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EDITED BY
Orsolya Valkó,
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Hungary

REVIEWED BY
Francesca Parrini,
University of the Witwatersrand,
South Africa
Francois Deacon,
University of the Free State,
South Africa

*CORRESPONDENCE
Dionísio Virgílio Roque
roque200781@gmail.com

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

Dionísio Virgílio Roque[1]*, Valério António Macandza[1], Ulrich Zeller[2], Nicole Starik[2] and Thomas Göttert[3]

[1]Department of Forestry Engineering, Faculty of Agronomy and Forest Engineering, Eduardo Mondlane University, Maputo, Mozambique, [2]Albrecht Daniel Thaer–Institute of Agricultural and Horticultural Sciences, Faculty of Life Sciences, Humboldt-Universität zu Berlin, Berlin, Germany, [3]Research Center [Sustainability–Transformation–Transfer], Eberswalde University for Sustainable Development, Eberswalde, Germany

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 is based on a systematic literature search, censuses reports, online databases, dung count transects, and camera trap surveys. We mapped all LH observations and movements using ArcGIS 10.1. 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 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 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 populations of LH. 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

large herbivores, historical distribution, movement patterns, species collapse, species restoration, ecological corridors, Limpopo National Park, current distribution

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 (International Union for Conservation of Nature [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, travelers, and naturalists recorded only historical occurrence of animals along well-traveled routes, and few traveled at night, thereby missing the nocturnal species (Boshoff et al., 2001). Furthermore, hunters might tend to over-interpret the behavior 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.

Archeological research has demonstrated that Iron Age communities settled in southern Africa by AD 200. 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, practiced 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 fifteenth and seventeenth centuries was one of gold mining and trade, which decreased at the beginning of the eighteenth century, and the ivory and wildlife skin trade began (Newitt, 1997; Madeiros, 2017). The increased ivory and wildlife skin trade along Transvaal and Limpopo River affected the distribution, migration, and other movements of wildlife in today's LNP and KNP (Huffman, 1996). Migrations of millions of ungulates were common until the nineteenth century in Africa (Roche, 2008). However, at the beginning nineteenth century these have declined dramatically in both number and size and many of those that still occur are believed to be 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 completely within 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 KNP in South Africa, Gonarezhou National Park (GNP) in Zimbabwe, Banhine National Park (BNP), and Zinave National Park (ZNP) in Mozambique, and the interstitial zone between these parks (Direcção Nacional das Áreas de Conservação [DINAC], 2003; Milgroom and Spierenburg, 2008). The GLTP consists of a network of transboundary ecosystems of African savannas (Direcção Nacional das Áreas de Conservação [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" (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 mid to late nineteenth 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; Mavhunga and Spierenburg, 2009). In the early twentieth 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 toward 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., 1966; Mavhunga and Spierenburg, 2009).

Wildlife has historically taken movements from KNP to LNP and vice versa (Pienaar et al., 1966; Mabunda et al., 2012). The construction of the KNP—LNP fence in 1976 impacted negatively the KNP, LNP, and GNP because it separated the LH population and blocked 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 removal of KNP–LNP fence sections in the early twenty-first century (Mabunda et al., 2012; Lunstrum, 2014) allowed wildlife to move freely between these parks (Mabunda et al., 2012). 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 use of land 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 twentieth and twenty-first 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 (Direcção Nacional das Áreas de Conservação [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, LNP defined six potential wildlife ecological corridors 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; Parque Nacional de Limpopo [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 selected LH species, (ii) to investigate how the distribution and movement patterns of LH have changed over time, and (iii) to discuss the suitability of proposed ecological corridors in the GLTP. We used scientific systematization to test the hypothesis that the proposed wildlife corridors are suitable. 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.

Materials and methods

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. 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 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°C and 30°C. Rainfall is low, presently ranging from 300 mm/year in the North to 500 mm/year in the South. Rainfall is also markedly seasonal with 95 percent of the yearly rainfall occurring in the wet season (Direcção Nacional das Áreas de Conservação [DINAC], 2003; 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 the red sand mantle, whereas alluvium and clay sediments characterize the Limpopo floodplains (Direcção Nacional das Áreas de Conservação [DINAC], 2003).

LNP has three main river systems with crucial impacts on the 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 has a large effect on the wildlife distribution (Direcção Nacional das Áreas de Conservação [DINAC], 2003). Subsistence farming, free grazing of livestock, and "bush meat poaching" (illegal hunting of wildlife for local consumption) characterize the settlements in the LNP (Andresen et al., 2014). Most of the population (around 20,000 people) is concentrated in 43 villages along the bank of the Limpopo River, where the alluvial soils are suitable

for agriculture (Bazin et al., 2016). The remaining inhabitants live in seven villages in the central area (Shingwedzi River) of the park (Milgroom and Spierenburg, 2008) and are slated to be resettled in an area outside the current LNP border termed the "buffer zone" (**Figure 1**; Massé, 2016). In these villages, there are about 9,000 head of domestic cattle (Serviço Distrital de Atividades Econômicas [SDAE], 2012) that share grazing areas with wildlife. The continuous matrixes of agricultural resettlements along the Limpopo River and Shingwedzi Valley (Andresen et al., 2014), and the KNP—LNP fence act as barriers to wildlife distribution and migrations in the GLTP.

Although wildlife populations were almost decimated due to Mozambique's civil war and decades of poaching (Hatton et al., 2001; Lunstrum, 2016), 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 (*Kobus ellipsiprymnus*), roan antelope (*Hippotragus equinus*), Lichtenstein hartebeest (*Alcelaphus lichtensteinii*) and impala (*Aepyceros melampus*)] 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 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 vast 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 migration routes are still blocked (Mabunda et al., 2003, 2012), there is little scientific evidence of LH movements through fence gaps (Andresen et al., 2012; Grossmann et al., 2014; Everatt, 2015).

