
+ data=mydata,family="binomial")
> summary(mod13)
> mod14<-glm(Presence~factor(Grazing)+factor(Habitat),
+ data=mydata,family="binomial")
> summary(mod14)
> mod15<-glm(Presence~factor(Grazing)+factor(Rainfall),
+ data=mydata,family="binomial")
> summary(mod15)
> mod16<-glm(Presence~factor(Habitat)+factor(Rainfall),
+ data=mydata,family="binomial")
> summary(mod16)
> mod17<-glm(Presence~factor(River)+factor(Settlement)+factor(Grazing),
+ data=mydata,family="binomial")
> summary(mod17)
> mod18<-glm(Presence~factor(River)+factor(Settlement)+factor(Habitat),
+ data=mydata,family="binomial")
> summary(mod18)
> mod19<-glm(Presence~factor(River)+factor(Grazing)+factor(Habitat),
+ data=mydata,family="binomial")
> summary(mod19)
```

```
> mod20<-glm(Presence~factor(Settlement)+factor(Grazing)+factor(Habitat),
+ data=mydata,family="binomial")
> summary(mod20)
> mod21<-glm(Presence~factor(River)+factor(Settlement)+factor(Rainfall),
+ data=mydata,family="binomial")
> summary(mod21)
> mod22<-glm(Presence~factor(River)+factor(Grazing)+factor(Rainfall),
+ data=mydata,family="binomial")
> summary(mod22)
> mod23<-glm(Presence~factor(Settlement)+factor(Grazing)+factor(Rainfall),
+ data=mydata,family="binomial")
> summary(mod23)
> mod24<-glm(Presence~factor(River)+factor(Habitat)+factor(Rainfall),
+ data=mydata,family="binomial")
> summary(mod24)
> mod25<-glm(Presence~factor(Settlement)+factor(Habitat)+factor(Rainfall),
+ data=mydata,family="binomial")
> summary(mod25)
> mod26<-glm(Presence~factor(Grazing)+factor(Habitat)+factor(Rainfall),
+ data=mydata,family="binomial")
> summary(mod26)
>mod27<-glm(Presence~factor(River)+factor(Settlement)+factor(Grazing)+
factor(Habitat),
+ data=mydata,family="binomial")
> summary(mod27)
>mod28<-glm(Presence~factor(River)+factor(Settlement)+factor(Grazing)+
factor(Rainfall),
+ data=mydata,family="binomial")
> summary(mod28)
>mod29<-glm(Presence~factor(River)+factor(Settlement)+factor(Habitat)+
factor(Rainfall),
+ data=mydata,family="binomial")
```

```
> summary(mod29)
> mod30<-glm(Presence~factor(River)+factor(Grazing)+factor(Habitat)+factor(Rainfall),
+ data=mydata,family="binomial")
> summary(mod30)
> mod31<-glm(Presence~factor(Settlement)+factor(Grazing)+factor(Habitat)+
factor(Rainfall),
+ data=mydata,family="binomial")
> summary(mod31)
> mod32<-glm(Presence~factor(River)*factor(Settlement),
+ data=mydata,family="binomial")
> summary(mod32)
> mod33<-glm(Presence~factor(River)*factor(Grazing),
+ data=mydata,family="binomial")
> summary(mod33)
> mod34<-glm(Presence~factor(Settlement)*factor(Grazing),
+ data=mydata,family="binomial")
> summary(mod34)
> mod35<-glm(Presence~factor(Habitat)*factor(Rainfall),
+ data=mydata,family="binomial")
> summary(mod35)
> mod36<-glm(Presence~factor(River)*factor(Settlement)*factor(Grazing),
+ data=mydata,family="binomial")
> summary(mod36)
> mod37<-glm(Presence~factor(River)*factor(Settlement)+factor(River)*factor(Grazing),
+ data=mydata,family="binomial")
> summary(mod37)
##############################################################################
#### Generating AIC (Akaike’s Information Criterion)
>AIC(mod1,mod2,mod3,mod4,mod5,mod6,mod7,mod8,mod9,mod10,mod11,mod12,mod13,mod14,mod15,mod16,mod17,mod18,mod19,mod20,mod21,mod22,mod23,mod24,mod25,mod26,mod27,mod28,mod29,mod30,mod31,mod32,mod33,mod34,mod35,mod36,mod37)
