

A Three Steps Workflow for Simulating Dispersal Trajectories and Assessing Landscape Connectivity: A Case Study on the Endangered African Wild Dog

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Abstract

Dispersal of individuals contributes to long-term population persistence, yet requires a sufficient degree of landscape connectivity. To date, connectivity has mainly been investigated using least-cost analysis and circuit theory, two methods that make assumptions that are hardly applicable during dispersal. Least-cost analysis assumes that animals move towards a known endpoint and are knowledgeable about the most favorable route to reach it. Circuit theory presumes a complete random walk and fails to incorporate directional persistence. While these assumptions can be relaxed by simulating dispersal movements spatio-temporally explicitly across the landscape of interest, a unified approach for such simulations is lacking.

Here, we present a simple three-step workflow to simulate dispersal movements and to assess connectivity starting from empirical GPS movement data. In step one, we use integrated step selection functions to fit a mechanistic movement model describing habitat and movement preferences of dispersing individuals. In step two, we apply the parameterized movement model to simulate dispersal trajectories. In step three, we derive three complementary connectivity maps: a heatmap that highlights frequently traversed areas, a betweenness map that pinpoints dispersal corridors, and a map of inter-patch connectivity that indicates the presence and intensity of functional links between habitat patches. As a case study, we applied the workflow to GPS data collected during dispersal of the endangered African wild dog (*Lycaon pictus*) inhabiting the Kavango-Zambezi Transfrontier Conservation Area (KAZA-TFCA).

Results from the case study show that wild dogs preferably disperse with directional persistence in the vicinity to water bodies, through areas with little human influence and sparse woodland cover. Dispersal simulations and subsequent connectivity maps revealed several dispersal hotspots and corridors across the extent of the KAZA-TFCA. Connectivity between NPs inside the KAZA-TFCA was good, yet few dispersers successfully moved from Zambia's NPs into neighboring areas. By rendering interactions between movement preferences and habitat preferences, our movement model substantially outperformed a previous model that omitted such interactions. While we simulated 80,000 dispersal trajectories in total, we found that metrics of connectivity only marginally changed beyond 10,500 simulations, suggesting that fewer simulations would have sufficed.

Ultimately, we show that a simulation-based approach that leverages on step-selection functions offers a simple yet powerful alternative to traditional connectivity modeling techniques. Such an approach not only makes fewer biologically unrealistic assumptions but also permits a more mechanistic understanding of dispersal and landscape connectivity. Our workflow is thus useful for a variety of applications in ecological, evolutionary, and conservation research.

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1 Introduction

1.1 Importance of Connectivity & Connectivity Models

Dispersal of individuals is a vital process that allows species to maintain genetic diversity (Perrin and Mazalov, 1999, 2000; Frankham et al., 2002; Leigh et al., 2012; Baguette et al., 2013), rescue non-viable populations (Brown and Kodric-Brown, 1977), and colonize unoccupied habitats (Hanski, 1999; MacArthur and Wilson, 2001). Importantly, the ability to disperse depends on a sufficient degree of landscape connectivity (Fahrig, 2003; Clobert et al., 2012), making the identification and protection of dispersal corridors that promote connectivity a task of fundamental importance (Nathan, 2008; Doerr et al., 2011; Rudnick et al., 2012). Identifying dispersal corridors not only necessitates a comprehensive understanding of the factors that limit dispersal movements, but also an appropriate model to estimate connectivity (Baguette et al., 2013; Vasudev et al., 2015; Hofmann et al., 2021a). To date, the most commonly used models to assess connectivity are least-cost path analysis (LCPA; Adriaensen et al., 2003) and circuit theory (CT; McRae, 2006; McRae et al., 2008). Unfortunately, both models rest on assumptions that appear unsuitable for dispersers, calling for the development of alternative approaches. One promising alternative to investigate dispersal and assess connectivity is to simulate dispersal from individual-based movement models (Diniz et al., 2019).

1.2 Issues with Traditional Connectivity Models

Traditional connectivity models make assumptions that are rarely met for dispersers. LCPA, for instance, assumes that individuals move towards a preconceived endpoint and choose a cost-minimizing route accordingly (Sawyer et al., 2011; Abrahms et al., 2017). While this assumption may be justifiable for migrating animals, it is unlikely to hold for dispersers, as dispersers typically move across unfamiliar territory towards an unknown endpoint (Koen et al., 2014; Cozzi et al., 2020). CT, on the contrary, posits that animals move according to a random walk, entailing that autocorrelation between subsequent movements cannot be rendered (Diniz et al., 2019). For dispersers, however, autocorrelated movements are regularly observed (Cozzi et al., 2020; Hofmann et al., 2021a), implying that dispersal trajectories are usually strongly directional. Moreover, because both models require static permeability or resistance surfaces as input, they are unable to reflect the temporal dimension of dispersal, meaning that statements about the expected duration for moving between habitat patches are impossible (Martensen et al., 2017; Diniz et al., 2019).

1.3 What about IBMMs?

The shortcomings inherent to LCPA and CT can be overcome by simulating dispersal from individual-based movement models (IBMMs) and by converting simulated trajectories into meaningful measures of connectivity (Diniz et al., 2019)). In contrast to LCPA and CT, IBMMs allow to explicitly simulate how individuals move across and interact with the encountered landscape (Kanagaraj et al., 2013; Clark et al., 2015; Allen et al., 2016; Hauenstein et al., 2019; Zeller et al., 2020), as well as to render potential interactions between movement behavior and habitat conditions (Avgar et al., 2016). This strictly shifts the focus from a structural to a more functional view on connectivity (Tischendorf and Fahrig, 2000; Kanagaraj et al., 2013; Hauenstein et al., 2019). Furthermore, IBMMs generate movement sequentially, i.e. they generate a series of steps, the temporal dimension of dispersal movements becomes explicit and allows to model autocorrelation between consecutive steps (Diniz et al., 2019). Finally, simulations from IBMMs do not enforce movement or connections towards preconceived endpoints, thereby preventing biases arising from misplaced endpoints. Despite these advantages, a unified framework to simulate dispersal and assess connectivity using IBMMs is lacking.

1.4 Proposed Solution: Three-Step Workflow

Here, we propose a simple three-step workflow for simulating dispersal and assessing landscape connectivity (Figure 1). In step one, we combine GPS movement data of dispersing individuals with relevant habitat covariates to fit a mechanistic movement model using integrated step selection functions (ISSFs, Avgar et al., 2016). ISSFs allow inference on the study species' habitat kernel (i.e. habitat preferences), its movement kernel (i.e. movement preferences/capabilities), and potential interactions between the two (Avgar et al., 2016; Fieberg et al., 2021). In step two, we simulate individual dispersal trajectories using the parametrized movement model. Comparable simulations have already been applied to estimate steady-state utilization distributions of resident individuals (Potts et al., 2013; Signer et al., 2017) and to model landscape connectivity, yet disregarding interdependencies between habitat and movement kernels (Clark et al., 2015; Zeller et al., 2020). Finally, in step three, we convert simulated trajectories into three complementary connectivity maps, each highlighting a different aspect of connectivity. The set of maps includes (i) a heatmap revealing areas that are frequently traversed by dispersers (e.g. Hauenstein et al., 2019; Zeller et al., 2020), (ii) a betweenness-map delineating dispersal corridors and bottlenecks (e.g. Bastille-Rousseau et al., 2018), (iii) and a map of inter-patch connectivity, depicting

the presence and intensity of specific connections, as well as the average dispersal duration required to connect corresponding habitat patches (e.g. Gustafson and Gardner, 1996; Kanagaraj et al., 2013).

