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Landscape connectivity for African elephants in the world's largest transfrontier conservation area: A collaborative, multi-scalar assessment

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Abstract

1. Landscape connectivity operates at a variety of scales, depending on the geography of the area in question and the focal species or ecological process under consideration.
2. Most connectivity studies, however, are typically focused on a single scale, which in the case of resistance-based connectivity modelling, is often the entire landscape or protected area (PA) network. This large, single-scale focus may miss areas that are important for connectivity at smaller scales and that can be documented via observed animal movements without resorting to landscape-wide statistical modelling and extrapolation approaches.
3. Here, we characterize landscape connectivity at three different scales (local/micro, inter-PA, and landscape-wide/macro), using observed animal movements rather than conventional resistance surface models, to produce a connectivity conservation blueprint for African elephants (*Loxodonta africana*) in the Kavango-Zambezi transfrontier conservation area (KAZA) in southern Africa. This analysis is based on an extensive, high-resolution GPS tracking database comprising approximately 4 million GPS locations from nearly 300 tagged elephants and their associated herds.
4. Our results show that high-fidelity elephant use of micro-corridors is typically—though not exclusively—related to directed movements towards water, often

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amidst heavy anthropogenic presence. Movement pathways that connected KAZA's core protected areas were longer and variable, with some channelled into narrow areas of use and others more dispersed across larger sub-landscapes. At the largest scale, a network analysis incorporating all used landscape grid cells revealed several clusters of large-scale movement corridors that connected distant parts of KAZA.

5. *Synthesis and applications*: Our three scales of analyses reveal disparate geographical priorities for connectivity conservation that collectively could help ensure the functional connectivity of KAZA for its largest inhabitants. Each scale will require its own set of inter-related conservation interventions, while further research into areas with sparse data collection, and other species of conservation concern, could reveal additional connectivity priorities at each scale.

KEYWORDS
animal movement, functional connectivity, landscape ecology, movement ecology

1 | INTRODUCTION

Landscape connectivity (the degree to which a landscape facilitates or impedes movement among resource patches; Fahrig et al., 2020) has received increasing attention in recent years from policy and research standpoints. From a policy perspective, the Post-2020 Global Biodiversity Framework (Xu, Cao, et al., 2021) prioritizes connectivity in several goals and targets, particularly the goal to conserve 30% of land and water in a system of well-connected protected and conserved areas, with an ongoing discussion surrounding indicators and measurement of such connectivity (Brennan et al., 2022; Saura et al., 2018; Theobald et al., 2022). From a research standpoint, connectivity studies are now common in the applied ecology and conservation literature (Kumar, Turnbull, et al., 2022). Typical workflows involve the development of a resistance layer from movement data, genetic information, point observations or expert opinion (Dutta et al., 2022), followed by circuit theory (Dickson et al., 2019) or least-cost analyses (Sawyer et al., 2011) to identify potential corridors or connectivity hotspots. These studies have helped inform conservation plans in which protected areas (PAs) and other important habitat patches are connected for individual species or species assemblages (e.g. Brodie et al., 2015; Dickson et al., 2013; Gangadharan et al., 2017).

Despite the proliferation of landscape connectivity studies, research has highlighted limitations with the conventional resistance modelling approach. These limitations include extrapolation of movement models, often based on limited sample sizes, to geographical scales far exceeding the conditions in which they were developed (Kumar, Turnbull, et al., 2022); an inability to represent significant variability among individuals, seasons, movement modes and geographic locations (Keeley et al., 2017; Kumar, Turnbull, et al., 2022); and the often poor ability of statistical models based primarily on remotely sensed information to reflect movements shaped by conspecific and interspecific interactions, memory and other unobservable factors (Brennan et al., 2018; Cífka et al., 2023; Merkle et al., 2019; Nuñez et al., 2022). In addition, connectivity modelling using a single, relatively coarse resistance layer for an entire landscape may be unable to capture important, finer-scale pockets of connectivity at daily, seasonal or home-range scales (Sawyer et al., 2011) that are also critical to maintain. The location of nodes (i.e. sources/destinations in least-cost and circuit theory analyses) in conventional connectivity analyses has a dominant effect on resulting patterns (Koen et al., 2014) which may also contribute to missing important areas for animal movement and connectivity at scales that are different from the scale of node placement, or if nodes are otherwise incorrectly placed. Omnidirectional methods, typically via circuit theory, can minimize node effects (Brennan et al., 2020), but few studies have validated these methods for multiple scales of movement (Dertien & Baldwin, 2023).

In light of these limitations, recent conceptual and methodological advances have charted various paths forward for landscape connectivity. Revisiting the earliest literature has led to the suggestion of three types of connectivity, with 'Noss connectivity' (i.e. structural connectivity) most closely aligned with typical approaches for assessing landscape connectivity (Fahrig et al., 2020). In contrast, Merriam connectivity (i.e. functional connectivity sensu stricto) refers to observed animal movements among landscape elements and, in combination with 'Hanski connectivity' (i.e. patch-level contributions to landscape occupancy and meta-population persistence), allows a full characterization of how connected a landscape is for a focal species. Resistance models parameterized with empirical movement data can estimate Merriam connectivity, but the resulting maps depict predicted, rather than observed, movements. Without resistance modelling and its attendant difficulties, Merriam connectivity is typically difficult or impossible to measure in large conservation landscapes, due to the enormous effort required to adequately sample a representative fraction of a target population with GPS tags (Fahrig et al., 2020, though see Donnelly et al., 2021), although mark–recapture studies can provide similar, albeit lower-resolution, connectivity estimates (e.g. Nightingale et al., 2023). Advances in simulating trajectories from models of individual animal movement hold great promise for characterizing Merriam connectivity (Kumar, Kaszta, et al., 2022; Schumaker & Brookes, 2018; Whittington et al., 2022), as does direct inference via network theory when adequate sampling of target populations is achievable (Bastille-Rousseau et al., 2018; Bastille-Rousseau & Wittemyer, 2020). However, examples of these advances remain rare in the landscape connectivity literature.