```

```
##################################################################################
#### Running Likelihood Ratio Test (LRT)###
> anova(mod1,mod2,test="LRT")
> anova(mod1,mod3,test="LRT")
> anova(mod1,mod4,test="LRT")
> anova(mod1,mod5,test="LRT")
> anova(mod1,mod6,test="LRT")
> anova(mod1,mod7,test="LRT")
> anova(mod1,mod8,test="LRT")
> anova(mod1,mod9,test="LRT")
> anova(mod1,mod10,test="LRT")
> anova(mod1,mod11,test="LRT")
> anova(mod1,mod12,test="LRT")
> anova(mod1,mod13,test="LRT")
> anova(mod1,mod14,test="LRT")
> anova(mod1,mod15,test="LRT")
> anova(mod1,mod16,test="LRT")
> anova(mod1,mod17,test="LRT")
> anova(mod1,mod18,test="LRT")
> anova(mod1,mod19,test="LRT")
> anova(mod1,mod20,test="LRT")
> anova(mod1,mod21,test="LRT")
> anova(mod1,mod22,test="LRT")
> anova(mod1,mod23,test="LRT")
> anova(mod1,mod24,test="LRT")
> anova(mod1,mod25,test="LRT")
> anova(mod1,mod26,test="LRT")
> anova(mod1,mod27,test="LRT")
> anova(mod1,mod28,test="LRT")
> anova(mod1,mod29,test="LRT")
> anova(mod1,mod30,test="LRT")
> anova(mod1,mod31,test="LRT")
```

```
> anova(mod1,mod32,test="LRT")
> anova(mod1,mod33,test="LRT")
> anova(mod1,mod34,test="LRT")
> anova(mod1,mod35,test="LRT")
> anova(mod1,mod36,test="LRT")
> anova(mod1,mod37,test="LRT")
### For saturated moedel
> anova(mod0,mod1,test="LRT")
> mod0<-glm(Presence~1,
+ data=mydata,family="binomial")
> summary(mod0)
##########################################################################
#### Assessing the overall fit of the best model using the Hosmer-Lemeshow (H-L) goodness of fit (best fitting model = mod25)###
#### Required package
library(generalhoslem)
> logitgof(mydata$Presence,fitted(mod25))
##########################################################################
#### Assessing Pseudo R square (McFadden)
#### Required package
> library(pscl)
> pR2(mod25)
##########################################################################
#### Model Validation
#### Building Confusion Matrix
> attri_predicted_value<-predict(mod25,type="response")
> attri_predicted_value
> pmod=predict(mod25,mydata)
> tab=table(pmod>0.5,mydata$Presence)
> tab
#### Predicted accuracy
> sum(diag(tab))/sum(tab)*100
```

4.6. References

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CHAPTER FIVE

5. General discussion, conclusion, and management implications

5.1. General discussion

In this study, I combined historical and current LH occurrence data (1500-2021) to (1) reconstruct the historical distribution and movement patterns of LH species, (2) assess the distribution patterns and the relative abundance of reintroduced LH, and (3) assess how ecological and anthropogenic factors influence the distribution of LH in the LNP landscape. The study results suggest connectivity between different habitats within the LNP despite intense human presence in the core area and buffer zone. Due to the connectivity among different habitats in the landscape, the study also revealed that some areas for wildlife distribution and transboundary movements from KNP to LNP used in the past are still being used. The distribution and movement patterns of LH from the historical to the current period are still affected by ecological and anthropogenic factors.