Study design

Spatial and temporal scales

For the distribution patterns of LH, the study area is restricted within the LNP park boundaries. However, because the ungulates exhibited a diversity of movement strategies, namely 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 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 mining and trade without wildlife pressure; at the beginning of the eighteenth century (peak of the colonial period), gold mining 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 country wide (Hatton et al., 2001; Dunham, 2004); 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 be focused on these species due to their high hunting value and thus, leaving out certain other species (Elton, 1872; Erskine, 1874; Sealous, 1908; Martinho, 1934; Sidney, 1965; Smithers and Tello, 1976; Dias, 1981). These species also represent different residence guilds (**Table 1**).

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 archeological information, journal articles, reports, mammals atlas, and books written by some of the literate pioneers—notably European explorers, travelers, naturalists, and big game hunters. Our primary sources of literature information include Mozambique's Historical Archive, Eduardo Mondlane University Library, and Systematic

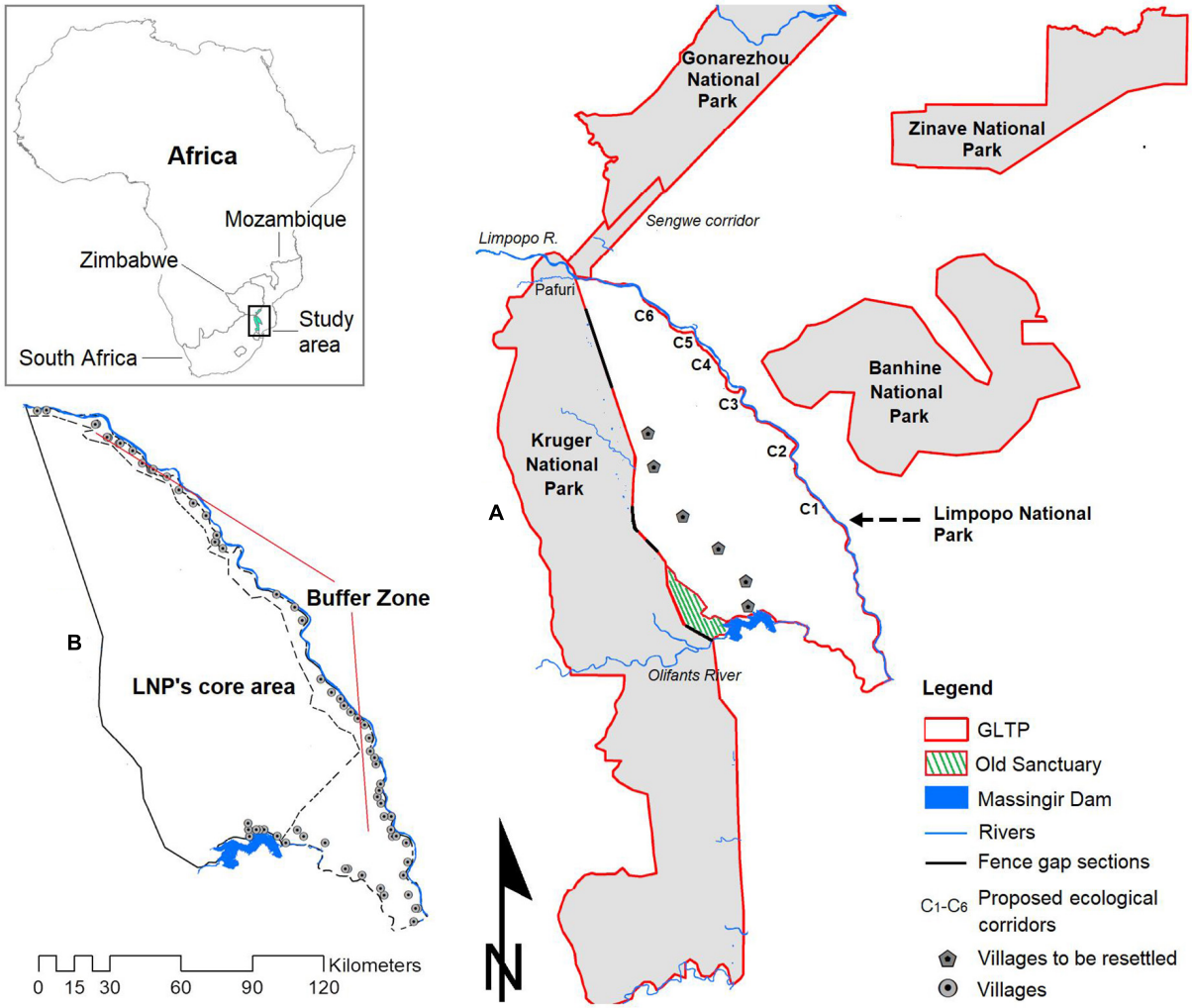

FIGURE 1
Overview of study area showing **(A)** the Great Limpopo National Park, removed fence sections, "scape sites," proposed ecological corridors, villages in the core area to be resettled in the buffer zone, and **(B)** the buffer zone with villages.

TABLE 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

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 the 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" (Global Biodiversity Information Facility [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; Grossmann et al., 2014; Administração Nacional das Áreas de Conservação [ANAC], 2018).

Current data

For the current period, we walked for 3 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 × 108 km^2 grid cells surveyed. We deployed one camera trap in each grid (Rovero et al., 2014; Debata and Swain, 2018) at 0.50–1.5 m in height on trees and shrubs. The cameras were active 24 h a day and took bursts of two successively high-resolution photos, 14 MP (4426 × 3312P) with a delay of 60 s 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 a total of 146 sampling units. Average length of camera deployment at each sampling unit was 69.5 days (*SD* = 31.2; min = 28; max = 122). Each camera trap 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 a total of 10,000 km^2 of the park with the camera traps and dung count transects.

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 a new ArcMap layer was created from the indicated occurrence and movement of species in the maps. The density of points and arrow directions related to the occurrence and movements of LH 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 we converted them to camera independent-observation (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). For the dung count transect, we considered as independent events the dungs 50 m apart. From camera trap and dung data, maps of species distribution were generated in ArcGIS.