As an empirical contribution to recent conceptual and methodological advances, we use an extensive, high-resolution database of GPS-collared African savanna elephants (*Loxodonta africana*) to evaluate multi-scale landscape connectivity in the Kavango-Zambezi transfrontier conservation area of southern Africa (hereafter, 'KAZA'). We assess connectivity directly at three scales (which we term micro-corridor, inter-PA, and macro-corridor), using approaches from the movement ecology and connectivity literature that do not rely on understanding the underlying habitat or matrix condition for elephants, or on resistance surface modelling or extrapolation. We examine multiple scales because connectivity is not only a species-specific attribute, but also an attribute specific to different movement processes that occur at different scales (e.g. long-distance dispersal versus short-distance movements for foraging; Riordan-Short et al., 2023). In KAZA, we examine 'micro-corridors' to identify small-scale movement corridors, 'inter-PA' pathways to identify areas important for connecting pairs of KAZA's protected elephant populations and 'macro-corridors' to identify areas important for connectivity across the entire set of GPS-collared elephant movement trajectories. Each scale represents a movement process whose maintenance is critical to effectively conserve elephants across the entire landscape, and by observing such multi-scale connectivity directly, factors that are difficult to incorporate via modelling and extrapolation (e.g. memory, social interactions and individual variability) may be better captured. This work therefore advances the current state of landscape connectivity research in two ways: (1) an explicit consideration of multiple scales of connectivity across a landscape; (2) direct assessment of Merriam connectivity via network theory and observed empirical movements using a very large sample of tagged animals. Our results provide a multi-scalar blueprint for conserving connectivity for elephants in KAZA, and can be updated as more information becomes available for elephants and additional species of conservation concern.

2 | MATERIALS AND METHODS

2.1 | Study site

KAZA spans parts of five southern African countries (Angola, Botswana, Namibia, Zambia, Zimbabwe) and at 520,000 km^2 is the world's largest terrestrial transfrontier conservation area. The landscape is a mosaic of protected areas, game reserves, hunting areas, communal lands, private leaseholds, tourism concessions and state or community forests. Most of KAZA is a mixture of savanna, woodland, dry forests, wetlands, floodplains and bushland ecoregions (Dinerstein et al., 2017). The transfrontier landscape contains about half (~228,000) of Africa's remaining savanna elephants (Bussière & Potgieter, 2023) and is considered a global conservation priority due to its exceptional biodiversity values (Tear et al., 2014). KAZA has strong seasonality, with ~600 mm of rain falling primarily during the November–April wet season, a pattern that shapes seasonal movements of migratory or nomadic herbivores (Bartlam-Brooks et al., 2013; Bennitt et al., 2022; Naidoo et al., 2016; Tshipa et al., 2017). Around 3 million people live in KAZA, many of whom practice subsistence agro-pastoralism (Salerno et al., 2020). Nature-based tourism has been viewed from KAZA's inception as a way to boost local economies and alleviate poverty (Suich, 2008), but despite benefitting tourism, wildlife, including elephants, impose substantial costs on local communities (Stoldt et al., 2020). Previous movement ecology and connectivity research on elephants in KAZA has focused on particular sub-landscapes across the transfrontier area and has documented long-range movements and migrations (Tshipa et al., 2017), as well as both natural and anthropogenic barriers to movement (Huang et al., 2022; Songhurst et al., 2016), especially the impact of veterinary fences on connectivity (Naidoo et al., 2022).

We collated data from existing elephant GPS collaring efforts within the relevant parts of the five countries that comprise KAZA. Collaring of elephants occurred in independent projects over a 15-year period, with all projects approved by the relevant government agencies in the country in question and following official guidelines for such efforts (see Buchholtz et al., 2019; Naidoo et al., 2022 for example descriptions of field protocols). Our multi-year approach focused on data-sharing for conservation results within a collaborative and contributing working group of research, governmental and practitioner peers. This process led to buy-in from most of the key stakeholders working on elephant conservation in KAZA and allowed us to amplify our movement data set to answer broader questions beyond what any single research group could have addressed (Sequeira et al., 2019). Ultimately the collaboration resulted in a combined data set of 3,994,208 GPS observations from 291 collared elephants (n = 266 Africa Wildlife Tracking, Pretoria, South Africa; n = 25 Vectronic Aerospace, Berlin, Germany) spanning 2009–2023, with 77% of observations recorded at 1-h intervals (range 15 min–12 h). All collared individuals were adults and included 158 females (usually found in breeding herds of 10–20 individuals) and 133 males. Sampling across the five KAZA countries was as follows: Angola = 19 animals collared; Botswana = 60; Namibia = 88; Zambia = 32; Zimbabwe = 92 (Table S1).

We assess connectivity at three scales: micro-corridors (small-scale movement corridors defined by the speed and directionality of elephant movement steps), inter-PA (the subset of pathways that connect pairs of KAZA's core protected areas) and macro-corridors (the most important grid cells, identified by betweenness centrality, for connectivity across the entire set of GPS-collared elephant movement trajectories).

2.2 | Micro-corridors

To guide hypotheses on the location of small-scale movement corridors (hereafter, 'micro-corridors'), we used data visualization techniques previously applied to transportation systems that involve the use of transparent white lines on a black background to highlight the direction and intensity of fine-scale movement trajectories (Cheshire & Uberti, 2014). Wildlife micro-corridors provide access to drinking water and other key seasonal resources for elephants in landscapes that are largely anthropogenic (Osipova et al., 2018; Songhurst et al., 2016). To identify micro-corridors, we first summarized the number of elephant movement steps (i.e. lines connecting consecutive GPS locations) passing through each cell of a 100-m resolution grid overlayed over KAZA (Figure 1). We further calculated the average speed of individuals passing through each grid cell, as well as the dot-product, which measures the degree of directed movement through a cell (Wall et al., 2013); values close to 1 indicate highly directional movement where most movement steps in a grid cell are parallel to one another. We then used a set of previously identified, well-studied micro-corridors in the Botswana part of KAZA (Songhurst et al., 2016) and examined grid cell-level data inside digitized corridor shapefiles to identify combinations of cell use, speed and dot product that were characteristic of micro-corridor movement. We used the 75% quantile to identify intensity-of-use levels of 1140 m/ha, speed levels of 1.34 km/h, and dot product values of 0.94 as thresholds above which micro-corridor movements were defined. Extracting grid cells with these values resulted in strong alignment with independently derived corridor pathways in the Okavango panhandle (see Figure S1 in Supporting Information; Songhurst et al., 2016). Using these threshold values, we subsequently identified and mapped 100-m grid cells across the entire KAZA landscape that contained these characteristics. Our definition of micro-corridor is thus a function of animal movement behaviour, rather than the physical characteristics of the landscape, an approach that has also been used for other species and geographic contexts (e.g. LaPoint et al., 2013; Wall et al., 2013).