At the end of the 18th century, the gradual decline of wildlife in Mozambique began because different groups of hunters led by Europeans had reached the interior of rural areas where they carried out large-scale wildlife hunting (Dias, 1961, Witter, 2010). In the 19th and 20th centuries, the center of the ivory and wildlife trophies trade was the junction between the Incomati and Olifantes Rivers. From this point, the border of this trade moved into the Great Limpopo region and extended to the North (Witter, 2010). The Maluleques tribe group with strong territorial dominance that had established itself in the current region of Makandezulu A and B of the LNP established a resource control centre through hunting areas: the Tsonga group controlled the hunting area in the north, and the Venda group controlled the south of the LNP. European commercial hunters were moved to the Greater Limpopo region from the Transvaal region because wildlife was abundant and there were no hunting restrictions (Mavhunga and Spierenburg, 2007). There was also an interest in connecting this area with the best ivory trade route in the Inhambane region along the Mozambican coast (Dias, 1961).

The decision to favour the protection of domestic animals rather than wild fauna in Mozambique and Rhodesia at that time led to a fierce fight against the tsetse fly (Mavhunga and Spierenburg, 2007). From the 1940s to 1960s, the strategies to combat tsetse flies differed in Rhodesia and Mozambique. Rhodesia focussed on the routes and means of spreading the infestation and in the fly habitat (Murray, 1995). All wildlife routes were blocked and the main wildlife habitats were intervened through fires and other measures to contain the tsetse fly, which affected LH movements and distribution. In Mozambique, the main focus was on the game as a vector of the fly. As a result, to the Portuguese authorities control of the game movement seemed far more important than controlling the movement of people (Allina-Pisano *et al.*, 1981). Until the late 1950s, the Portuguese government considered slaughtering (culling) game the main method of tsetse control in Mozambique. Dias (1961) listed five culling operations carried out between 1949 and 1969, in which a total of 126,721 animals were killed. Elephants were destroyed in large numbers, and the culling process was also an economically attractive option.

The quantity and quality of the historical written records used to reconstruct the LH historical distribution and movement patterns in the LNP varies in terms of the spatial coverage achieved and the quantity and quality of the information that comprises each record. The main reason for this variation is the non-systematic manner in which the historical written records were taken in the past. According to Boshoff *et al.* (2016), the main factors that introduce complications are 1) not all areas covered by the study were visited by literate pioneers, European explorers, travellers, naturalists, and big game hunters (while some areas received relatively many such people, others received few or none), 2) species observed records were made by individual literate pioneers, European explorers, travellers, naturalists, and big game hunters on a highly selective and irregular basis, and therefore, the amount of information (physical description, behaviour, habitat and locality) that was recorded by the same or different observers differ greatly, 3) very few of these observers recorded the absence of species

For the present study, the extent and frequency of historical records varies considerably among them as the literate pioneers, European explorers, and big game hunters, were focused on species of high value for hunting and thus, leaving out certain other species. However, I believe that these problems have been ameliorated, at least to some extent, because the study clearly defined the location, record, and reference (Roque *et al.*, 2022) and mapped only the records on the acceptable identification and precise locality categories, leaving out questionable identification, imprecise locality categories, and unmappable records (Skead, 2007); Boshoff and Kerley, 2010, 2013; Boshoff *et al.*, 2016). Furthermore, it was highlighted in chapter two (Roque *et al.*, 2022) that results on the distribution and movement patterns of the studied species should be viewed as of a preliminary nature since the indicated patterns can be strengthened and gaps filled if and when new written records for the different periods under study are discovered.

Currently, the restoration process of different LH species has already started in the LNP. However, it is still in an early and vulnerable stage and appears to be more linked with the availability of habitat features (Roque *et al.*, 2021) and precipitation (Roque *et al.*, in press). Some studied species, such as white rhino, giraffe, blue wildebeest, and eland, appeared to have a relatively slow recovery. Giraffes and blue wildebeest were reintroduced from 2001 to 2008, but these species have suffered from intense poaching for meat and traditional ceremonies after the establishment of the LNP. This was because by that time the number of anti-poaching control posts was low, and the park had not yet implemented the Wildlife Intensive Protection Zone (PNL, 2012). Eland was not actively reintroduced in the LNP, and this can further explain the poorest restoration as the population of this species depends up on the passive reintroduction through KNP-LNP fence gaps. The main reason for the white rhino extinction in LNP was the excessive hunting (Dunham, 2004).