Records that mention the occurrence of LH and allude to movements by one or more study species were mapped using ArcGIS 10.1. 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 patterns of species distribution. We depicted the LH occurrence in graduated symbols of four classes in ArcGIS 10.1 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 number of observations in a period, the more widely distributed the species. Thus, we calculated the species observations by reference as the total records of species in a period divided by the total number of references. 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 completely fenced in 1976 (Mabunda et al., 2003, 2012). After this year, the movements occurred only through fence-removed sections and "gap sites." We generated maps of movements for each LH species from the 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 (Dunham, 2004; 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 10.1 to indicate the area of movement and its direction. Each movement area depicted on the maps represents a 5 km of radius as we assumed the species can disperse within 5 km of the sighting (Stoldt et al., 2020). To assess the suitability 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 we compared 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 others areas between the two parks (Macandza and Ruiz, 2012; Parque Nacional de Limpopo [PNL], 2012). A total of 70 historical literature passages, six hand-drawn maps, 13 digital maps (**Supplementary Tables 1, 2**), 36 online records from the Global Biodiversity Information Facility (GBIF), 1,459 records from camera traps, 386 records from dung counts and 1,162 records from censuses which mention, or allude to LH occurrence and movements, were found in the study area.

Results

The taxa dealt with in this study (seven LH species with a body mass > 150 kg) are listed in **Table 1**. Species distribution and movement patterns are grouped and described based on their degree of similarity in terms of diet or movement guild. We also consider significant zones (North, South, Center, West, and East) of the Limpopo National Park (LNP).

Prehistoric and start of the colonial period (1500)

In this period, all species except the white rhino (*Ceratotherium simum*) were sporadically recorded in the present-day LNP. African elephant (*Loxodonta africana*) and eland (*Tragelaphus oryx*) were recorded in the Pafuri region of the LNP. African buffalo (*Syncerus caffer*), plains zebra (*Equus quagga*), and blue wildebeest (*Connochaetes taurinus*) were sporadically recorded in the Pafuri region of the present-day LNP and extreme northwest of the present-day LNP. Giraffes (*Giraffa camelopardalis*) were only recorded 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 2A–7A**).

The peak of the colonial period (1800–1975)

In 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

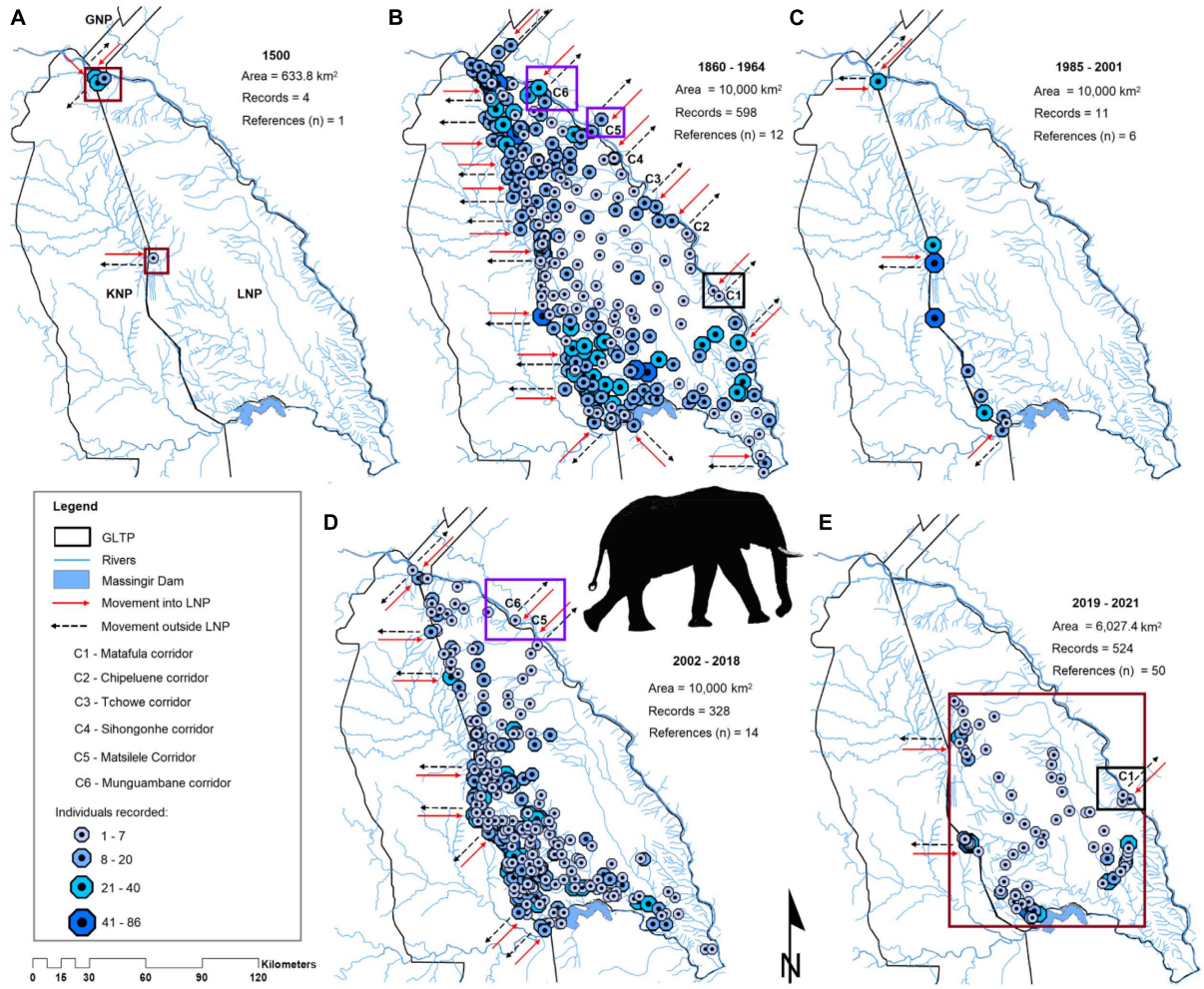

FIGURE 2
African elephant distribution and movement patterns in the LNP, **(A)** prehistoric/start of the colonial period, **(B)** peak of the colonial period **(C)** post-colonial/civil war/intense poaching period, **(D)** proclamation of GLTP period, and **(E)** current period. The area (km^2) represents 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)**, 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.

elephant showed much more movements and used areas that overlap all the proposed ecological corridors (Figures 2B–8B).