2.3 | Inter-PA pathways

We considered KAZA's core protected areas to be all national parks ($n = 19$) along with Moremi Game Reserve in northern Botswana, the globally significant Okavango Delta's premier PA (see Figure S2 for labelled map of core PAs and other key landscape features). Understanding PA connectivity is a key research and policy aim from global to local scales, but the data to comprehensively evaluate actual animal movements that link PAs is rarely available (Fahrig et al., 2020; Sequeira et al., 2019). Here, for each pair of core PAs ($n = 190$), we extracted and mapped all elephant movement pathways that connected them. Pathways began at the point of exit of one PA and ended when the animal reached the second PA, regardless of the length of time reaching the second PA took. We buffered each pathway by 500 m to account for deviations in actual animal location versus observed GPS points and interpolated tracks (Merkle et al., 2023). We then converted each pathway from a buffered line to a 500-m resolution raster and summed all rasters together, with the final layer reflecting the number of inter-PA pathways passing through each 500-m grid cell in KAZA.

2.4 | Macro-corridors

We used spatially explicit network methods (Bastille-Rousseau et al., 2018) to circumvent the limitations of typical resistance-based connectivity analysis pipelines described in the Introduction, allowing us to make inference on large-scale connectivity directly. In particular, our approach takes advantage of the massive GPS collar sampling effort across the KAZA landscape, which rendered a modelled and extrapolated resistance surface unnecessary. Using R package MoveNT (Bastille-Rousseau et al., 2018), we calculated a grid cell-level measure of betweenness centrality (Minor & Urban, 2007). Betweenness-centrality measures the number of times a focal grid cell falls on the shortest pathway between two other grid cells; grid cells that fall in between many others therefore have high betweenness-centrality scores, reflecting their position as important conduits within a network. Previous research has demonstrated that betweenness centrality can be a good proxy for landscape connectivity in various settings (e.g. Mueller et al., 2014), including for elephants (Bastille-Rousseau & Wittemyer, 2020). We divided the surface of KAZA into 500-m (the average step length of 1-h relocations; Bastille-Rousseau et al., 2018) resolution grid cells and for each individual elephant calculated the betweenness centrality of every grid cell within the animal's entire movement trajectory. We then summed betweenness-centrality scores over all individuals and interpreted the resulting layer for spatial patterns that may reflect areas of high connectivity across the KAZA landscape. These 'macro-corridors' thus reflect the most significant parts of the landscape for elephant movement in the context of all observed movements across the entire KAZA transfrontier conservation area.

Lastly, we resampled the micro-corridor layer to the same 500-m resolution as the inter-PA and macro-corridor layers and identified those grid cells containing high values at one, two or all three connectivity scales. For inter-PA connectivity and macro-corridors, we selected the top 0.1% of grid cell values to identify the highest priority connectivity cells at each scale, and used those for subsequent overlap. Visual examination of this threshold confirmed that it captured the main patterns at each of the three scales (see Section 3), whereas lowering the threshold (e.g. to the top 1%) diluted the patterns and resulted in an overly dispersed set of 'high priority' connectivity grid cells.