Although the LNP has communities in the core area and the buffer zone, the study results disclosed that some areas for wildlife distribution and transboundary movements from KNP to LNP used in the past are still being used. According to Bennett (2003), the level of connectivity perception varies between species. Some species are tolerant to human land use and can live in and freely move through a patchwork of degraded natural habitats and anthropogenic environments, while others avoid degraded habitats. Species may tolerate human presence and different land use when the connectivity among high-quality habitats, resources (food and water), and conditions (safety and shelter) are available. It appears to be the case in the LNP landscape where the anthropogenic disturbances (human settlements and cattle grazing areas) seemed to either (partially) prevent the LH occurrence or show the potential for human-wildlife conflict risk. The people in the LNP core area are scheduled to be resettled in the buffer zone by 2006 (ANAC, 2022). As time passes, the people number will increase in the buffer zone, pushing the LNP biodiversity and its associated ecosystem services flow in the context of uncertainty. Since the results showed that some historical areas of LH distribution and movements are still in use, it can teach a valuable lesson in the LNP management practice for further development of the GLTP. The management effort is to integrate LNP into a wider GLTP landscape (ANAC, 2022). These can be achieved by incorporating a social-ecological approach into this wider landscape approach. According to Palomo *et al*. (2014), social-ecological may bring protected areas more in line with the needs of society, promoting regional landscape planning beyond the limits of the protected area and integrating the effects of drivers of change in ecosystems with social and ecological sciences that might improve the management of protected areas and their surrounding landscapes. It would allow investigating/quantifying the potential human-wildlife conflict risk at finer spatial scales to improve future management in the GLTP.

5.2. Conclusions

Mozambique's wildlife suffered a decline for centuries due to multiple causes. The overriding reason is that wildlife has experienced a turbulent history that varies from massive culling by veterinary services allegedly to protect livestock from Rinderpest and diseases transmitted by ticks and tsetse fly, trophy hunting, increasing human settlements, wars, to the uncontrolled hunting for bush meat by rural communities (Martinho, 1934; Dias and Rosinha, 1971; Dias, 1981; Hatton *et al*., 2001; Ntumi *et al*., 2009; Madeiros, 2017). After the civil war (1976-1992), Mozambique conservation areas remained abandoned, with no management, with intense poaching activities (MICOA, 1997, 2014; Hatton *et al*., 2001), leading to dramatic wildlife decline.

This research was designed with the broad aim of contributing towards a better understanding of historical and current distribution and movement patterns of large herbivores (LH) in the Limpopo National Park (LNP) landscape, thereby creating a basis and providing evidence for the management and further development of the Great Limpopo Transfrontier Park (GLTP). The specific objectives included: 1) to reconstruct the historical distribution and movement patterns of large herbivores species in the Limpopo National Park, 2) to assess the distribution patterns and the relative abundance of reintroduced large herbivores in the Limpopo National Park, and 3) to assess how ecological and anthropogenic factors influence the distribution of large herbivores in the Limpopo National Park landscape. The key questions addressed in this study are: 1) did the distribution and movements of large herbivores change over time in the LNP? 2) what are the main drivers in the distribution of LH in Limpopo National Park? and 3) is the GLTP's ecological objective of managing the LNP to re-establish the transboundary wildlife movements being achieved?