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 2C–7C).

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

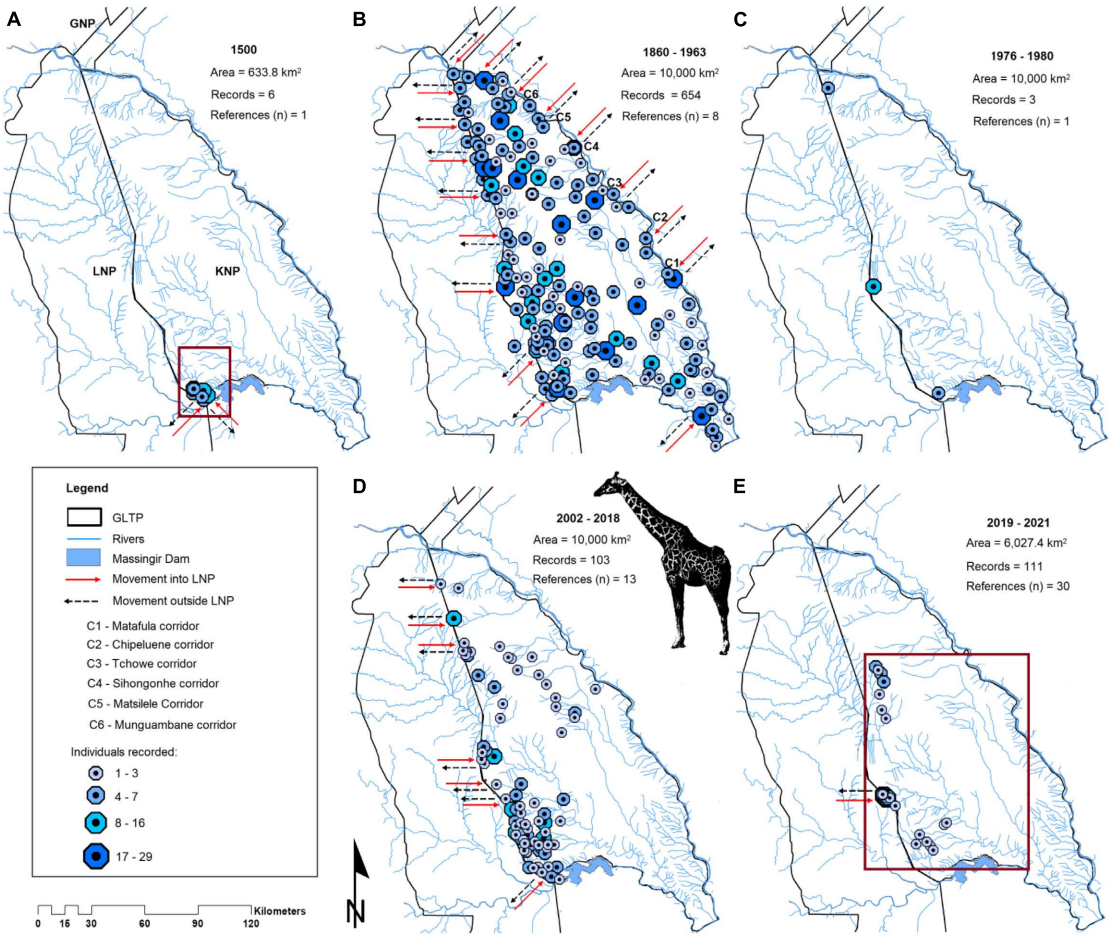

FIGURE 3
Giraffe distribution and movement patterns in the LNP, **(A)** prehistoric/start of the colonial period, **(B)** peak of the colonial period **(C)** post-colonial/civil war/intense poaching period, **(D)** proclamation of GLTP period, and **(E)** current period. The area (km^2) represents the spatial covered by the references, the record is the observation of the species and the reference is the species observation source, 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.

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. Elephant and wildebeest used some of the proposed ecological corridors—Chipeluene, Matsilele, and Munguambane corridors that were also used in the historical period (Figures 2D–8D).

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 2E–7E).

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 Great Limpopo Transfrontier Park to the current period. However, there are species-specific differences in the process of LH recovery: 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 current period (Figure 9).