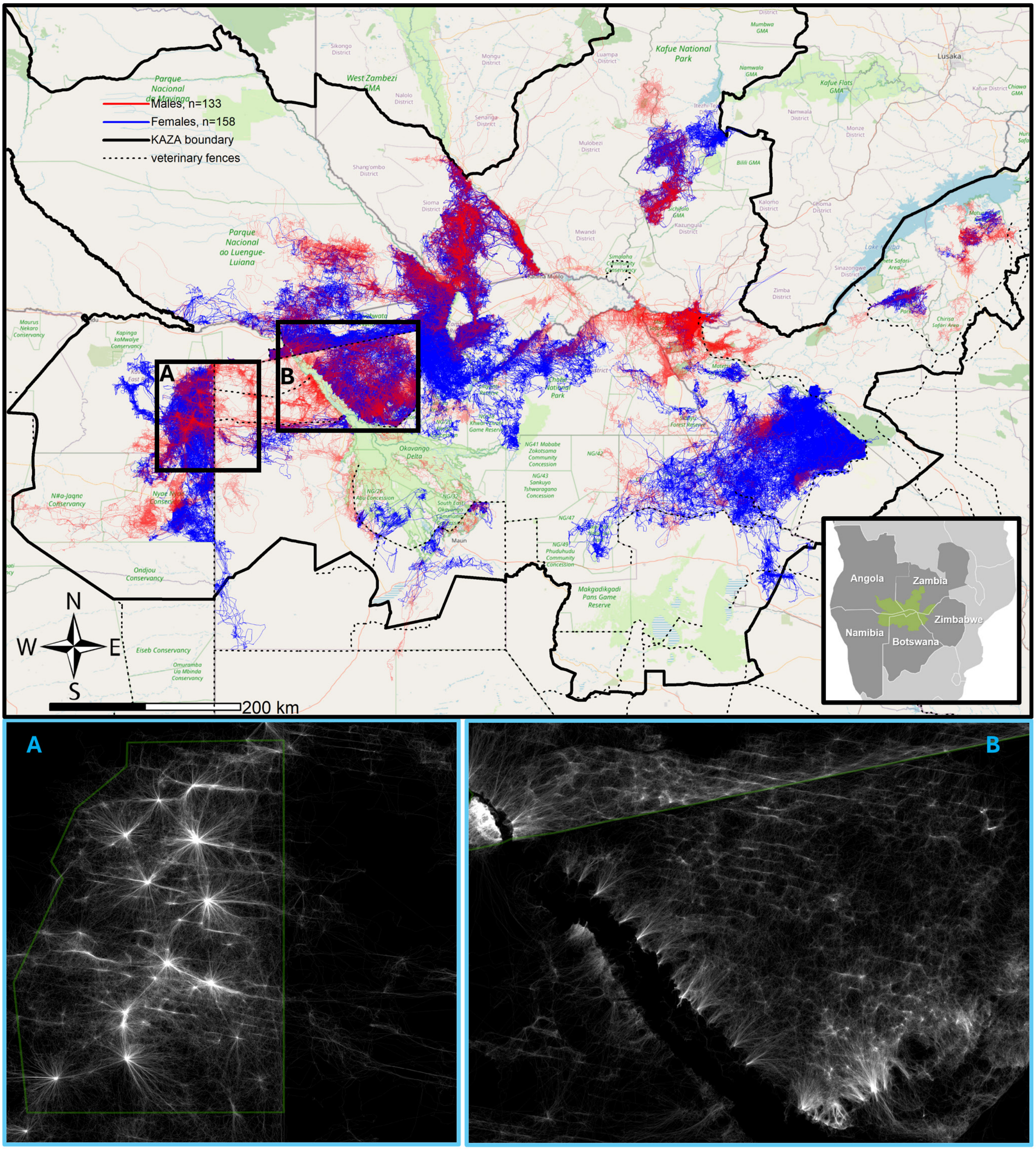

FIGURE 1 GPS sampling of African elephants in the Kavango-Zambezi transfrontier conservation area (KAZA). Upper panel: Location of elephant movement trajectories used in our analyses ($n=133$ males, red lines; $n=158$ females, blue lines. Background from Open Street Map, green polygon on inset locator map shows location of KAZA in southern Africa. Veterinary fences are shown in dashed black lines. Lower panels: Brighter colours indicate greater degree of overlap of GPS-derived movement trajectories. (A) Artificial waterpoint use in Khaudum National Park, Namibia. (B) Micro-corridor use (arrow-like features to the west and south), Okavango Panhandle, Botswana.

3 | RESULTS

Areas with low GPS sample coverage within our elephant movement database in part reflected locations in KAZA where elephants are transient, absent or occur at low densities (e.g. Mavinga National Park in Angola, anthropogenic landscapes between Sioma Ngwezi and Kafue National Parks in Zambia). Three of KAZA's 20 core PAs were not well-covered by our sampling, including Mangetti (Namibia) and Makgadikgadi Pans (Botswana) National Parks, where elephant densities are low and where we had no GPS collars deployed. In contrast, elephant densities are high in Moremi Game Reserve (Botswana) but we had only sparse GPS coverage here ($n=5$ individuals, 3722 GPS points). Elephants also live in high densities in the NG11/NG13 concessions of northern Botswana (Figure 1B), but this region is not a strict PA, and previous research has shown that the substantial elephant population here is largely confined by veterinary fences and human settlements along the Okavango river (Naidoo et al., 2022; Pozo et al., 2017; Songhurst et al., 2016). Overall, there was a moderate and statistically significant correlation between our GPS coverage and dry-season elephant densities recorded during a recent census of elephants across KAZA (see Supporting Information).

3.1 | Micro-corridors

Examination of the grid cells across KAZA that had similar elephant movement characteristics to those of the Okavango Panhandle micro-corridor system revealed numerous micro-corridors falling into three categories: (1) Directed movements to/from water, such as in the Okavango Panhandle region (Figure 2D), other areas along the Okavango, Kwando, Zambezi and Chobe-Linyanti rivers, and artificial water points in Khaudum National Park (Figures 1A and 2B) and north-western Zimbabwe (Figure 2A); (2) Directed movements along fences, with fences thus acting as barriers but also channelling movements alongside them (Xu, Dejid, et al., 2021). This is particularly prevalent along the Namibia-Botswana border fence in Bwabwata National Park (e.g. Figure 2D), but also alongside other fences in Namibia and Botswana; and (3) Pinchpoints and directed movements reflecting

