

# Flooding of the Okavango Delta influences Connectivity for Dispersing African Wild Dogs

David D. Hofmann<sup>1,2,§</sup>  Dominik M. Behr<sup>1,2</sup>  John W. McNutt<sup>2</sup>

Arpat Ozgul<sup>1</sup>  Gabriele Cozzi<sup>1,2</sup> 

January 5, 2023

<sup>1</sup> Department of Evolutionary Biology and Environmental Studies, University of Zurich,  
Winterthurerstrasse 190, 8057 Zurich, Switzerland.

<sup>2</sup> Botswana Predator Conservation Program, Private Bag 13, Maun, Botswana.

§ Corresponding author: david.hofmann2@uzh.ch

**Running Title:** Seasonal Flooding of the Okavango Delta and its Consequences for  
African Wild Dog Dispersal and Connectivity

**Keywords:** movement, connectivity, seasonality, dispersal, conservation, permeability

## Abstract

Climate change is expected to profoundly impact the life history of wild-living animal populations. While the impact of climate change on the demographics of local subpopulations has been studied repeatedly, little is known about the consequences of environmental change on dispersal and connectivity.

We capitalize on a “natural experimental setup”, the flood-pulse driven environmental change across the Okavango Delta in northern Botswana, to investigate the impact of changing environmental conditions on dispersal patterns and connectivity of the endangered African wild dog (*Lycaon pictus*). For this, we simulate dispersal trajectories across the landscape of the Okavango Delta under two extreme environmental scenarios; one assuming a maximum flood extent, one assuming a minimum flood extent.

During maximum flood, we observe a reduction in connectivity and an increase in dispersal durations between distinct habitat patches. Notably, dispersal into the central habitats of the Okavango delta is reduced by 80% during maximum flooding. At minimum flooding, conversely, the delta reveals vital dispersal corridors and increases chances of successful dispersal into neighboring habitat patches by xx percent. Furthermore, we find that dispersers get pushed into different zones of potential human-wildlife conflict depending on the flood extent.

Climate change is expected to critically impact water-cycles across the globe, including the flood-pulsing dynamics of the Okavango delta. Our results suggest that anticipating and taking into account such changes in environmental conditions is key when developing and implementing conservation strategies, especially when the aim is to improve connectivity. Besides this, our analysis also provides important insights towards a better understanding of the conservation needs for the African wild dog and demonstrates the usefulness of individual-based dispersal simulations as a pertinent conservation tool to study impacts of environmental change on dispersal success.

# Contents

<b>1</b>	<b>Introduction</b>	<b>1</b>
1.1	Climate Change and Dispersal . . . . .	1
1.2	Connectivity . . . . .	1
<b>2</b>	<b>Materials and Methods</b>	<b>5</b>
2.1	Study Area . . . . .	6
2.2	Spatial Habitat Layers . . . . .	6
2.3	Dispersal Model . . . . .	7
2.4	Source Areas and Emigration Zones . . . . .	8
2.5	Dispersal Simulation . . . . .	8
2.6	Dispersal Prospects and Connectivity . . . . .	8
<b>3</b>	<b>Results</b>	<b>9</b>
3.1	General . . . . .	9
3.2	Heatmaps . . . . .	9
3.3	Betweenness . . . . .	10
3.4	Inter-Patch Connectivity . . . . .	10
<b>4</b>	<b>Discussion</b>	<b>10</b>
4.1	Conclusion . . . . .	13
<b>5</b>	<b>Authors' Contributions</b>	<b>14</b>
<b>6</b>	<b>Data Availability</b>	<b>14</b>
<b>7</b>	<b>Acknowledgements</b>	<b>14</b>