1.5 Case Study

We showcase the application of the proposed workflow (Figure 1) using GPS movement data collected on dispersing individuals of the endangered African wild dog (*Lycaon Pictus*). The African wild dog is a highly mobile species whose population persistence heavily relies on the availability of large, natural or semi-natural landscapes and a sufficient degree of connectivity among remaining subpopulations. Once common throughout sub-Saharan Africa, this species has disappeared from much of its historic range, largely due to human persecution, habitat fragmentation, and disease outbreaks (Woodroffe and Sillero-Zubiri, 2012). Wild dogs typically disperse in single-sex coalitions (McNutt, 1996; Behr et al., 2020) and are capable of dispersing several hundred kilometers (Davies-Mostert et al., 2012; Masenga et al., 2016; Cozzi et al., 2020). Although previous studies have investigated connectivity using LCPA (Hofmann et al., 2021a) or CT (Brennan et al., 2020), a more comprehensive and mechanistic understanding of connectivity is missing for this species (but see Creel et al., 2020). With fewer than 6,000 free-ranging wild dogs remaining in fragmented subpopulations (Woodroffe and Sillero-Zubiri, 2012), reliable information on landscape connectivity is essential for the conservation of this endangered carnivore. Here, we use GPS data of 16 dispersing wild dogs originating from a free-ranging population in northern Botswana to parametrize a mechanistic movement model, which we then employed to simulate 80,000 dispersal trajectories across the landscape of the world’s largest transboundary conservation area, the Kavango-Zambezi Transfrontier Conservation Area (KAZA-TFCA). We anticipated that simulations based on our three-step workflow would overcome several of the above highlighted conceptual shortcomings of traditional connectivity models and provide a more comprehensive view on dispersal behavior and landscape connectivity.

2 Methods

2.1 Study Area

Our simulation of dispersal trajectories and assessment of connectivity spanned across the entire Kavango-Zambezi Transfrontier Conservation Area (KAZA-TFCA), an area of approximately 1.3 Mio. km² (Figure 2a and b). The KAZA-TFCA is the world’s largest

transboundary conservation area and comprises parts of Angola, Botswana, Namibia, Zimbabwe, and Zambia, thus hosting a rich diversity of landscapes, ranging from savannah to grassland and from dry to moist woodland habitats. In its center lies the Okavango Delta, a dominant hydro-geographical feature and the world's largest flood-pulsing inland delta. Large portions of the KAZA-TFCA are formally protected in the form of national parks (NPs) or other protected areas, yet considerable human-dominated landscapes (e.g. roads, agricultural sites, and settlements) remain.

2.2 Data Collection and Preparation

2.2.1 GPS Data

We collected GPS movement data on 16 coalitions of dispersing African wild dogs (7 female and 9 male coalitions) between 2011 and 2019 from a free-ranging population in northern Botswana (details on the data collection can be found in Cozzi et al. (2020) and Hofmann et al. (2021a)). To delineate periods of dispersal, we determined the exact timing of emigration from the natal pack and settlement in a new territory using direct field observations and through visual inspection of the net squared displacement (NSD) metric. The NSD metric measures the squared Euclidean distance of a GPS relocation to a reference point (Börger and Fryxell, 2012), which we set to the center of the territory of each dispersers' natal pack. Thus, dispersal was deemed to have started once an individual left its natal territory and ended once the NSD metric remained constant, indicating settlement. Because behavior during dispersal is more pertinent to landscape connectivity than behavior during residence (Elliot et al., 2014; Abrahms et al., 2017), we only considered data collected during dispersal for our analysis. During dispersal, GPS collars recorded a fix every 4 hours and regularly transmitted data over the Iridium satellite system. To ensure regular time intervals between GPS fixes, we removed any fixes that were not successfully obtained at the desired 4-hour schedule (allowing for a tolerance of \pm 15 minutes). We then converted the fixes ($n = 4'169$) into steps, where each step represented the straight-line movement between two consecutive GPS fixes (Turchin, 1998).

2.2.2 Habitat Covariates

We represented the physical landscape in our study area by the habitat covariates *water-cover*, *distance-to-water*, *woodland-cover*, *shrub/grassland-cover*, and *human-influence*. To render the seasonal dynamics in water-cover of major water bodies for the extent of the Okavango Delta, we applied an algorithm that enabled us to obtain weekly updated raster-

layers for water-cover and distance-to-water from MODIS satellite imagery (Wolski et al., 2017; Hofmann et al., 2021a). This algorithm is now implemented in the `floodmapr` package (available on GitHub; <https://github.com/DavidDHofmann/floodmapr>). To ensure a consistent resolution across habitat covariates, we coarsened or interpolated all layers to a resolution of 250 m x 250 m. A detailed description of how we prepared each habitat covariate is provided in Hofmann et al. (2021a).

Besides habitat covariates, we computed movement metrics that we used as movement covariates in the ISSF models (Avgar et al., 2016; Fieberg et al., 2021). Specifically, we computed for each step the step length (`sl`), its natural logarithm (`log(sl)`), and the cosine of the relative turning angle (`cos(ta)`). Moreover, we created the binary variable `LowActivity`, indicating whether a step was realized during periods of low wild dog activity (09:00 to 17:00 local time) or high wild dog activity (17:00 to 09:00 local time, following Cozzi et al., 2012). We performed all data preparations, spatial computations, and statistical analysis in R, version 3.6.6 (R Core Team, 2020). Some helper functions were written in C++ and imported into R using the `Rcpp` package (Eddelbuettel and François, 2011; Eddelbuettel, 2013).

2.3 Step 1 - Movement Model

We used ISSFs (Avgar et al., 2016) to parametrize a mechanistic movement model for dispersing wild dogs. More specifically, we paired each realized (i.e. observed) step with 24 random steps, so that a realized step plus its 24 random steps formed a 25-step-stratum that received a unique identifier. As suggested by Avgar et al. (2016), we generated random steps by sampling random turning angles from a uniform distribution $(-\pi, +\pi)$ (which is equivalent to a von Mises distribution with location and concentration parameters; $\mu = \kappa = 0$) and step lengths from a gamma distribution that was fitted to realized steps (scale $\theta = 6'308$ and shape $k = 0.37$).

Along each realized and random step, we extracted values from the habitat covariate layers using the `velox` package (Hunziker, 2021) and we computed averages of each covariate along the steps. We further calculated the movement metrics `sl`, `log(sl)`, and `cos(ta)` for each step. To facilitate model convergence, we standardized all continuous covariates to a mean of zero and a standard deviation of one. Correlations among covariates were low ($|r| < 0.6$; Latham et al., 2011), so we retained all of them for modeling.