In southern Africa, historical accounts (Martinho, 1934; Du Plessis, 1969; Smithers and Tello, 1976; Plug, 1982; Carruthers *et al*., 2008; Ntumi *et al*., 2009; Boshoff and Kerley, 2010; Boshoff *et al*., 2016) suggest that large herbivores were most abundant and widely distributed throughout the region until the beginning of the colonial interference (Carruthers *et al*., 2008). Ungulates migration and dispersal movements in this period were also common (Dingle and Drake, 2007; Roche, 2008; Owen-Smith *et al*., 2020; Kauffman *et al*., 2021). Combining past and current wildlife information can assist and guide the species restoration to areas from which they have become extinct (IUCN, 2001; Boshoff *et al*., 2016; Stoldt *et al*., 2020). Stalmans *et al*. (2019) demonstrated the potential for rapid post-war recovery of large herbivores, given sound protected area management, but also suggested that restoration of community structure takes longer and may require active intervention. However, reconstructing past distribution and movement patterns of LH is difficult in any part of southern Africa because species distribution data is scarce for most taxa (Du Plessis, 1969; Smithers and Tello, 1976; Carruthers *et al*., 2008; Ntumi *et al*., 2009; Boshoff and Kerley, 2010, 2013; Boshoff *et al*., 2016; Neves *et al*., 2018, 2019; Stalmans *et al*., 2019).

In Chapter 2, I attempted to reconstruct the historical distribution and movement patterns of LH species in different periods and assess the use of proposed ecological corridors in the LNP. Based on these foundations, I used scientific systematization to test the hypothesis that the distribution areas and movement routes of LH in the LNP have changed over time such that most of the suitable sites for these species in the past are no longer available. The results of this chapter revealed a dramatic collapse of LH populations between the peak of the colonial period and the post-colonial/civil war period (1800-2001), followed by a slight recovery from the post-proclamation of GLTP to the current period (2002-2021). The results also gave scientific evidence concerning the functioning of some proposed wildlife corridors in the LNP. The dramatic collapse of LH during the civil war period, followed by variable species-specific recovery rates during the post-war decades reported in this study, were reported previously (Ntumi *et al*., 2009; Stalmans *et al*., 2019). This finding suggests that the white rhino, although reintroduced in the park, probably did not survive the intense poaching suffered from 2010 to 2015 (Lunstrum, 2014; Büscher and Ramutsindela, 2015). The eland fluctuates from census to census, ranging from unseen to visualization of less than six individuals (Stephenson, 2013; Grossman *et al.*, 2014; ANAC, 2018; Roque *et al.*, 2021). The limitation of this Chapter was the sporadic observation of LH at the prehistoric/start of the colonial period. This prevented a suitable reconstruction of LH assemblages in this period. Since no information on past LH occurrence was digitalized for GLTP, the hand-drawn maps used may have added potential errors in the species geo-referencing.

In Chapter 3, I assessed the distribution patterns and the relative abundance of reintroduced large herbivores in the LNP. The quality of the release site, the habitat requirements of the translocated species, the availability and quality of surrounding habitats, including connectivity and linkages at the landscape scale, and the predator occurrence and abundance (Sinclair et al., 2003; Valeix *et al.*, 2009) play a crucial role in the reintroduction success (Scillitani *et al.*, 2013; Richardson *et al.*, 2015). Based on this, I hypothesized that the current distribution and abundance of large herbivores in the Limpopo National Park landscape are associated with the availability of the habitat types rather than the historical reintroduction site (Old Sanctuary). The key findings of Chapter 3 were:

1. The relationship between the ecological parameters [relative capture index (RAI), species richness (S), and naïve occupancy, species-specific and guild-specific response patterns] strongly responded to habitat features than the initial release site of LH (Old Sanctuary);
2. The potential predator species in the LNP have not yet reached population sizes that might have a significant impact or cause a measurable effect on the distribution pattern of ungulates.