# 1 Introduction

## 1.1 Climate Change and Dispersal

Climate change is expected to profoundly impact ecosystems worldwide with far-reaching consequences for species living therein (Ozgul et al., 2010; Radchuk et al., 2019; IPCC, 2022). By altering environmental conditions, climate change affects animal behavior (Fuller et al., 2016), resource availability (Durant et al., 2007), population dynamics (Paniw et al., 2021), and the distribution of wild living animal populations (Thomas et al., 2004; Thuiller et al., 2006). One life-history pathway through which species potentially mediate the effects of environmental change is dispersal (Anderson et al., 2012), i.e. the movement of individuals away from their natal location to the site of first reproduction (Clobert et al., 2012). The ability to disperse enables species to adapt to climate change by tracking favorable habitat conditions (Raia et al., 2012) or by shifting into a different region of their fundamental niches (Kokko, 2006). Dispersal furthermore provides resilience against changing conditions by safeguarding genetic diversity (Frankham et al., 2002; Leigh et al., 2012; Baguette et al., 2013), facilitating the colonization empty habitats (Gustafson and Gardner, 1996; Hanski, 1999; MacArthur and Wilson, 2001), and promoting the reinforcement of weakened and small subpopulations (Brown and Kodric-Brown, 1977).

## 1.2 Connectivity

While dispersal offers a means to offset the demographic consequences of climate change (Kokko, 2006; Hodgson et al., 2009; Travis et al., 2013), it itself is a function of climatic and environmental conditions (e.g. (Elliot et al., 2014; Behr, 2020)). The link between dispersal and the environment can either be indirect, for example if the propensity of individuals to disperse depends on environmental conditions, or direct, when the biophysical environment through which dispersers move affects dispersal prospects (Travis et al., 2013). The latter case highlights that dispersal is also inextricably linked to the concept landscape connectivity (Baguette et al., 2013), which is understood as the degree by which the landscape facilitates or impedes movements (Taylor et al., 1993). A sufficient degree of landscape connectivity is therefore a critical prerequisite of successful dispersal (Fahrig, 2003). Unfortunately, the continued degradation and destruction habitats worldwide continues to imperil the dispersal ability of many species and increases the prospects of inbreeding, genetic risk and of local extirpation due to stochastic events (Melbourne and Hastings, 2008; Sawyer et al., 2011). Combined, these factors limit species ability to adapt to changing environmental conditions

(Fahrig, 2003). Conservation strategies that aim to facilitate dispersal by improving landscape connectivity are thus often viewed as pinnacle of conservation strategies to combat the adverse effects of climate change (Heller and Zavaleta, 2009).

In recent years, there has been a growing body of research that uses animal relocation data to identify movement corridors and assess connectivity at large scales (Chetkiewicz et al., 2006; Doerr et al., 2011; Squires et al., 2013; Elliot et al., 2014; Benz et al., 2016; Osipova et al., 2019). Identification of potential corridors relies on the estimation of permeability (respectively resistance) surfaces, which return the ease or willingness at which the focal species traverses a specific landscape (Sawyer et al., 2011). Such surfaces are typically created on the basis of habitat preferences, which can be estimated using a suite of selection functions (Boyce et al., 2002; Fortin et al., 2005; Cushman and Lewis, 2010). In selection functions, habitat preferences are inferred by comparing spatial covariates (e.g. environmental and anthropogenic) at locations visited by the animal to the same spatial covariates at randomly selected locations in the animal's availability domain (Zeller et al., 2012; Thurfjell et al., 2014). Importantly, selection functions rely on adequate landscape and GPS relocation data that are representative of the process being studied (Diniz et al., 2019). More specifically, GPS relocation data collected on dispersing individuals has been shown to outperform GPS relocation data collected on resident individuals when aiming at detecting large scale dispersal corridors (Elliot et al., 2014; Diniz et al., 2019). However, few connectivity studies have partitioned their GPS relocation data according to behavioral modes (e.g. resident vs. dispersing) of the studied species (Wilson et al., 2012; Vasudev et al., 2015). As such, most permeability surfaces upon which dispersal corridors are identified are created using GPS relocation data that were collected on resident individuals. This introduces severe biases and substantially reduces the power to reveal meaningful movement corridors, for dispersing individuals have different needs and drives compared to resident individuals (Killeen et al., 2014; Elliot et al., 2014; Cozzi et al., 2020). Consequently, these biases have limited our ability to assess the adequacy of the boundaries of protected areas in securing connectivity for their protected species.