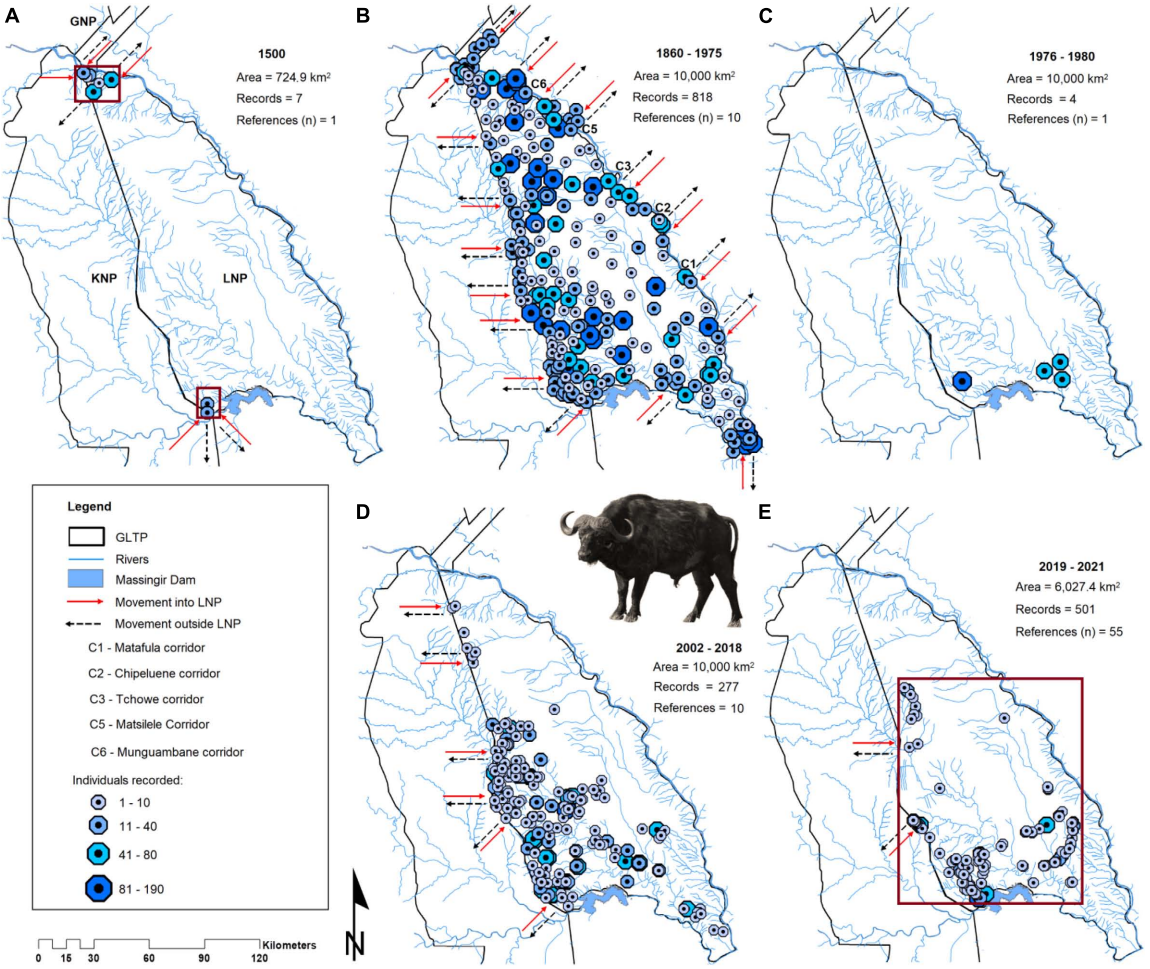

FIGURE 4
African buffalo distribution and movement patterns in the LNP, **(A)** prehistoric/start of the colonial period, **(B)** peak of the colonial period **(C)** post-colonial/civil war/intense poaching period, **(D)** proclamation of GLTP period, and **(E)** current period. The area (km^2) represents the spatial covered by the references, the record is the observation of the species and the reference is the species observation source, 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.

Discussion

This study provides the first attempt to describe the historical distribution and movement patterns of selected large herbivore (LH) species in Limpopo National Park (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 massively 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; Tello, 1977; Dias, 1981; East, 1999; Ntumi et al., 2009; Madeiros, 2017).

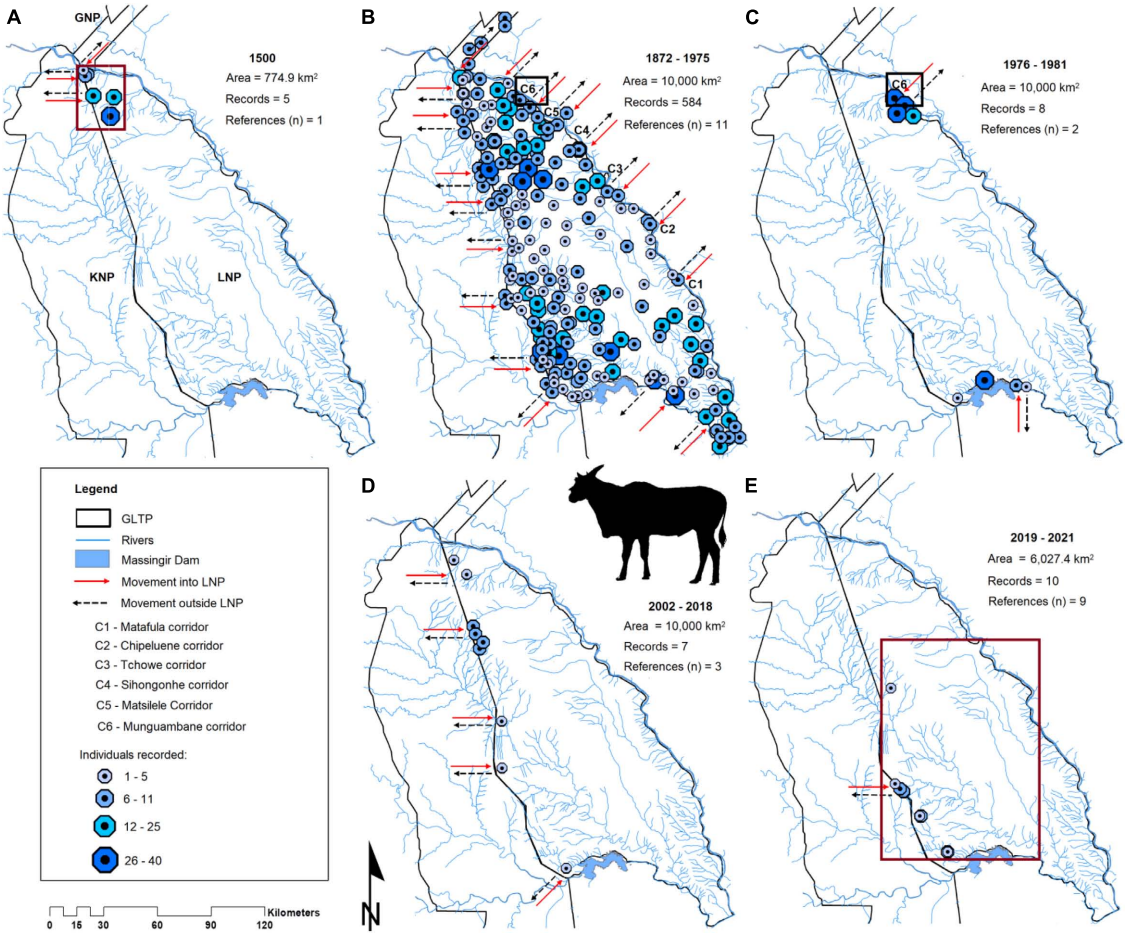

FIGURE 5
Eland distribution and movement patterns in the LNP **(A)** prehistoric/start of the colonial period, **(B)** peak of the colonial period **(C)** post-colonial/civil war/intense poaching period, **(D)** proclamation of GLTP period, and **(E)** current period. The area (km^2) represents the spatial covered by the references, the record is the observation of the species and the reference is the species observation source, dark red rectangles represent the area covered by reference in periods **(A,E)**, 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.