To contrast realized steps (scored 1) and random steps (scored 0), we assumed that animals assigned a selection score $w(x)$ to each step (Equation 1; Fortin et al., 2005). $w(x)$

depended on the step's associated covariates (x_1, x_2, \dots, x_n) and on the animal's preferences (i.e. relative selection strengths; Avgar et al., 2017) towards these covariates ($\beta_1, \beta_2, \dots, \beta_n$):

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \dots + \beta_n x_n) \quad (\text{Equation 1})$$

The probability of a step i being realized was then contingent on the step's selection score, as well as on the selection scores of all other step in the same stratum:

$$P(Y_i = 1 | Y_1 + Y_2 + \dots + Y_i = 1) = \frac{w(x_i)}{w(x_1) + w(x_2) + \dots + w(x_i)} \quad (\text{Equation 2})$$

To estimate preferences (i.e. the β -coefficients), we used mixed effects conditional logistic regression analysis (Muff et al., 2020) that we implemented using the r-package `glmmTMB` (Brooks et al., 2017). The method introduced by Muff et al. (2020) allows to model random slopes, yet requires to fix the variance of the stratum specific intercept to a large value. Hence we fixed the stratum specific intercept variance to an arbitrary high value of 10^6 . We used disperser identity to model random slopes for all covariates.

The covariate structure of the movement model was based on a habitat selection model that was previously developed for dispersing wild dogs (hereafter referred to as *base model*, Hofmann et al., 2021a). In the base model, no interactions among habitat covariates and movement covariates were considered. Hence, we expanded the base model and allowed for interactions between all movement covariates and habitat covariates, thus reflecting that movement behavior may depend on habitat conditions (details in Appendix A1). To determine the most parsimonious movement model among model candidates, we ran stepwise forward model selection based on Akaike's Information Criterion (AIC, Burnham and Anderson, 2002). Finally, we validated the predictive power of the most parsimonious model using k-fold cross-validation for case-control studies as described in Fortin et al. (2009). This validation proves a significant prediction in case the Spearman rank correlation of predicted step-ranks and associated frequencies under the movement model is significantly greater than under the assumption of random preferences (details in Appendix A2).

2.4 Step 2 - Dispersal Simulation

We used the most parsimonious movement model to simulate individual dispersal trajectories within the study area. The simulation of a dispersal trajectory resembled an “inverted” ISSF and was set up as follows. (1) We defined a random source point and assumed a random

initial orientation of the simulated animal. (2) Starting from the source point, we generated 25 random steps by sampling turning angles from a uniform distribution $(-\pi, +\pi)$ and step lengths from our fitted gamma distribution. Similarly to the empirical data, each random step represented a 4 hours straight-line movement. To prevent unreasonably large steps, we restricted sampled step lengths to a maximum of 35 km (i.e. the farthest dispersal distance traveled within 4 hours in our data). (3) Along each random step, we extracted and averaged values from the different habitat covariate layers and calculated movement covariates (as explained under Step 1). To ensure compatible scales with the fitted movement model, we standardized extracted values using means and standard deviations from the empirical data. (4) We applied the parametrized movement model to predict the selection score $w(x)$ for each step using Equation 1 and we converted predicted scores into probabilities using Equation 2. (5) We randomly sampled one of the generated random steps based on assigned probabilities and determined the animal's new position. We repeated steps (2) to (5) until 2,000 steps were realized.

To mitigate edge effects and to deal with random steps leaving the study area, we followed Koen et al. (2010) and artificially expanded all covariate layers by a 100 km wide buffer zone. Within the buffer zone, we randomized covariate values by resampling values from the original covariate layers. Through this buffer zone, simulated dispersers were able to leave and re-enter the main study area. In cases where random steps crossed the outer border of this buffer zone, we resampled steps until they fully lied within the buffer zone, essentially forcing individuals to remain within the expanded study area.

For the simulation, we distributed 80,000 source points within the study area. Of these, 50,000 were located inside protected areas that were larger than the average home range of resident wild dog packs (i.e. $> 700 \text{ km}^2$; Pomilia et al., 2015), while the remaining 30,000 were placed randomly inside the buffer zone, mimicking potential immigration into the study area (Figure S1).

To ensure reliable connectivity estimates, we determined the number of simulated dispersal trajectories required for connectivity to reach a “steady state” across the entire study area. For this purpose, we distributed 1,000 rectangular “checkpoints”, each with an arbitrary extent of 5 km x 5 km at random coordinates within the study area (excluding the buffer). We then determined the relative frequency at which each checkpoint was traversed by simulated dispersal trajectories (hereafter referred to as relative traversal frequency) as we gradually increased the number of simulated trajectories from 1 to 50,000. To assess variability in the relative traversal frequency, we repeatedly subsampled 100 times from all

50'000 trajectories and computed the mean traversal frequency across replicates, as well as its 95% prediction-interval for each checkpoint. We considered connectivity to have reached a steady state once the width of the prediction-interval dropped below a value of 0.01 for all checkpoints.

2.5 Step 3 - Connectivity Maps

2.5.1 Heatmap

To identify dispersal hotspots within the study area, we created a heatmap indicating the absolute frequency at which each raster-cell was traversed by simulated dispersal trajectories (e.g. Pe'er and Kramer-Schadt, 2008; Hauenstein et al., 2019; Zeller et al., 2020). Specifically, we rasterized all simulated trajectories onto a raster with 1 km x 1 km resolution and tallied resulting layers into a single map. If the same trajectory crossed a raster-cell twice, we only counted it once to reduce biases due to individuals that were surrounded by unfavorable habitat and therefore “moved in circles”. To achieve high performance rasterization, we used the R-package `terra` (Hijmans, 2021).

2.5.2 Betweenness Map

To pinpoint movement corridors and bottlenecks, we converted simulated trajectories into a network and calculated betweenness scores for all raster-cells in the study area (Bastille-Rousseau et al., 2018). Betweenness is a pertinent metric for connectivity as it measures how often a specific network-node (in our case a raster-cell) lies on a shortest path between any other pair of nodes (Bastille-Rousseau et al., 2018). To convert simulated trajectories into a network, we followed Bastille-Rousseau et al. (2018) and overlaid the study area (including the buffer) with a 5 km x 5 km raster, where the center of each raster-cell served as node in the final network. To identify edges (i.e. connections) between the nodes, we used the simulated trajectories and determined all transitions occurring from one node to another, as well as the frequency at which those transitions occurred. This resulted in an edge-list that we translated into a weighted network using the r-package `igraph` (Csardi and Nepusz, 2006). The weight of each edge was determined by the frequency of transitions, yet because `igraph` handles edge weights (ω) as costs, we inverted the traversal-frequency through each raster-cell by applying $\omega = \frac{\text{mean}(\text{TraversalFrequency})}{\text{TraversalFrequency}_i}$. Consequently, regularly used edges received small weights (i.e. low costs) and vice versa. Finally, we used the weighted network to calculate betweenness scores for all network nodes.

2.5.3 Inter-Patch Connectivity Map

To examine the presence and intensity of functional links (i.e. connections) between specific patches inside the KAZA-TFCA, we calculated inter-patch connectivity between NPs (e.g. (Gustafson and Gardner, 1996; Kanagaraj et al., 2013)). The decision to only consider NPs as potential “patches” was purely out of simplicity and does not imply that connections between other protected areas do not occur. To quantify inter-patch connectivity, we computed the relative frequency at which dispersers originating from one NP successfully moved into another NP. We considered movements as successful if an individual’s dispersal trajectory intersected with the target NP at least once. For each trajectory we also recorded the number of steps required to reach the first intersection with the respective NP, allowing us to compute the average dispersal durations from one NP to another. In summary, we determined *if* and *how often* dispersers moved between certain NPs, as well as *how long* individuals had to move to make these connections.