To study connectivity, various modeling techniques have emerged Etherington (2016); Diniz et al. (2019). Initially, the techniques were limited to studying structural aspects of connectivity by focusing on the composition and configuration of habitat patches, while ignoring species' responses to the landscape matrix (Tischendorf and Fahrig, 2000; Doerr et al., 2011). With the increasing availability of telemetry data and methods to study habitat and movement preferences (Boyce et al., 2002; Fortin et al., 2009; Cushman and Lewis,

2010; Avgar et al., 2016), however, the focus has shifted towards more functional aspects of connectivity (Tischendorf and Fahrig, 2000; Doerr et al., 2011). Currently, the most prominent *functional* connectivity models are least-cost path analysis (LCPA, Adriaensen et al., 2003) and circuit theory (CT, McRae et al., 2008), two graph-based methods that estimate conductance of the landscape by means of a resistance (or inversely permeability) surface (Zeller et al., 2012). Because both approaches make assumptions that are rarely met by dispersing individuals, individual-based movement models (IBMMs) have also gained some momentum recently (Kanagaraj et al., 2013; Allen et al., 2016; Hauenstein et al., 2019; Diniz et al., 2019; Zeller et al., 2020; Unnithan Kumar et al., 2022a,b; ?). In these models, movement of individuals is explicitly simulated and connectivity metrics are derived based on the simulated dispersal paths. IBMMs provide great modeling flexibility and are thus considered powerful tools for examining connectivity under different landscape configurations (Littlefield et al., 2019).

Irrespective of the chosen method, connectivity is often modeled as a snapshot in time that fails to render dynamic environmental change. However, some recent studies have shown that connectivity may differ substantially depending on season ... some examples.

Unfortunately, our understanding how changing environmental conditions influence connectivity and dispersal is limited (Kokko, 2006; Travis et al., 2013). Because collecting information on dispersing animals is difficult and because it is difficult to assess how changing environmental conditions affect connectivity...

Ashrafzadeh et al. (2019) found that climate change is likely to substantially reduce connectivity for mountain newts in Iran. Similarly, Luo et al. (2021) predicted significant reductions in connectivity for the giant spiny frog in South-East Asia.

However, failing to take into account potential changes in climatic and environmental conditions imperils our ability to design cost-effective conservation strategies.

Here, we used naturally occurring seasonal flood-cycles to approximate the likely changes in connectivity that will arise under amplified climatic conditions due to climate change. While a better understanding of the ODS flooding regime under global change is of major interest, reliable predictions remain challenging due to the complex interplay between climate, anthropogenic water use, animal behavior, and topography of the region.

Climate change could lead to the disruption of existing dispersal corridors and the emergence of new dispersal barriers but may also provide possibilities to access previously unsuitable dispersal routes. Designing and implementing effective conservation strategies that aim to improve landscape connectivity, such as habitat restoration or the creation of wildlife

corridors, requires better understanding of such dynamics.

Albeit the impacts of climate change on connectivity cannot be directly estimated, one can study how changing environmental conditions due to seasonality influence patterns of dispersal and connectivity.

Habitat degradation and fragmentation lead to isolated subpopulations that have a high associated risk of extinction due to stochastic events and generally decreased genetic variability (Melbourne and Hastings, 2008).

More recently, individual-based movement models (IBMMs) have been uprising and are recommended for their ability to incorporate several crucial realities of animal behavior, such as, for example, autocorrelation, that are by omitted by necessity using resistance-based approaches (?Unnithan Kumar et al., 2022b). Botswana is among the countries most heavily influenced by climate change .

For multispecies approaches to connectivity within the KAZA-TFCA, see Brennan et al. (2020) and Lines et al. (2021).