Our results give reason to assume that there is scientific evidence of the functionality of proposed ecological corridors for wildlife movements to BNP and ZNP and vice-versa 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 was also used by the 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.

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 report the occurrence of

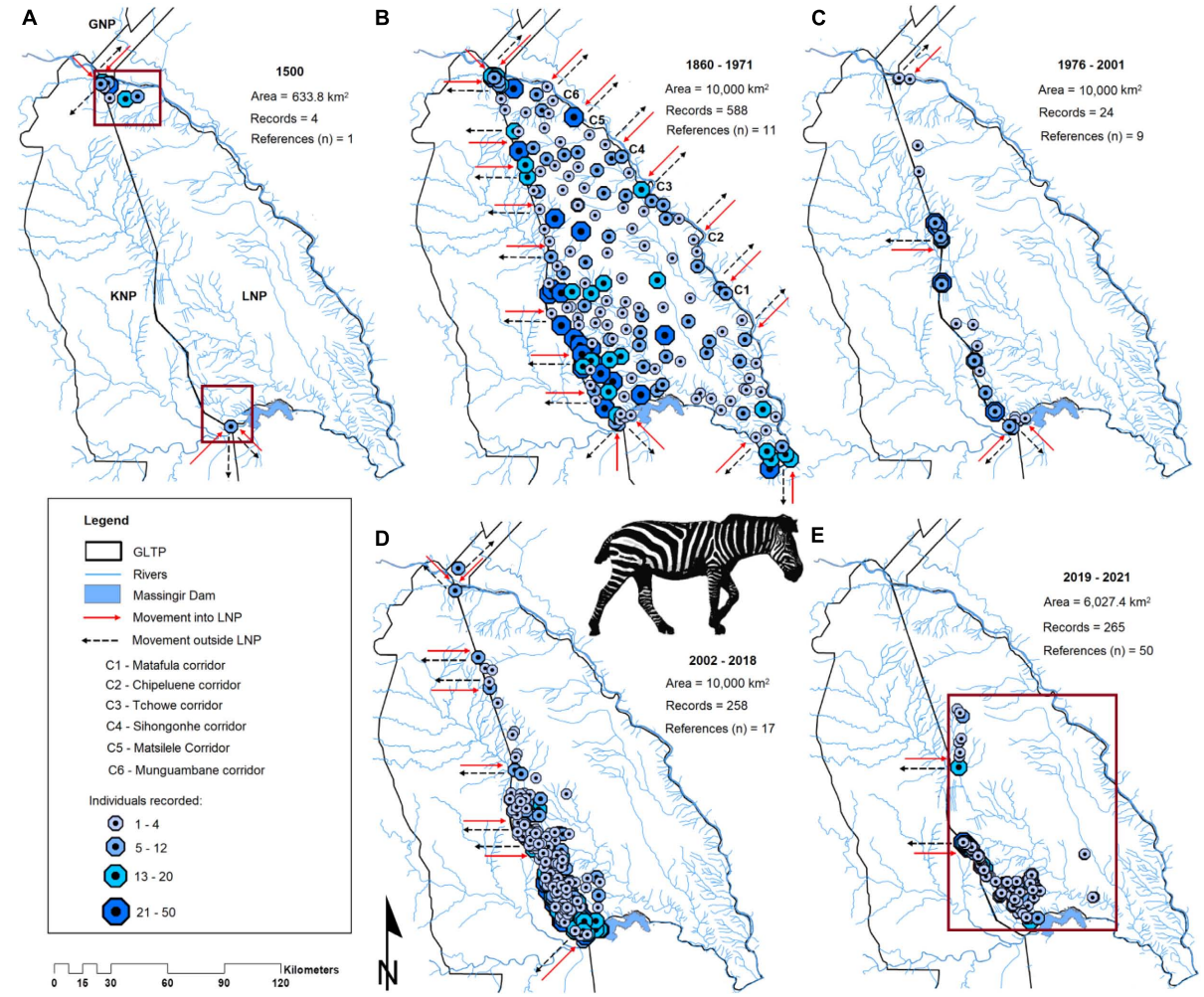

FIGURE 6
Plain's zebra distribution and movement patterns in the LNP, **(A)** prehistoric/start of the colonial period, **(B)** peak of the colonial period **(C)** post-colonial/civil war/intense poaching period, **(D)** proclamation of GLTP period, and **(E)** current period. The area (km^2) represents the spatial covered by the references, the record is the observation of the species and the reference is the species observation source, 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.

LH 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.

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.