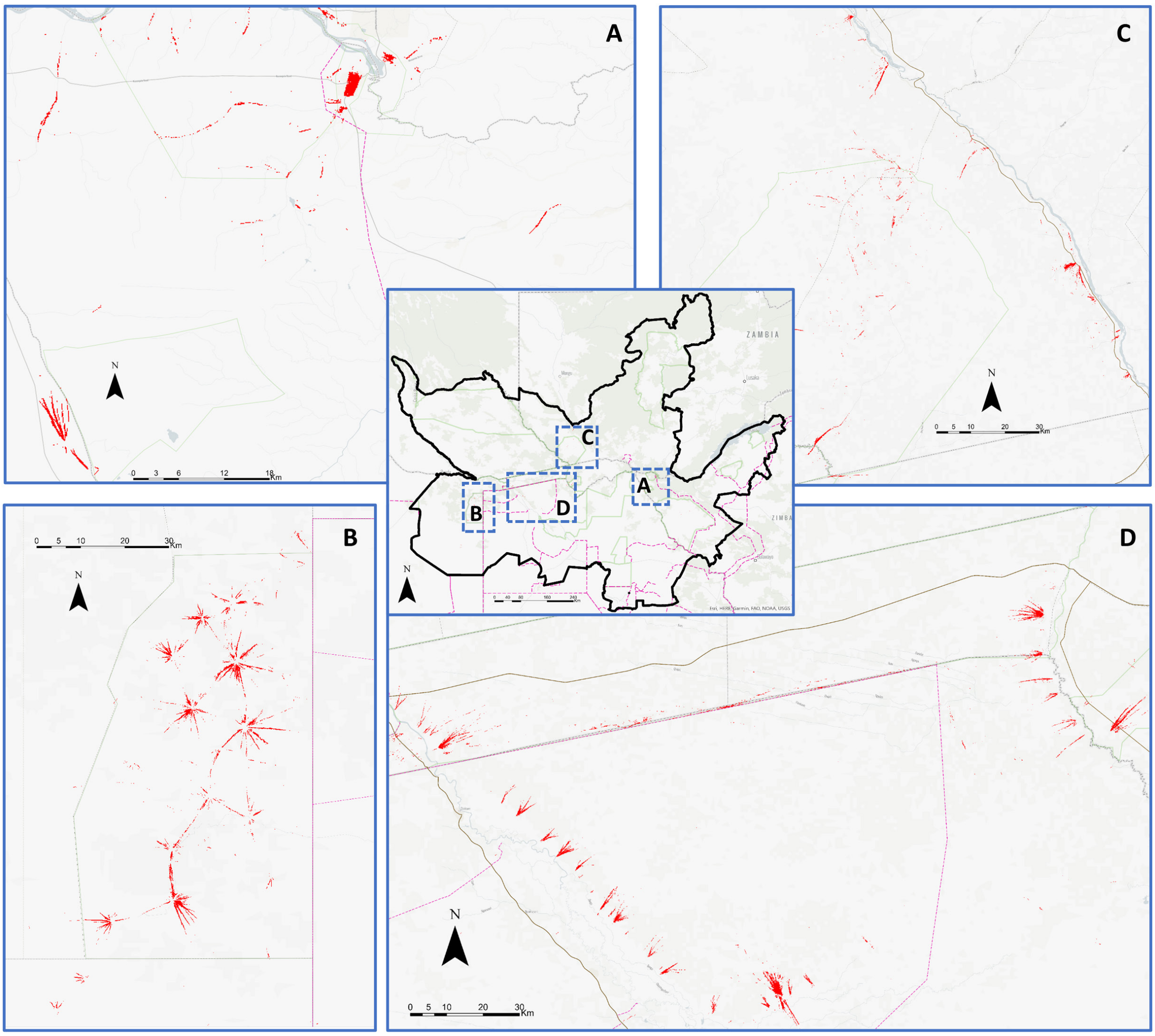

FIGURE 2 Micro-corridor locations (red) arising from analyses of speed and directionality for 291 GPS-collared elephants in the Kavango-Zambezi transfrontier conservation area. (A) Northwestern Zimbabwe; (B) Khaudum National Park, Namibia; (C) Sioma Ngwezi National Park and surroundings, Zambia; (D) Okavango Panhandle and Kwando River environs, Botswana and Namibia. Veterinary fences in each panel are shown in dashed pink lines; brown lines show major roads.

elephant movement across (e.g. roads) or between (e.g. agricultural areas) human-modified parts of the landscape. For example, the clear, sharp corridors along the Namibia/Zambia/Angola border that occur between agricultural fields (Figure 2C), and in/near urban areas such as Victoria Falls and Livingstone (Figure 2A). These micro-corridor movements tended to be relatively short in length (e.g. 4–7 km in the Okavango Panhandle region); however, fast and directed movements of up to 60 km also occurred along fences.

3.2 | Inter-PA pathways

The number of elephant movement pathways connecting pairs of core PAs in KAZA varied from 0 to 1597, with a mean of 28 and a median value of 0 (77% of all PA pairs had no observed pathways connecting them). Mapping these movement pathways highlighted priority areas for inter-PA connectivity that fell into two broad categories (Figure 3). Areas of concentrated inter-PA movements included landscapes between Sioma Ngwezi and Mudumu National Parks (Figure 3A), Bwabwata and Mudumu National Parks (Figure 3B), and a PA complex on the Zimbabwe and Botswana borders that includes Chobe, Kazuma Pan, Zambezi, Victoria Falls and Mosi-oa-Tunya National Parks (Figure 3C). In these landscapes, movement pathways were channelled into corridors either by densely settled anthropogenic areas (Figure 3A), along permanent rivers (Figure 3B), or both (Figure 3C). In contrast, Figure 3D (Khaudum–Bwabwata National Parks), Figure 3E (Nkasa Rupara–Chobe National Parks), and Figure 3F (Hwange–Nxai Pan National Parks) are larger wildlands with multiple dispersed pathways connecting PAs, where elephants traverse dryland landscapes with low human populations and few barriers to movement.

3.3 | Macro-corridors

The betweenness-centrality analysis highlighted movement corridors and known areas of high use in well-studied parts of Zambia (Chibeya et al., 2021), Namibia (Brennan et al., 2020; Naidoo et al., 2018) and Zimbabwe (Tshipa et al., 2017), lending confidence to its surrogacy for landscape connectivity at the transfrontier scale. In particular,