3 Results

3.1 Movement Model

The most parsimonious movement model consisted of movement covariates, habitat covariates and several of their interactions, suggesting that movement behavior during dispersal depended on habitat conditions (Figure 3a, Table S1 and Table S2). Although multiple models received an AIC weight ≥ 0 (Table S1), we only considered results from the most parsimonious model for simplicity. This decision only marginally influenced subsequent steps as all models with positive AIC weights retained similar covariates (Table S1). Plots that aid with model interpretation are provided in Figure S2. Under average conditions, dispersing wild dogs avoided moving through water, woodlands, and areas dominated by humans, but preferred shrublands or grasslands (Figure 3a). Dispersers realized shorter steps (indicating slower movements) in areas covered by water or woodland, while realizing larger steps in areas dominated by shrubs or grass (Figure 3a). Moreover, dispersing wild dogs moved faster during twilight and at night (i.e. between 17:00 and 09:00 o’clock) than during the rest of the day (Figure 3a). Although dispersers showed a preference for directional movements (i.e. low turning angles), especially when moving quickly, they did less so in proximity to humans or water, resulting in more tortuous movements in such areas (Figure 3a).

The k-fold cross-validation of the movement model showed that the final model substantially outperformed a random guess and suggested reliable predictions (confidence intervals

of $\bar{r}_{s,realized}$ and $\bar{r}_{s,random}$ do not overlap). Moreover, the model correctly assigned high selection scores to realized steps (Figure 3b), indicating a good fit between predictions and observations. Compared to the base model ($\bar{r}_{s,realized} = -0.55$; $95\% - CI = [-0.57, -0.52]$; Hofmann et al., 2021a), the inclusion of several interactions between movement and habitat covariates significantly improved model performance ($\bar{r}_{s,realized} = -0.65$; $95\% - CI = [-0.67, -0.64]$).

3.2 Dispersal Simulation

Dispersal simulations based on the most parsimonious movement model proved useful for assessing landscape connectivity. Of the 50,000 simulated dispersal trajectories with starting point within the main study area, only 4.5% reached a map boundary, suggesting minimal biases due to boundary effects. Moreover, our examination of the relative traversal frequency across all checkpoints showed that connectivity reached a steady state after 10,500 simulated dispersal trajectories (Figure S3). Although variability in relative traversal frequency kept decreasing as we increased the number of simulated dispersers, the marginal benefit of additional trajectories diminished quickly (Figure S3).

3.3 Heatmap

The heatmap (Figure 4), which resulted from the sum of all simulated dispersal trajectories, showed that several extensive regions within the KAZA-TFCA were frequently traversed by dispersing wild dogs (median traversal frequency inside KAZA-TFCA = 166, IQR = 274, Figure S6a), whereas areas beyond the KAZA-TFCA boundary were rarely visited (median traversal frequency outside KAZA-TFCA = 61, IQR = 133, Figure S6a). Most notably, the region in northern Botswana south of the Linyanti swamp appeared as highly frequented dispersal hotspot (median traversal frequency = 987, IQR = 558). Nevertheless, the presence of extensive water bodies, such as the Okavango Delta, the Makgadikgadi Pan, and the Linyanti swamp, restricted dispersal movements and limited realized connectivity within the KAZA-TFCA. Similarly, high human density, roads, and agricultural activities in Zambia's and Zimbabwe's part of the KAZA-TFCA limited dispersal movements in those countries. Outside the KAZA-TFCA, the most heavily used regions included the areas inside the Central Kalahari NP in Botswana, the area south-west of the Khaudum NP in Namibia, and the area surrounding the Liuwa Plains NP in Zambia. Although the heatmap facilitated the identification of areas frequently traversed by simulated dispersers, it seemed impractical to pinpoint dispersal corridors.

3.4 Betweenness

The betweenness map (Figure 5) revealed distinct dispersal corridors that run within the KAZA-TFCA. Again, northern Botswana emerged as a wild dog dispersal hub that connected more remote regions in the study area. Towards east, the extension of this corridor ran through Chobe NP into Hwange NP. From there, a further extension connected to Matusadona NP in Zimbabwe. Northwest of the Linyanti ecosystem, a major corridor expanded into Angola, where it split and finally traversed over a long stretch of unprotected area into Zambia’s Kafue NP. Several additional corridors with lower betweenness scores emerged, yet most of them ran within the KAZA-TFCA boundaries (median betweenness inside KAZA-TFCA = 6.947×10^6 , IQR = 54.311×10^6 , Figure S6b). In general, there were few corridors that directly linked the peripheral regions of the KAZA-TFCA and passed through unprotected areas outside the KAZA-TFCA (mean betweenness outside KAZA-TFCA = 2.685×10^6 , IQR = 9.891×10^6 , Figure S6b). Compared to the heatmap, the betweenness map facilitated the identification of dispersal corridors between habitat patches.

3.5 Inter-Patch Connectivity

The inter-patch connectivity map showed that the relative frequency at which simulated dispersal trajectories moved from one NP to another varied, as did the average dispersal duration required to make these connections (Figure 6). Overall, inter-patch connectivity between NPs in Angola, Namibia, Botswana, and Zimbabwe appeared to be high; between 54% and 87% of individuals originating from a NP in these countries successfully moved into some other NP (Figure S7a). Conversely, only 19% of the dispersers leaving from a NP in Zambia managed to find a route into some other NP (Figure S7b). Prior to reaching another NP, individuals from Angola, Namibia, Botswana, Zimbabwe, and Zambia had to move for an average of 630, 640, 940, 1045, and 890 steps, respectively. For some NPs, we also detected imbalances between the number of ingoing and outgoing links, hinting at possible source-sink dynamics. From Chobe NP, for instance, 510 individuals reached Moremi NP, yet the opposite route was only realized by 340 individuals. However, relative to the number of simulated individuals, these numbers imply fractions of 50% and 68%, respectively. Furthermore, it appeared that the dispersal corridor between Angola’s NPs and the Kafue NP in Zambia identified in Figure 6 is only rarely realized.

4 Discussion

4.1 Short Summary

We used empirical data from a free-ranging population of African wild dogs to demonstrate the application of a three-step workflow to simulate dispersal trajectories and assess landscape connectivity. In step one, we used ISSFs to parametrize a fully mechanistic movement model describing how dispersing wild dogs move through the landscape. In step two, we employed the movement model to simulate 80,000 dispersal trajectories across the extent of the KAZA-TFCA, the world’s largest transboundary conservation area. In step three, we translated the simulated trajectories into three complementary connectivity maps, each emphasizing a different aspect of landscape connectivity (e.g. frequently traversed areas, critical dispersal corridors and bottlenecks, and the presence and intensity of functional links between suitable patches). Importantly, such simulations from ISSFs overcome several conceptual shortcomings inherent to more traditional connectivity modeling techniques, such as LCPA and CT.