In Chapter 4, I investigated how ecological factors (distance to perennial rivers, habitat types, and rainfall) and anthropogenic factors (distance to settlements and cattle grazing areas) influence the distribution of LH species surveyed over 21 years. The distribution of LH in the landscape is affected by three broad classes of mechanisms: biotic bottom-up mechanisms related to resources supply (Fryxell, 1991; Sinclair, 2003; Fryxell *et al.*, 2004), biotic top-down mechanisms involving predators and diseases (Sinclair *et al.*, 2003; Grange and Duncan, 2006) and the interactions of both classes (Anderson *et al.*, 2010). Based on findings from previous studies addressing abiotic and biotic factors regulating the distribution of herbivores (e.g. Chirima *et al*., 2013), I predicted that the ecological factors (habitat types, rainfall, and perennial rivers) would positively influence the distribution of LH, while anthropogenic factors (settlements and cattle grazing areas) would negatively influence. The key findings of Chapter 4 were:

1. Habitat types and rainfall were the most influential factors shaping positively the pattern of LH distribution in the LNP. Lebombo North, Pumbe Sandeveld, and Rugged Veld were the habitat types positively associated with the prevalence of LH. Large herbivores were prevalent in 0-450 and > 450-500 mm areas of average rainfall;
2. Some species (zebras, kudus, and impalas) tended to avoid settlements, while others (elephants, buffalos, and nyala) are attracted to settlements due to crops as alternative food resources and overlap in the water resources use with humans in the dry season, leading to increase the risk of human-wildlife conflicts. This finding reveals a high probability of human-wildlife conflict in the future if the issue of human population resettlement is not well planned in the LNP.

Overall, this study revealed a dramatic collapse of LH populations of LH between the peak of the colonial period and the post-colonial/civil war period (1800-2001. However, there is evidence of the re-establishment of wildlife transboundary movements in the GLTP across some proposed ecological corridors. These corridors link the LNP with Banhine and Zinave National Parks and the interstitial zone between these parks, allowing dispersal movements in the Great Limpopo Transfrontier Park and Conservation Area (ANAC, 2022). The availability of resources (food and water) in different habitat types explains the distribution of LH in the LNP. Anthropogenic disturbances (livestock keeping) retract the prevalence of most species. The study results give reason to assume that restoration of LH in the LNP is in an early state. Furthermore, this recovery process is slow, where the LH population are vulnerable due to anthropogenic disturbances. Therefore, it is necessary to put a continuous effort into the restoration process through an adaptive management approach. This approach will allow managers to learn from the process of managing and thereby continuously adapt and improve their management concerning human settlements to reduce human-wildlife conflicts and impacts on high-value habitats, allow wildlife dispersal to the East and North, improve the functionality of proposed corridors, and mitigate the poaching and human-wildlife conflicts.

5.3. Management implications

According to the LNP Management Plan (ANAC, 2022), the ecological objectives of the LNP are: (i) to maintain the current “wilderness” (in the sense of natural or near-natural, largely un-transformed) character of the LNP and to manage it as a globally important conservation area within a framework of minimum management intervention, whilst ensuring the maintenance and natural evolution of ecosystem structure and function, (ii) to ensure the LNP’s integration into the GLTP planning and development framework, thereby contributing to the judicious and sustainable natural resource management of the region. These ecological objectives of LNP are embedded within the ecological goals of the GLTP. Accordingly, the ecological goals of GLTP with ecological impact on biodiversity conservation (Bazin *et al*., 2016; ANAC, 2022) is to holistically manage the Limpopo ecosystem to ensure the connectivity of habitats to re-establish historical transboundary movements and migration routes of wildlife and other ecosystem functions that have been disordered by fences and incompatible legislation. About 7,000 people live in seven villages in the core area (Shingwedzi Valley) of LNP (ANAC, 2022), awaiting resettlement in the buffer zone (Massé, 2016). People in settlement villages practice subsistence farming, livestock keeping, bush meat poaching, firewood extraction, and pole extraction for house and livestock corral buildings (Andresen *et al*., 2014; ANAC, 2018). The factors limiting LH distribution and movements at the landscape scale appear to be human settlements (crop resources) and other associated activities, such as livestock keeping and the KNP-LNP fence in the western extension. At the habitat scale, resources and conditions seem to be limiting factors in LH distribution and movements. Accordingly, based on the study findings, I suggest that management in the LNP should reduce human pressure on wildlife in the core area and ecological corridors in the short term and in the medium or long term should improve the habitats conditions and LH restocking. Therefore:

- The human resettlements of the Shingwedzi Valley to the buffer zone should consider the movement patterns of elephants around villages and how the species use the areas around villages in the GLTP (Cook *et al*., 2015). This management action will reduce the illegal hunting of wildlife for local consumption, which increases as the human population increases. It will also reduce the potential human-wildlife conflict risk due to competition with cattle on grass and water along the river.