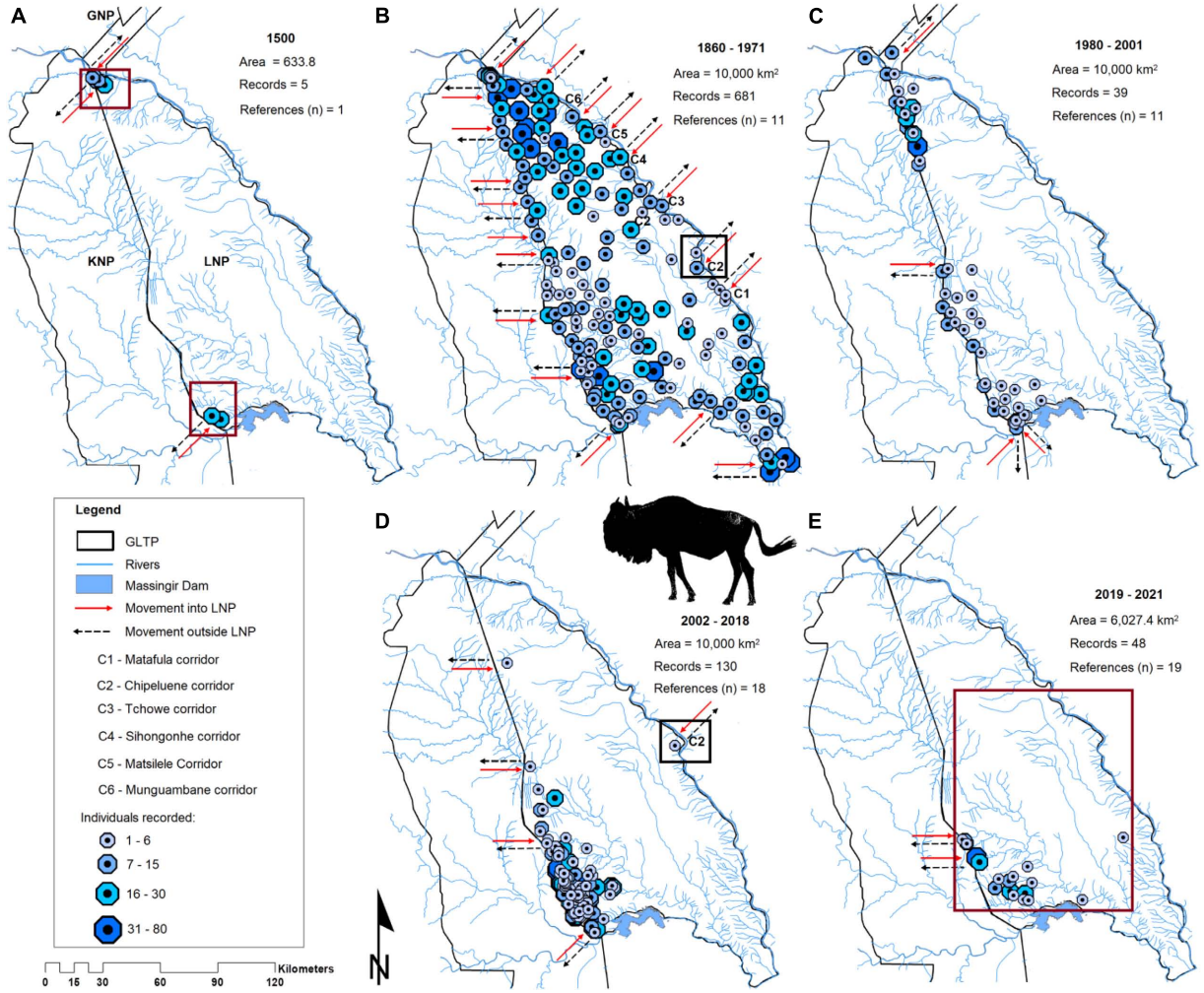

FIGURE 7
Blue wildebeest distribution and movement patterns in the LNP, **(A)** prehistoric/start of the colonial period, **(B)** peak of the colonial period **(C)** post-colonial/civil war/intense poaching period, **(D)** proclamation of GLTP period, and **(E)** current period. The area (km^2) represents the spatial covered by the references, the record is the observation of the species and the reference is the species observation source, dark red rectangles represent the area covered by reference in periods **(A,E)**, 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.

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

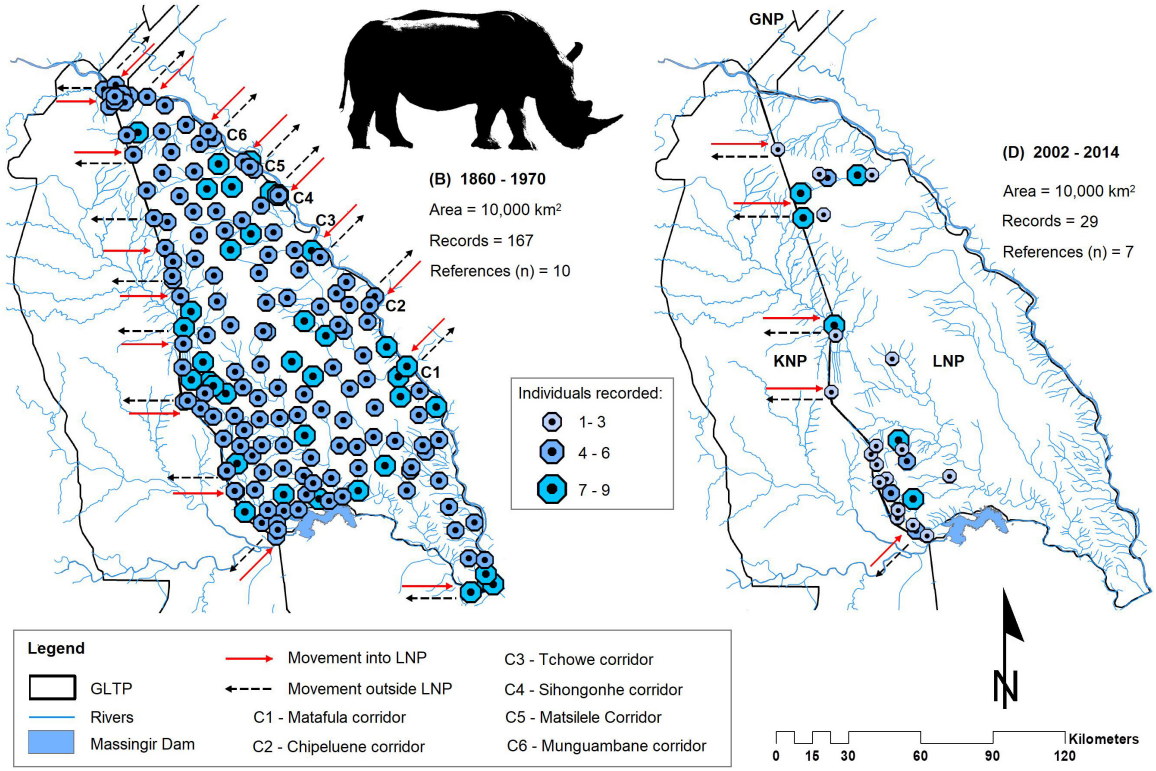

FIGURE 8
White rhino distribution and movement patterns in the LNP, (B) peak of the colonial period, and (D) proclamation of GLTP period. The area (km^2) represents the spatial covered by the references, the record is the observation of the species and the reference is the species observation source. GLTP, Great Limpopo National Park; GNP, Gonarezhou National Park; KNP, Kruger National Park; LNP, Limpopo National Park.