4.2 Movement Model

Our results on habitat preferences showed that dispersers avoid areas dominated by humans and covered by water, but select for regions with open grassland in the vicinity to water bodies. This largely complied with previous studies that investigated habitat selection by dispersing wild dogs (Davies-Mostert et al., 2012; Masenga et al., 2016; Woodroffe et al., 2019; O’Neill et al., 2020; Hofmann et al., 2021a). However, by also accounting for movement preferences, we were able to model several additional complexities common to dispersal. For instance, by including an interaction between turning angle and step length we could accommodate that dispersers exhibit step lengths that are correlated with turning angles, meaning turning angles are smaller when individuals move fast. Although similar autocorrelations could be incorporated by sampling step lengths and turning angles from copula probability distributions (Hodel and Fieberg, 2021a,b), the ISSF framework allowed us to conveniently include correlations in the movement model. We only considered first order autocorrelation, i.e. correlation between two consecutive steps, although higher order autocorrelation is conceivable and may be desirable to model (Dray et al., 2010; McClintock et al., 2012). This will, however, require vast amounts of GPS data that are not interrupted by missing fixes; something that is rarely achieved in reality (Graves and Waller, 2006). The power and flexibility of ISSFs to model additive effects between habitat and movement covariates

(Avgar et al., 2016; ?) furthermore allowed us to formally capture that dispersing wild dogs move slower and more tortuous in areas covered by water, something that surely was to be expected. Overall, the inclusion of interactions between habitat and movement covariates in our movement model lead to a significant improvement in predictive performance compared to an earlier model that omitted such interactions (Hofmann et al., 2021a).

4.3 Simulation

Our simulation of 80,000 dispersal trajectories moving 2'000 steps across the KAZA-TFCA required five days of computation on a desktop machine (AMD Ryzen 7 2700X processor with 8 x 3.6 GHz and 16 logical cores, 64 GB of RAM). The long simulation time was primarily caused by the massive extent of the study area considered (ca. 1.8 Mio km²) and the large number of trajectories simulated. Most connectivity studies focus on smaller study areas (e.g. Kanagaraj et al., 2013; Clark et al., 2015; McClure et al., 2016; Abrahms et al., 2017; Zeller et al., 2020) and will therefore achieve faster simulation times (given the same spatial resolution across covariates). We also believe that fewer simulated trajectories will often suffice, as the relative traversal frequency by simulated trajectories through randomly placed checkpoints across our study area converged already after 10,500 runs. The number of required simulations to achieve reliable estimates of connectivity will, however, vary depending on the structure of the landscape and the dispersal behavior of the focal species (Gustafson and Gardner, 1996). For species that disperse short distances through homogeneous environments, few simulations may suffice to gauge connectivity, whereas for species that disperse over long distances through heterogeneous habitats, a large number of simulations will be required to sufficiently explore the spectrum of possible routes.

4.4 Maps

Each of the three connectivity maps derived from simulated dispersal trajectories highlighted a different aspect of landscape connectivity. The heatmap was most suitable for pinpointing frequently traversed areas and showed that an exceptionally large number of dispersers moved through the regions of the Moremi NP and the Chobe NP in northern Botswana. (Hofmann et al., 2021a) previously identified the same area as potential dispersal hotspot using LCPA, however, it was not clear whether this was the consequence of the central location of the region and connections being enforced between predefined start and endpoints. Contrary to LCPA, a simulation-based approach as presented here does not require predefined endpoints because endpoints, as endpoints emerge naturally from the

simulated dispersal trajectories. Not having to predefine endpoints is especially useful for dispersal studies, as known endpoints are usually an unrealistic assumption (Elliot et al., 2014; Abrahms et al., 2017; Cozzi et al., 2020). At the same time, simulations permit to detect potential routes that do not necessarily lead into suitable habitats (Dwernychuk and Boag, 1972; Van der Meer et al., 2014) and into areas with a high susceptibility for human-wildlife conflicts (Cushman et al., 2018).

In contrast to the heatmap, the betweenness map emphasized relatively narrow and linear movement routes and thus facilitated the identification of discrete movement corridors. The resulting map reinforced our notion that Botswana plays a central role for the establishment of connections into more remote regions of the KAZA-TFCA. While, in this case, both the heatmap and the betweenness map attributed a high importance to northern Botswana, little consensus was found for other regions. For instance, the stretch of unprotected land between Luengue-Luiana NP in Angola and the Kafue NP in Zambia was characterized by a high betweenness-score, but at the same time received a low heatmap score. These contrasts highlight the complementary nature of the presented connectivity maps and emphasize the value of consulting multiple metrics when assessing connectivity.

Finally, we produced a map of inter-patch connectivity. The map depicted the frequency at which simulated individuals moved between NPs as well as the average duration (in steps) required to realize them. Calculating dispersal durations was possible because dispersal trajectories were simulated spatially and temporally explicitly, something that is currently impossible with LCPA or CT. An explicit representation of time enables answerings questions such as: “*How long will it take a disperser to move from A to B?*” or “*Is it possible for a disperser to move from A to B within X days?*”. Moreover, it yields opportunities to study how seasonality affects connectivity and to investigate whether dispersal corridors exist seasonally or all-year round (*dynamic connectivity*; Zeller et al., 2020). With LCPA or CT, seasonality can currently only be incorporated by repeatedly running a connectivity analysis using an array of seasonal permeability surfaces (e.g. Benz et al., 2016; Osipova et al., 2019). In contrast, simulations from ISSFs allow the environment to change “as the dispersers move”, so that simulated trajectories can dynamically respond to seasonal fluctuations in the environment.

4.5 Disadvantages of ISSF Simulations

Despite the many benefits and great flexibility offered by simulations from ISSFs, one also must be aware of the associated non-trivial but important modeling decisions. Here, we

will further elaborate on four modeling decisions concerning: (1) the number of simulated individuals, (2) the location of source points, (3) the simulated dispersal duration, and (4) behavior at map boundaries.

(1) When simulating dispersal trajectories, the modeler needs to decide on the number of simulated individuals. A higher number is always desirable, as each additional trajectory provides information about landscape connectivity. However, each additional simulation entails computational costs, so a trade-off needs to be managed. Here, we followed Signer et al. (2017) who suggested to simulate additional individuals only until the metrics of interest converge towards a steady state. The exact number of required individuals might, however, vary depending on the target metric and the anticipated connectivity map. Consequently, more sophisticated target metrics tailored for each of the presented connectivity maps need to be developed in the future.

(2) To initiate dispersers, a modeler needs to provide a set of source points at which the virtual disperser will be released. We placed source points within protected areas large enough to sustain viable wild dog populations, implicitly assuming wild dogs primarily survive in large, formally protected areas (Woodroffe and Ginsberg, 1999; Davies-Mostert et al., 2012; Woodroffe and Sillero-Zubiri, 2012; Van der Meer et al., 2014). We lacked precise knowledge about the presence and abundance of wild dogs in the different protected areas, so we distributed source randomly points within them. In cases where such data is available, source points could be distributed accordingly, reflecting that the number of simulated trajectories does not necessarily scales with the size of the source area. Alternatively, source points could be distributed homogeneously and only later be weighted when deriving connectivity metrics. In any case, the challenge of selecting meaningful source points is not unique to individual-based simulations but also applies to LCPA or CT.