Say that wild dogs are keystone predators and an umbrella species for conservation

Unfortunately, little is known about the specific responses of different species to climate change, especially for regions most vulnerable to altered conditions (Paniw et al., 2021).

Earlier studies demonstrating the importance of rendering seasonal change include Chetkiewicz and Boyce (2009), who use resource selection functions to demonstrate that connectivity differs for Ursus actor and Puma concolor and Mui et al. (2017), who showed that connectivity for turtles changes depending on the season, and Kaszta et al. (2021), who show monthly differences in elephant's habitat selection using path-selection functions.

Only if there

The challenges associated with studying dispersing animals have thus far impaired the collection of data of dispersers at the appropriate temporal and spatial scale (Graves et al., 2014; Vasudev et al., 2015) and weakened our ability to project dispersal prospects under changing environmental conditions into the future. Nevertheless, a more comprehensive understanding of dispersal under changing environmental conditions is critical for designing effective conservation strategies in the light of climate change. By predicting and modeling dispersal patterns under different scenarios, we can better anticipate the impacts of climate change on species and design effective conservation strategies to protect them. This is especially important for endangered species that are already at the verge of extinction.

The Okavango delta in Southern Africa poses a unique opportunity to study the impacts of environmental change on species dispersal ability and connectivity in a large scale natural

experiment setup. According to projections by the IPCC, Botswana and its surroundings are among the most vulnerable to climate change. While global temperatures are expected to increase by xx degrees until the end of the 21st century, For example, Engelbrecht et al. (2015) predicts an increase between 4 and 6°C for regions in southern Africa. One of the keyspone predators and an umberella species for conservation efforts in this ecosystem is the African wild dog (*Lycaon pictus*). This species heavily relies on dispersal for long-term persistence. The African wild dog is a lightly built canid lives in cohesive packs comprising up to 20 individuals. Wild dogs are social breeders and the majority of reproduction is monopolized by the dominant alpha couple who are supported by subordinates in taking care of their pups. The species exhibits strong inbreeding avoidance, hence juvenile individuals born into the pack disperse in same-sex sibling coalitions after reaching sexual maturity (McNutt, 1996; Behr, 2020). Notably, the African wild dog is the sole extant representative of its genus and thus considered as high-priority species for conservation efforts (Leigh et al., 2012). However, fragmentation and destruction of their historic habitat may have decreased dispersal success for this species and thus jeopardizes connectivity (Leigh et al., 2012). Since the impacts of climate change are not uniformly distributed across the planet, but particularly pronounced at high latitudes and arid ecosystems, the species may be seen as most vulnerable to such ecosystem shifts.

#### Talk about Zeller und Osipova

Here, we capitalize on the previously parameterized dispersal model by ? and use dispersal simulations to investigate dispersal success and connectivity patterns for African wild dogs under two extreme scenarios; one assuming maximum flooding of the Okavango delta and one assuming minimum flooding of the Okavango delta. Given that water poses a barrier to dispersing individuals, we anticipated that dispersal prospects and connectivity during maximum flood are low. During minimum flood, in contrast, we expect to reveal the presence of several dispersal corridors that may be used to freely and quickly move between remaining habitat patches.

## 2 Materials and Methods

We conducted all analyses using the programming language R (R Core Team, 2022). Any spatial data manipulation was completed using the **terra** (Hijmans, 2022) and **spatstat** packages (Baddeley et al., 2015). Several helper functions for the simulation algorithm were written in C++ and imported to R using the **Rcpp** package (Eddelbuettel and François, 2011). Figures were generated using **ggplot2** (Wickham, 2016), **igraph** (Csardi and Nepusz,

2006), and `ggnetwork` (Briatte, 2021). All R-scripts used to conduct our analyses are provided through an online repository.