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 flies 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), and 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. Sidney (1965) and Child and Savory (1964), 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).

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 the (iii) 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;

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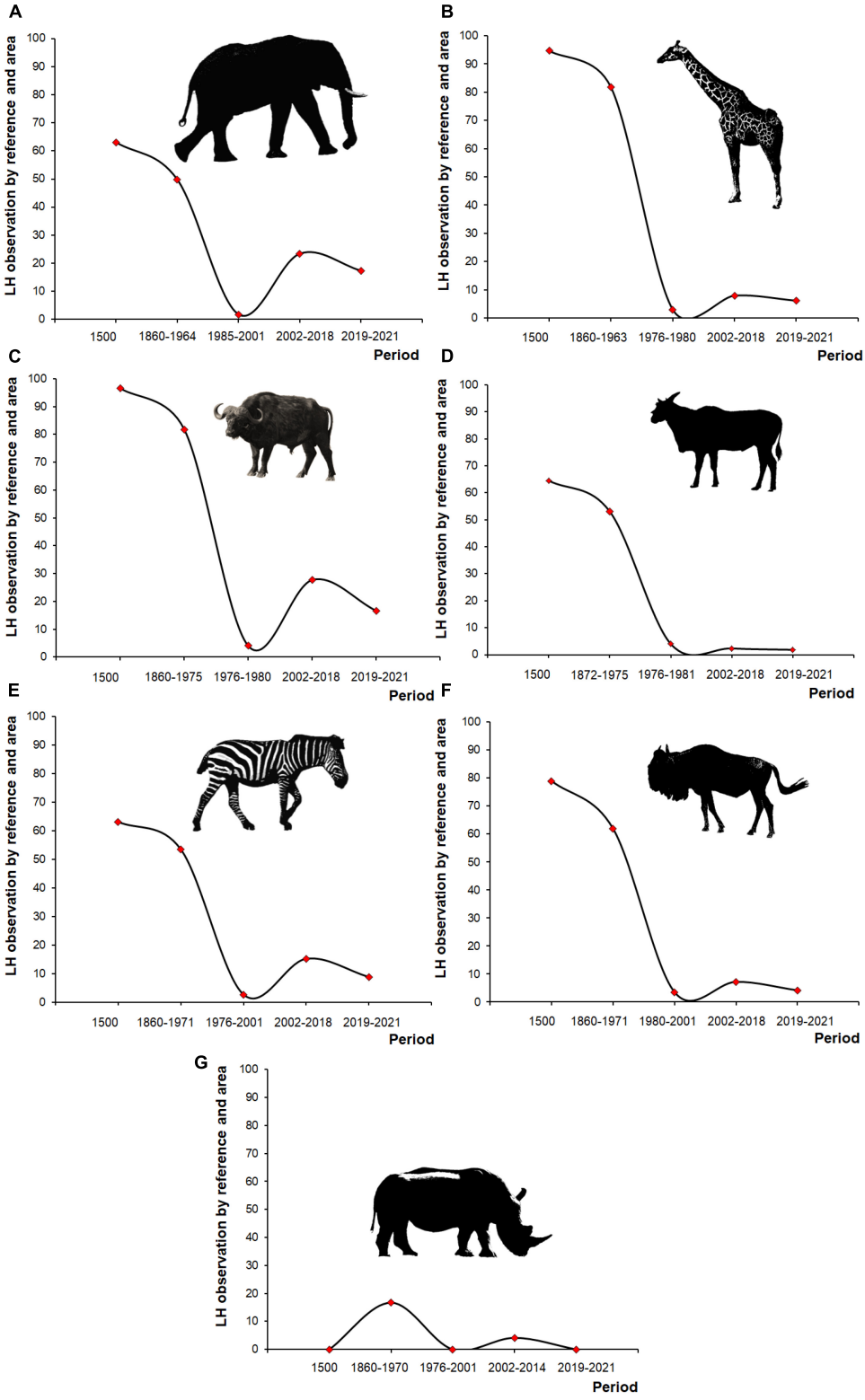

FIGURE 9

Relationship between species observation by references and the total area covered in different study periods of **(A)** 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, total area covered by the references in each period.

Ntumi et al., 2009). This further reduced the large herbivores' range.

Definitely the civil war (1976–1992) ended up with the rest of the wildlife as it forced the government's abandonment of most protected areas and 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, on 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.

Proclamation of Great Limpopo Transfrontier Park 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 (Grossmann 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), Grossmann et al. (2014), Administração Nacional das Áreas de Conservação [ANAC] (2018), and 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; Grossmann et al., 2014; Administração Nacional das Áreas de Conservação [ANAC], 2018), reveal 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 show also behavior similar to blue wildebeest. However, these species according to LNP Park Warden, have suffered from intense poaching for meat and traditional ceremonies at least 10 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 (Parque Nacional de Limpopo [PNL], 2012; Grossmann 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) and 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), and 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 nature 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 on the topic in question as it simultaneously reveals the dramatic collapse of large herbivores in the Limpopo National Park and the process of their restoration. 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 migration patterns.

Data availability statement

The original contributions presented in this study are included in the article/**Supplementary material**, further inquiries can be directed to the corresponding author/s.

Author contributions

DR was mainly responsible for the field survey, data collection, analysis, and manuscript writing. VM was responsible for manuscript revision and field research coordination. UZ was accountable for manuscript revision and funding acquisition. NS was responsible for data collection and manuscript revision. TG was accountable for data collection, analysis, and manuscript revision. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.978397/full#supplementary-material

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