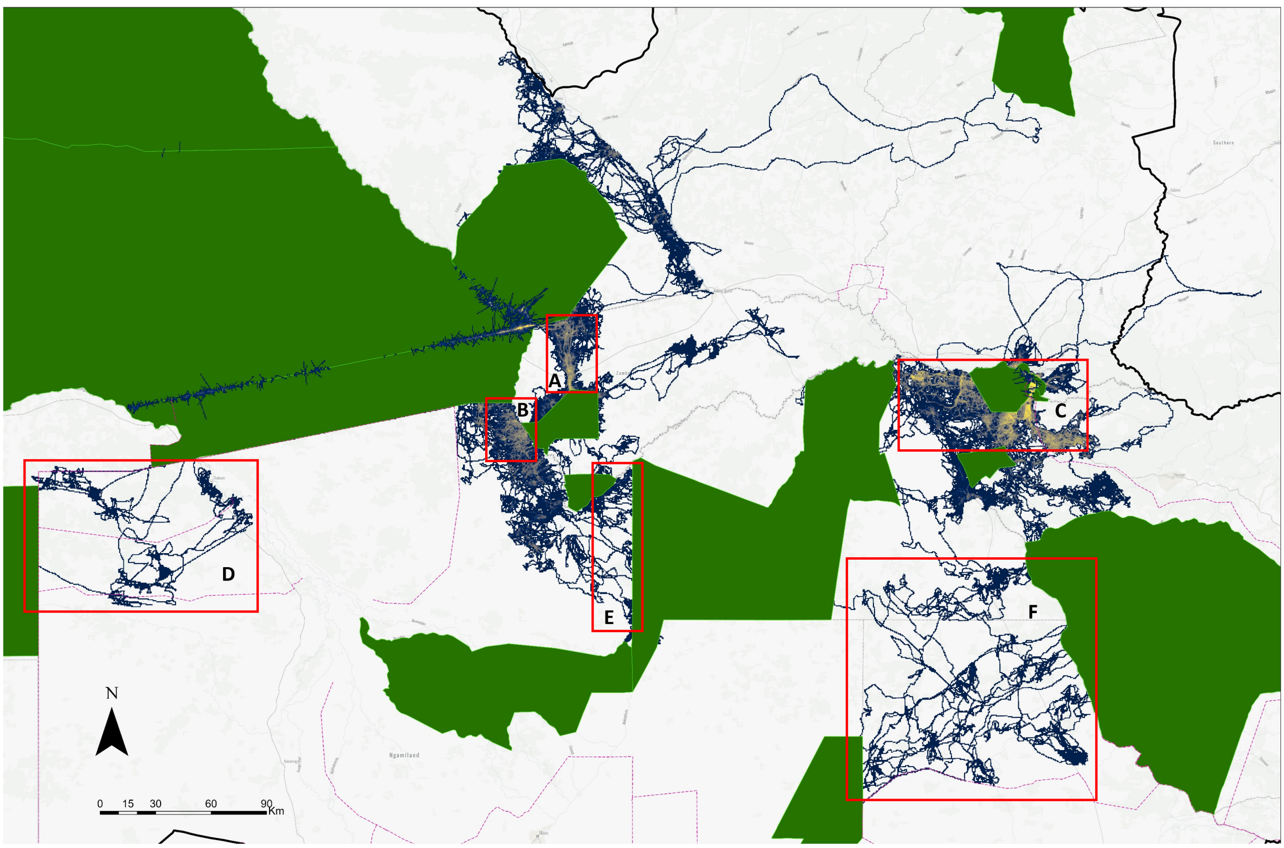

FIGURE 3 Elephant pathways connecting core protected areas (dark green polygons) in the Kavanzo-Zambezi (KAZA) transfrontier conservation area. Warmer colours = greater number of pathways. (A) The Sobbe corridor between Sioma Ngwezi National Park, Zambia and Mudumu National Park, Namibia; (B) High density of pathways between Bwabwata and Mudumu National Parks, Namibia, via northern Botswana; (C) High densities of pathways between a cluster of protected areas in northwestern Zimbabwe; (D) Dispersed pathways between Khaudum and Bwabwata National Parks, Namibia, via northern Botswana; (E) Dispersed pathways between multiple national parks in Namibia and Chobe National Park, Botswana; (F) Dispersed pathways between Hwange National Park, Zimbabwe and Nxai Pan National Park, Botswana. Veterinary fences are shown in dashed pink lines and the KAZA boundary in heavy black lines. See Figure S2 for location of named parks.

the central part of KAZA had a high density of transfrontier macro-corridors (Figure 4). This included parts of Bwabwata National Park along the veterinary border fence with Botswana, Sioma Ngwezi National Park and adjacent areas in Zambia, both sides of the Kwando River in Namibia and Botswana (including the Sobbe corridor on communal land in Namibia, along with multiple macro-corridors in Botswana's Ngamiland region), and a variety of pathways connecting Namibia and Botswana with Angola's Luengue-Luiana National Park (Figure 4A). A second cluster of high betweenness-centrality pathways occurred between Hwange National Park in Zimbabwe and Nxai Pan National Park in Botswana, reflecting large-scale inter-PA pathways and the importance of unprotected lands in northern Botswana for migratory elephants (Tshipa et al., 2017; Figure 4B). Secondary pockets of high betweenness-centrality grid cells also occurred in Khaudum National Park (Figure 4C), the eastern part of the Okavango panhandle (Figure 4D), the Victoria Falls–Zambezi–Mosi-oa-Tunya–Chobe cluster of national parks in Zimbabwe and Botswana (Figure 4E), and a return pathway between Sioma Ngwezi and Kafue National Parks in Zambia (Figure 4F).

3.4 | Areas of overlap

Of the 6595 cells that were a priority for at least one of the three connectivity scales, 204 cells (3%) were considered priorities at two levels, and only 2 (0.03%) were priorities for all three scales. Multi-scale connectivity priority cells were clustered in the Kwando River surroundings (Figure 5A) and in the Zambezi–Mosi-oa-Tunya–Victoria Falls–Kazuma Pan national park cluster in Zimbabwe (Figure 5B).

4 | DISCUSSION

Our assessment of landscape connectivity for African elephants in KAZA shows how observed movement data at multiple scales can provide insights for connectivity conservation and the management of functional landscapes. There were limited areas within KAZA where priorities at one scale overlapped with those at other scales; these areas have strong evidence for their connectivity importance and thus are clear priorities for conservation. However, most (>95%) grid cells identified as a priority at one scale did not overlap with connectivity priorities at other scales. A singular focus on any one scale would therefore miss important locations that support elephant movement at other scales and that are therefore required to conserve the complete landscape connectivity portfolio. Disaggregating connectivity to multiple scales can sharpen our understanding of which areas are important to what types of movements and suggest more specific actions to conserve them. In addition, by freeing ourselves from methods that rely on resource

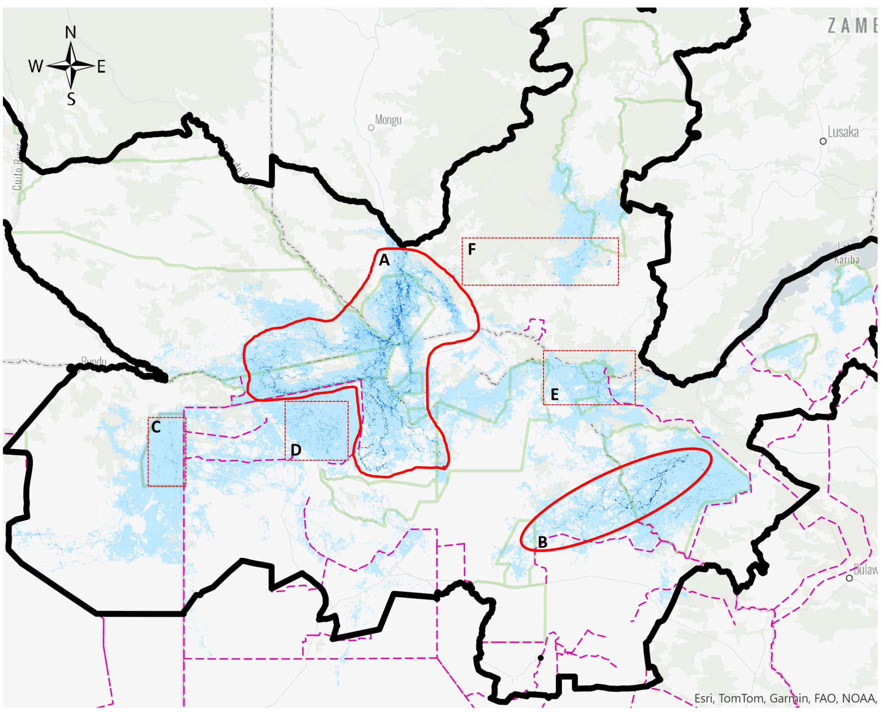

FIGURE 4 Betweenness-centrality macro-corridor scores that reflect long distance, landscape-wide connectivity for elephants in the Kavango-Zambezi (KAZA) transfrontier conservation area. Darker shades represent higher values. (A) High landscape-scale connectivity in the Kwando River Wildlife Dispersal Area. (B) High landscape-scale connectivity between Hwange National Park, Zimbabwe and Nxai Pan National Park, Botswana. (C–F) Sub-landscapes with moderate betweenness-centrality values. Veterinary fences are shown in dashed pink lines, green outlines are core protected areas, and heavy black lines indicate KAZA boundary. See Figure S2 for location of named parks.