- Of the six ecological corridors (Munguambane, Matsilele, Sihogonhe, Tchowe, Chipeluene e Matafula) proposed for wildlife movements (PNL, 2012), three were recommended for implementation based on the analysis of the ecological and socio-economic characteristics (Macandza and Ruiz, 2012) and four were found being used by LH after the proclamation of GLTP to the current period based on historical analysis and camera traps (Roque *et al*., 2021, 2022). The four proposed corridors confirmed in this study (Roque *et al*., 2022) include two identified as intact by Macandza and Ruiz (2012). Thus, an Intensive Protection Zones (IPZ) similar to the West LNP with enough anti-poaching control posts and well-trained human-wildlife conflict teams should be established on these corridors confirmed by both studies. These management actions will avoid the disconnection between the corridors and the main habitats, ensuring their functionality for LH movements and reducing potential human-wildlife conflicts.
- The resettlement will increase the human population in the buffer zone over the years and intensify the blocking of wildlife corridors. However, when the LH restoration reaches an advanced state in the longer term, the importance of the LNP as a key component of the GLTP landscape will become clear. Therefore, the park should ensure that wildlife movement corridors remain open and accessible for wildlife to move freely, keeping villages and human activities at least 20 km away from the wildlife corridors. This management action will avoid land degradation through human impact around the wildlife corridors and allow large herbivores to access Limpopo River resources such as water and the alluvial floodplain in the dry season, and probably stimulate wildlife movements towards the objectives for the wider GLTFCA (dispersal movements to BNP and ZNP).
- Nwambia Sandveld and Shrubveld on Calcrete are the largest habitat types occupying 80% of the park (Stalmans *et al*., 2004). They are also the highest grass biomass production in the LNP (Ribeiro *et al*., 2019). Notwithstanding having these food resources, they are the least preferred habitats by LH due probably to human encroachment and lack of water throughout the dry seasons (Dunham, 2004; ANAC, 2022). Furthermore, these habitats establish a connection between areas of

greater concentration of LH (Lebombo North, Pumbe Sandveld, and Rugged Veld) and the proposed corridors to BNP, ZNP, and other LH dispersal areas between the two parks. Therefore, I suggest measures in the long term that reduce human impacts, such as avoiding land degradation and fragmentation within and around or adjacent to these habitats. This management action will promote LH's use of these habitats as they will easily access water in the Limpopo River.

- It has been 20 years since the active reintroduction of LH took place in LNP, and the restoration process remains slow and vulnerable (Roque *et al*., 2022) because poaching, human encroachment, and livestock keeping still harm wildlife (Andresen *et al*., 2014; ANAC, 2022). Therefore, rather than relying only on wildlife passive movements through KNP-LNP fence gaps, the park should actively translocate some species (eland, sable antelope, blue wildebeest, and white rhino) that show low recovery trend (Roque *et al*., 2021, 2022). This management measure will accelerate LH restoration in the park. However, this action should be combined with the Limpopo National Park law enforcement capacity strengthening to prevent the decline of reintroduced species due to poaching.
- The study findings suggest connectivity between different habitats within the LNP despite the intense human presence in the core area and buffer zone, highlighting the potential human-wildlife conflict risk. Some connectivity areas remain the same from historical periods. Therefore, I suggest further research on connectivity in the larger GLTP through GPS tracking of LH species. It would allow the definition of corridors from the KNP-LNP fence (West) towards the interstitial area between the BNP and ZNP (East), as also quantifying the potential risk of human-wildlife conflict at finer spatial scales to improve future management in the LNP and GLTP.
- The results revealed that some habitats (Pumbe Sandveld, Lebombo North, and Mopane Rugged Veld) are determinant in the prevalence of LH. However, these habitats have a smaller surface area in the park. Therefore, I suggest future studies on predicting habitat suitability and estimating ecological carrying capacity in the LNP. These measures may allow the park to design measures to prevent habitat degradation through overgrazing.

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