(3) The use of ISSFs to simulate dispersers requires deciding on the number of simulated steps (i.e. dispersal durations). If sufficient dispersal data of the focal species has been collected, dispersal durations can be sampled from observed dispersal events. Due to the low number of observed dispersal events, we opted against this solution and instead simulated all individuals for 2,000 steps, which is at the upper end of observed dispersal durations (Davies-Mostert et al., 2012; Masenga et al., 2016; Cozzi et al., 2020; Hofmann et al., 2021a). This approach also has the advantage that it allowed us to subsample simulated trajectories to shorter durations after their simulation and to investigate the sensitivity of our connectivity maps with respect to exact dispersal durations (Figures S4 and S5).

(4) Unless simulated dispersal trajectories are strongly drawn towards a point of attrac-

tion (e.g. Signer et al. (2017)), some trajectories will inevitably approach a map boundary where one of the generated random steps might leave the study area. In this case, one solution would be to simply terminate the simulation of the affected trajectory, implicitly assuming that the respective animal left the study area permanently. However, this approach might become problematic in cases where individuals are released near map borders, as already a single random step leaving the study area will break the simulation, thus biasing connectivity along map borders. Instead of breaking the simulation, we created a buffer zone (Koen et al., 2010) and resampled random steps until they fully lied within the study area. This approach proved an effective solution to overcome problems with boundary effects.

4.6 Conclusion

In summary, we proposed and applied a simple three-step workflow that relies on ISSF-analysis and enables the simulation of dispersal trajectories and the assessment of landscape connectivity. The proposed workflow overcomes several of the conceptual shortcomings inherent to LCPA and CT, such as the assumption of known endpoints, and provides a highly flexible tool for investigating connectivity. With this work, we hope to have sparked interest in the application, optimization, or creation of methods to investigate dispersal movements and connectivity via individual-based simulations, while at the same time stressing some of the non-trivial modeling decisions involved.

5 Authors' Contributions

D.D.H., D.M.B., A.O. and G.C. conceived the study and designed methodology; D.M.B., G.C., and J.W.M. collected the data; D.D.H. and D.M.B. analysed the data; G.C. and A.O. assisted with modeling; D.D.H., D.M.B., and G.C. wrote the first draft of the manuscript and all authors contributed to the drafts at several stages and gave final approval for publication.

6 Data Availability

GPS movement data of dispersing wild dogs is available on dryad (Hofmann et al., 2021b). Access to R-scripts that exemplify the application of the proposed workflow using simulated data are provided through Github (<https://github.com/DavidDHofmann/DispersalSimulation>). In addition, all codes required for the African wild dog case study will be made available through an online repository at the time of publication.

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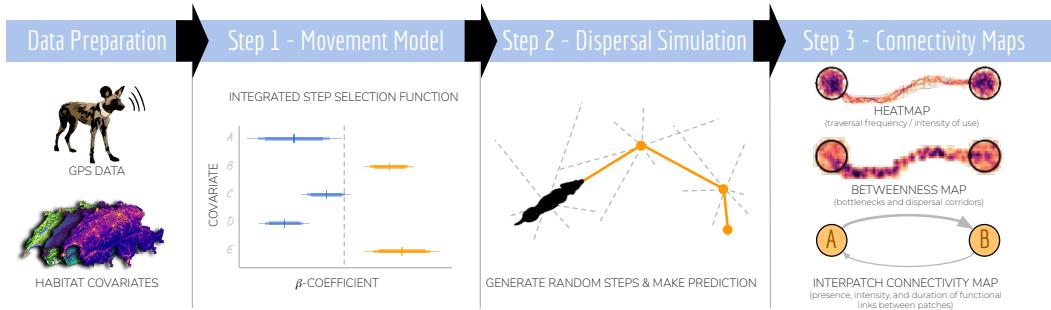


Figure 1: Flowchart of the simulation-based connectivity analysis as proposed in this article. First, GPS data and habitat covariates must be collected. The combined data is then analyzed in an integrated step selection model, which enables the parametrization of the focal species' habitat and movement kernels and results in a mechanistic movement model. The parametrized model is then treated as an individual-based movement model and used to simulate dispersal trajectories. Ultimately, simulated trajectories serve to produce a set of maps that are pertinent to landscape connectivity. This includes a heatmap, indicating the traversal frequency across each spatial unit of the study area, a betweenness map, highlighting movement corridors and bottlenecks, and, finally, an inter-patch connectivity map, where the frequency of connections and their average duration can be depicted.

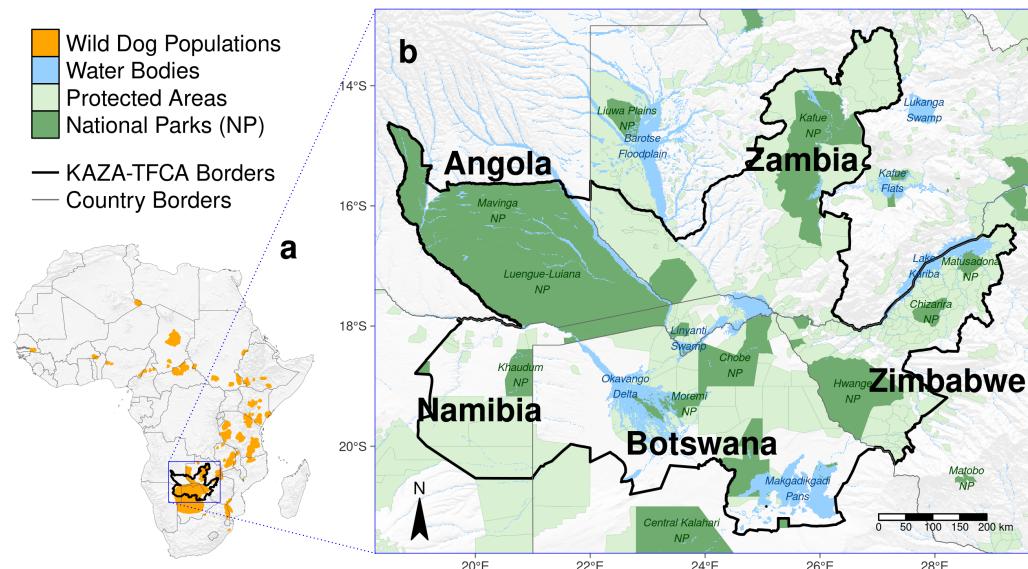


Figure 2: Illustration of the study area located in southern Africa. (a) The study area was confined by a bounding box spanning the entire KAZA-TFCA which comprises parts of Angola, Namibia, Botswana, Zimbabwe, and Zambia. (b) The KAZA-TFCA currently represents the world's largest terrestrial transfrontier conservation area, covering a total area of 520'000 km². Its main purpose is to re-establish connectivity between already-existing NPs (dark green) and other protected areas (light green).