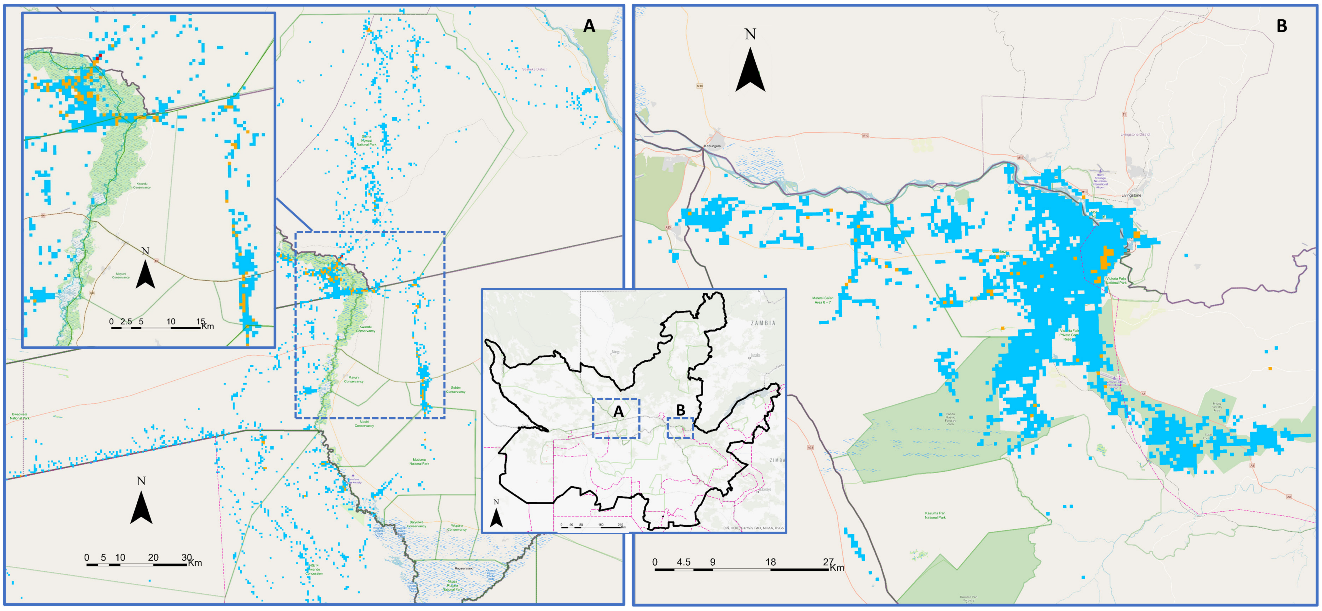

FIGURE 5 Priority locations (500-m grid cells) for connectivity at one scale (blue, $n=6389$), two scales (orange, $n=204$) and all three scales (red, $n=2$). (A) Kwando River Wildlife Dispersal Area; (B) Zambezi–Mosi-oa-Tunya–Victoria Falls–Kazuma Pan National Parks cluster, Zimbabwe. Veterinary fences are shown in dashed pink lines. Background from Open Street Map. See Figure S2 for location of named parks.

selection-based resistance modelling, we can identify connectivity conservation priorities where animals actually move, regardless of whether those movements occur in areas considered habitat, non-habitat or some gradient thereof. Our approach may be particularly useful in identifying movements that occur in areas typically identified as high resistance in resource selection connectivity models, such as small-scale corridors that support daily access to water resources through high human-use landscapes.

Direct connectivity inference using observed movement data, as in strict Merriam connectivity, requires a level of sampling that few studies in conservation landscapes can attain (Fahrig et al., 2020). Our study compiled data from one of the largest samples of collared elephants in any African landscape, but despite this sample size, even these data may not be fully representative, in terms of spatial, temporal and individual variability (Lamb et al., 2023), of elephant movements in KAZA. For example, recent research documenting elephant movement trajectories throughout southern Africa indicated substantial connections in the Botswana part of KAZA between Moremi Game Reserve and Chobe National Park, as well as some pathways connecting Makgadikgadi and Nxai Pan National Parks (Huang et al., 2022). Areas between these two sets of adjacent PAs should therefore be considered high priority inter-PA pathways despite not falling within our own data set. These areas notwithstanding, the statistically significant correlation of our GPS coverage with elephant densities estimated from a recent transfrontier aerial survey (Bussière & Potgieter, 2023) suggests our database is spatially representative of most areas where elephants are distributed in good numbers in KAZA. In terms of temporal representation, our data span 14 years (2010–2023) and are therefore likely to capture movements under a wide range of temporally varying environmental conditions. Whether our movement data set from $n=291$ animals represents the full spectrum of individual variability is most difficult to assess, however several recent studies on various taxa have independently concluded that sample sizes of greater than 100 tagged animals can be sufficient to accurately represent population-level estimates of movement and connectivity parameters (Lamb et al., 2023; Roberts et al., 2018; Sequeira et al., 2019).

Our extensive elephant movement database allowed us to make direct inference on connectivity in KAZA, rather than relying on conventional modelling and extrapolation. Data from large-scale GPS collaring efforts are increasingly being used to document—rather than model—movement phenomena such as migration (Kauffman et al., 2021), dispersal (Woodroffe et al., 2020), and nomadism (Nandintsetseg et al., 2019) in conservation landscapes. Furthermore, while remaining a minority portion of the connectivity literature, there are increasing examples of large tagging studies allowing direct inference for connectivity in various taxa, including marine turtles (Kot et al., 2022), waterbirds (Martín-Vélez et al., 2020), and sea birds (Gray & Olsen, 2023; Lamb et al., 2019). While we expect this trend to continue, models of animal movement will nonetheless remain important tools for examining landscape connectivity under future scenarios describing climate warming and anthropogenic development (Cushman et al., 2016; Duporge et al., 2022). Recent advances in individual animal movement simulations from agent-based and step selection models offer potential to quantify Merriam connectivity in less data-rich systems by observing the number of simulated pathways connecting areas of interest; that is, an in silico analog to the empirical observations we present here (Kumar, Kaszta et al., 2022; Schumaker & Brookes, 2018; Whittington et al., 2022).