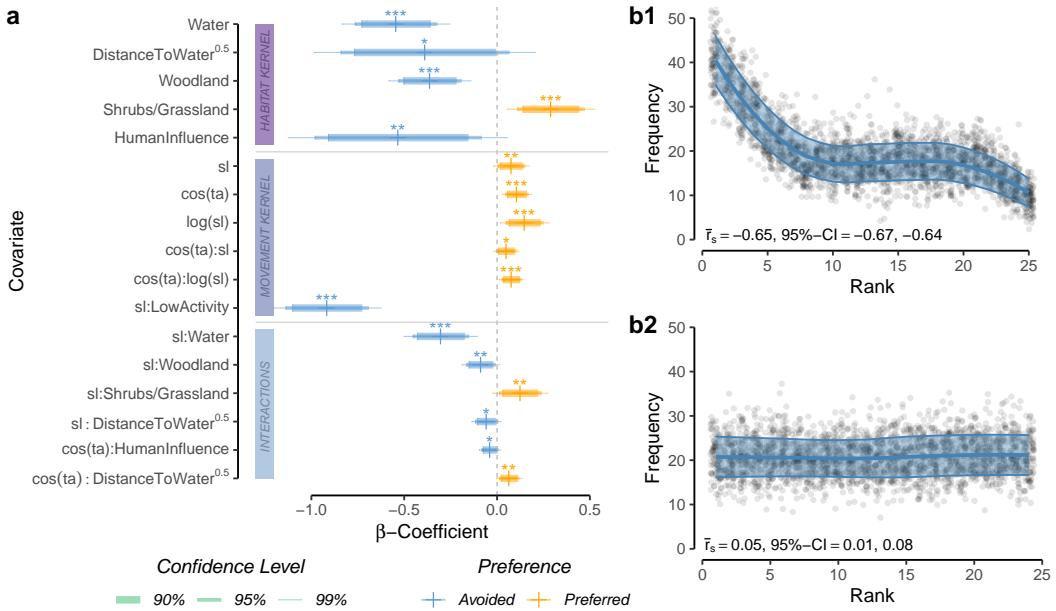


Figure 3: (a) Most parsimonious movement model for dispersing wild dogs. The model comprises a habitat kernel, a movement kernel, as well as their interactions. The horizontal line segments delineate the 90%, 95%, and 99% confidence-intervals for the respective β -coefficients. Significance codes: * $p < 0.10$, ** $p < 0.05$, *** $p < 0.01$. (b) Results from the k-fold cross validation procedure. The upper plot shows rank frequencies of realized steps according to model predictions with known preferences, whereas the lower plot shows rank frequencies of realized steps when assuming random preferences. The blue ribbon shows the prediction interval around a loess smoothing regression that we fitted to ease the interpretation of the plots. The significant correlation between rank and associated frequency in (b1) highlights that the most parsimonious model successfully outperforms a random guess (b2) and assigns comparably high selection scores to realized steps.

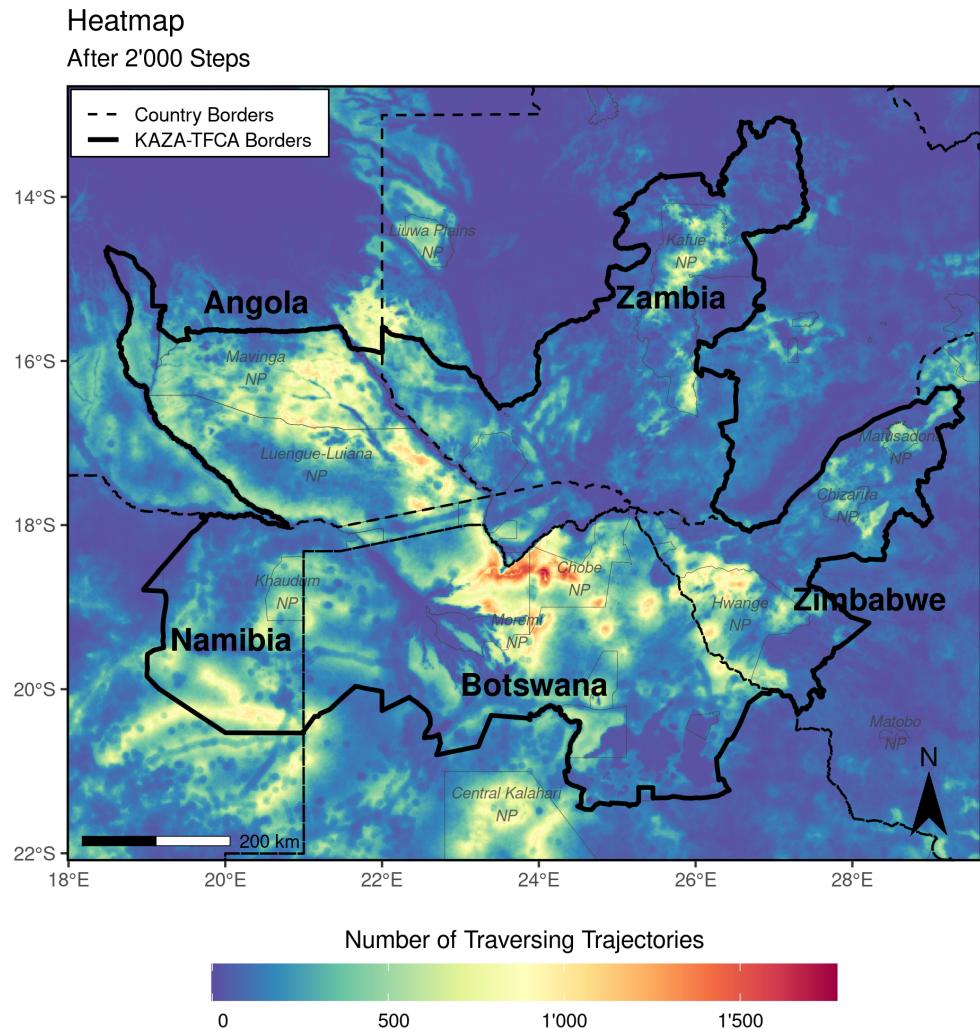


Figure 4: Heatmap showing traversal frequencies of 80'000 simulated dispersers moving 2'000 steps across the KAZA-TFCA. Simulations were based on an integrated step selection model that we fitted to the movement data of dispersing African wild dogs. To generate the heatmap, we rasterized and tallied all simulated trajectories. Consequently, the map highlights areas that are frequently traversed by virtual dispersers. For spatial reference we plotted a few selected NPs (dark gray). Additional heatmaps showing the traversal frequency when individuals move fewer than 2'000 steps are provided in Figure S4.

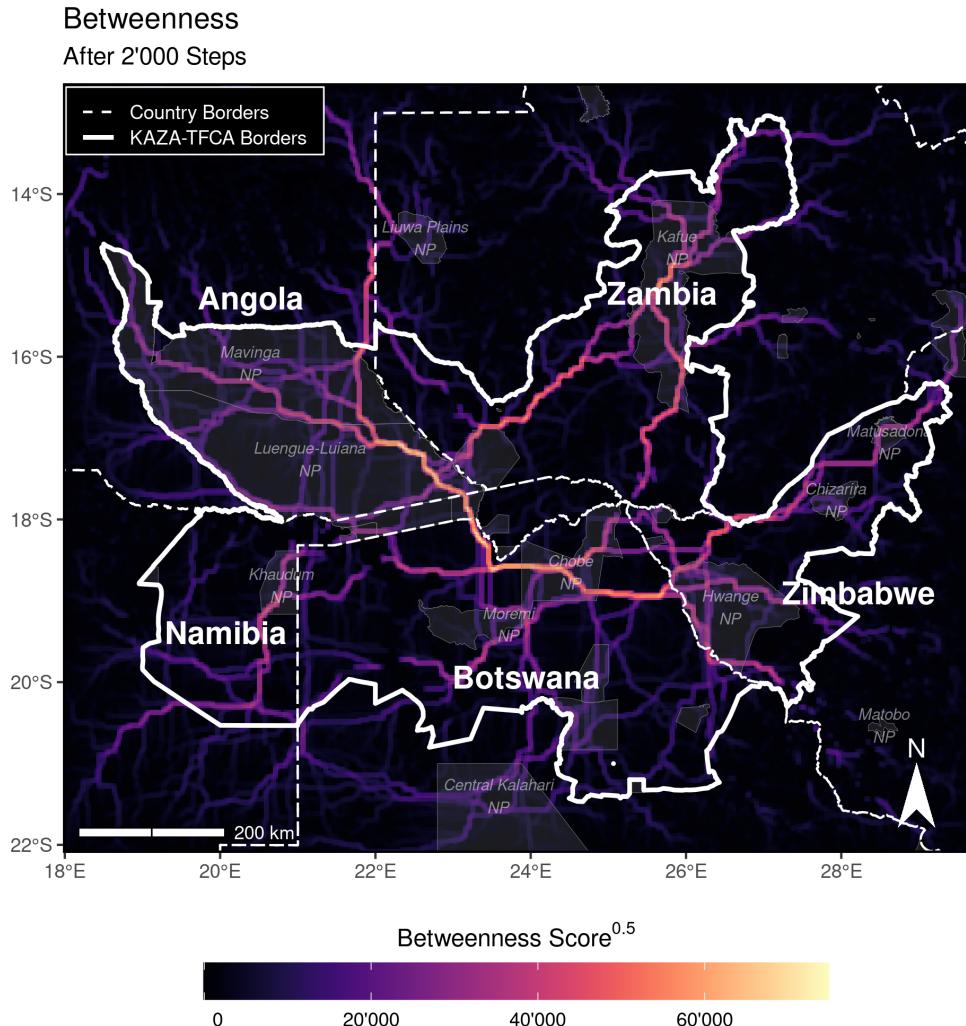


Figure 5: Map of betweenness scores, highlighting distinct dispersal corridors and potential bottlenecks across the extent of the KAZA-TFCA. Betweenness measures the number of shortest paths traversing through each node (raster-cell). Hence, a high betweenness score indicates that the respective area is exceptionally important for connecting different regions in the study area. The metric is therefore useful to pinpoint discrete movement corridors (Bastille-Rousseau et al., 2018). Note that we square-rooted betweenness scores to improve visibility of corridors with comparably low scores. Additional betweenness maps showing betweenness scores when individuals move fewer than 2'000 steps are provided in Figure S4.

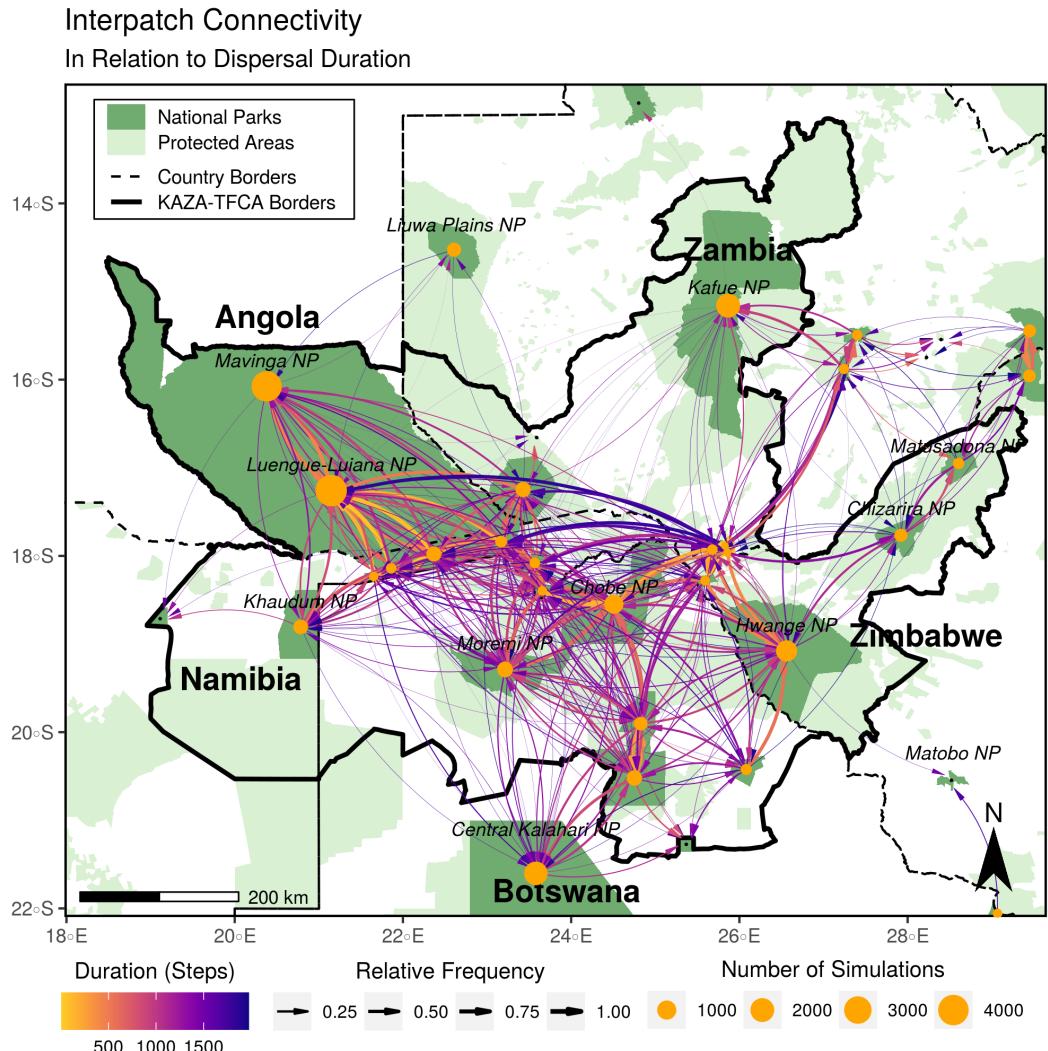


Figure 6: Map of inter-patch connectivity, highlighting connections between NPs (dark green). Yellow bubbles represent the center of the different NPs and are sized in relation to the number of simulated dispersers originating from each park. Black dots represent NPs that were smaller than 700 km² and therefore did not serve as source areas. Arrows between NPs illustrate between which NPs the simulated dispersers successfully moved and the color of each arrow shows the average number of steps (4-hourly movements) that were necessary to realize those connections. Additionally, the line thickness indicates the relative number of dispersers originating from a NP that realized those connections. Note that a similar network view could be adopted to investigate connectivity between other protected areas need not to be restricted to NPs.