Effectively conserving the three scales of connectivity we have documented will require complementary conservation approaches. Micro-corridors are easiest to target geographically but may also be the most difficult or costly to maintain in a functionally intact condition, as human–wildlife conflict here is likely the most acute of all scales (Songhurst et al., 2023), owing to their setting within anthropogenic land uses. Elephant movements in micro-corridors are predominantly to access critical resources (we do not consider the micro-corridors along fences to be conservation priorities), but are greatly impacted by human activity and risk avoidance, which are essential to consider for maintaining micro-corridor function (Songhurst et al., 2016; Vogel et al., 2020). Alleviating human–wildlife conflict, appropriate land-use zoning, and generating a flow of economic benefits to incentivize conservation among local communities are key micro-corridor actions identified in several internal KAZA processes (KAZA TFCA Secretariat, 2019, 2023). A number of such interventions are already underway in KAZA (e.g. Buchholtz et al., 2019; Gross et al., 2021; La Grange et al., 2022; Ministry of Environment Forestry and Tourism, 2021; Parker & Osborn, 2006). For example, our micro-corridor results will be used in an upcoming land-use project to aid in the designation and zoning of elephant corridors along the Zambezi river, building off work by land authorities and NGOs in Botswana (FAO and IUCN SSC HWCCSG, 2023; Songhurst et al., 2016).

The two areas containing the most significant proportion of macro-corridor pathways in KAZA (Figure 4A,B) correspond to the Kwando River and the Hwange-Makgadikgadi-Nxai Pan 'Wildlife Dispersal Areas' (WDAs), which are loose geographical constructs intended to focus conservation attention in important sub-landscapes within KAZA (KAZA TFCA Secretariat, 2014). A key pinchpoint for both macro-corridor and inter-PA connectivity in the Kwando River WDA is the Sobbe corridor (Figure 3A), currently threatened by conflicting legal frameworks that are resulting in private land claims and clearing of vegetation on communal land. The Kwando River WDA also contained the only two (adjacent) grid cells in the entire transfrontier landscape that were a priority for all three connectivity scales; this occurred within the Maunga community corridor in Zambia near the Angola and Namibia borders (Figure 2C). Both the Sobbe and Maunga corridors are examples of how tiny patches of land can make outsized contributions to connectivity at much larger scales, and both will require substantial conservation effort to ensure these contributions persist. The Victoria Falls and Livingstone urban areas in the Zambezi—Mosi-oa-Tunya WDA also had high clusters of micro-corridor and inter-PA connectivity priorities, indicating the need for urban elephant corridor conservation and management, as in other parts of KAZA (Adams et al., 2017).

The removal of 30 km of the Botswana-Namibia border fence in 2001 appears to have restored inter-PA and macro-corridor connectivity along the Kwando River in Angola, Namibia and Botswana. Additional fence realignment or decommissioning will be necessary if connectivity is to be similarly improved in the Khaudum-Ngamiland WDA (Figure 3D), where elephant movement between Khaudum and Bwabwata National Parks is very limited due to veterinary fences (KAZA TFCA Secretariat, 2023; Naidoo et al., 2022). Specific conservation measures to secure inter-PA connectivity in KAZA will depend on whether channelled pathways among PAs (e.g. Figure 3A–C) or more dispersed and diffuse pathways (e.g. Figure 3D–F) are present. In the latter case, a focus on mitigating the effects of fencing and livestock, the maintenance of intact landscapes free of large-scale human development and anti-poaching efforts will provide the best chance of conserving larger-scale connectivity among KAZA's core protected areas and across its wilderness regions.

While the results presented here are for elephants, they could be adapted to additional species via multi-species connectivity efforts within KAZA (Brennan et al., 2020), and can also be updated if additional elephant GPS data become available. Furthermore, these movement-based estimates are a baseline against which connectivity inference from other approaches, such as seasonal aerial surveys (Fynn et al., 2014), genetic/genomic sampling (de Flamingh et al., 2023), and counts from satellite imagery (Duporge et al., 2021) or aerial-borne photography (Lamprey et al., 2020) can be compared. The KAZA elephant sub-working group, under whose auspices this work was conducted, comprises a large group of elephant conservationists whose diverse expertise has contributed to a detailed, interdisciplinary understanding of elephant connectivity in KAZA. In addition to the constraints on connectivity discussed here, the threats to elephant persistence in KAZA include poaching (Schlossberg et al., 2019), competition associated with the livestock industry (Thomson et al., 2013), human–elephant conflict resulting from human settlement expansion and attendant landscape conversion (Buchholtz et al., 2019), increasing disease (Foggin et al., 2023), and a warming, drying landscape under human-caused climate change that may further limit surface water for wildlife (Schaffer-Smith et al., 2022). Further collaborative efforts marshalling multidisciplinary perspectives across a variety of scales and wildlife species will be necessary to address these threats and fulfil KAZA's vision as a connected transfrontier conservation landscape.

AUTHOR CONTRIBUTIONS

Robin Naidoo, Piet Beytell, Angela Brennan, John Carter, Kerryn D. Carter, Simon Chamaillé-Jammes, Richard Hoare, Malvern Karidozo, J. Werner Kilian, Tinaapi Hilary Madiri, Graham McCulloch, Nyambe Nyambe, Loki Osborn, Russell Taylor, Arnold Tshipa and Anna Songhurst conceived the ideas and designed methodology. Piet Beytell, John Carter, Kerryn D. Carter, Simon Chamaillé-Jammes, Brian Chilambe, Richard Hoare, Novald Iiyambo, Donovan Jooste, Malvern Karidozo, J. Werner Kilian, Daphine Madhlamoto, Graham McCulloch, Norman Monks, Isaac Mudimba, Nobesuthu Ngwenya, Loki Osborn, Michael Pelham, Letlhogonolo Phologo, Robert Reid, Miguel Savituma, Maurice Schutgens, Twakundine Simpamba, Stuart Slabbert, Amanda Stronza, Arnold Tshipa and Anna Songhurst collected the data.

Robin Naidoo, Angela Brennan, Anna Songhurst and Russell Taylor analysed the data; Robin Naidoo, Anna Songhurst and Russell Taylor led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

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DATA AVAILABILITY STATEMENT

Spatial data layers for micro-corridors, inter-PA pathways and macro-corridors are available via the Open Science Framework, https://doi.org/10.17605/OSF.IO/AWSXG (Naidoo et al., 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Summary statistics of elephant samples across 5 countries in the Kavango-Zambezi transfrontier conservation area.

Figure S1. Alignment of elephant micro-corridors (violet) identified by grid cell-level thresholds of intensity of use, speed and dot-product in the Kavango-Zambezi transfrontier conservation area with micro-corridor pathways (black lines—low use; orange lines—medium use; red lines—heavy use) independently identified by ground-based observations (Songhurst et al., 2016).

Figure S2. Map of the Kavango-Zambezi transfrontier conservation area, with labels for key features mentioned in the main text.

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