## 2.1 Study Area

The study area for this analysis was focused on the Okavango delta (OD) and its surroundings in Southern Africa, comprising parts of Angola, Namibia, Botswana, Zimbabwe, and Zambia (Figure 1). The OD is the world’s largest inland delta and the main driver of seasonal environmental change in the region. While our primary focus lied on the immediate surroundings of the Okavango Delta, we considered a large rectangular extent stretching from 20°30' E to 26°E. (totaling to an area of 300'000 km<sup>2</sup>) to accommodate for the long distance dispersal events commonly observed in African wild dogs (e.g. Davies-Mostert et al., 2012; Masenga et al., 2016; Cozzi et al., 2020). The flood-pulsing rhythm of the OD is mainly dictated by precipitation in the catchment areas of the Angolian highlands, where rainwater is collected and channeled into the OD through the Okavango River. Although precipitation in Angola peaks between December and March, water only slowly descends through the Okavango river and its distributaries, reaching the distal ends of the delta in July or August, where the water percolates at the Thamalakane and Kunyere Faults. At minimum extent, the flood covers an area of 3'600 km<sup>2</sup>, during maximum flood more than 9'000 km<sup>2</sup>. Vegetation in the study area is dominated by mopane forest, mixed acacia woodland, and grassland. Human influence is low and mainly concentrated around small villages at the western periphery of the delta as well as the city of Maun at the south-eastern tip of the OD. Large portions of land are dedicated national parks, game reserves or forest reserves. The study area is also part of the world’s largest transboundary conservation initiative, the Kavango-Zambezi Transfrontier Conservation Area, which aims to restore connectivity between protected areas in Southern Africa.

## 2.2 Spatial Habitat Layers

We represented the physical landscape through which dispersers could move by a set of spatially referenced habitat layers, each resolved at 250m x 250m. The set of layers included water-cover, distance-to-water, tree-cover, shrub/grassland-cover, and a human influence layer depicting anthropogenic influences through villages, roads, and agriculture. A detailed description of the different habitat layers is provided in ???. Importantly, the water-cover and derived distance-to water layers were generated using MODIS Terra MCD43A4 satellite imagery that was classified using a “floodmapping” algorithm developed by (Wolski et al.,

2017) and available through the R-package `floodmapr`. The algorithm allowed us to generate almost weekly updated “floodmaps”, thus providing detailed information about the flood-extent at any given point in time. In total, we generated 700 floodmaps between the years 2000 and 2019. Based on these maps, we generated a minimal and maximum flood scenario. To create the minimum flood scenario, we averaged the 50 floodmaps with smallest flood extent and generated a binary image using areas that were inundated in at least 50% of the maps. Similarly, we created an average image for high flood using the 50 most flooded maps. The final maps are depicted in Figure 2.

### 2.3 Dispersal Model

Our dispersal model was based on a previously parametrized and validated integrated step-selection function (iSSF, Avgar et al., 2016) fitted to GPS data of dispersing AWDs (?). In step selection functions (SSFs, Fortin et al., 2005), observed GPS locations are converted into steps (the straight-line traveled between two GPS recordings (Turchin, 1998)) and compared to a set of *random* steps in a (mixed effects) conditional logistic regression framework (Fortin et al., 2005; Thurfjell et al., 2014; Muff et al., 2020; Fieberg et al., 2021). The model presented in (?) used dispersal data of 16 dispersing African wild dogs from a free-ranging wild dog population in northern Botswana. GPS data during dispersal was collected at 4-hourly intervals and translated into steps of similar duration. Observed steps were then paired step with 24 random steps that were generated using a uniform distribution for turning angles  $(-\pi, +\pi)$  and step lengths from a gamma distribution fitted to observed steps (scale  $\theta = 6'308$  and shape  $k = 0.37$ ). It was then assumed that animals assigned to each observed and random step a selection score of the form (Fortin et al., 2005):

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

Where  $(x_1, x_2, \dots, x_n)$  represent the covariate values along each of the steps and the  $(\beta_1, \beta_2, \dots, \beta_n)$  are the animal’s relative selection strengths Avgar et al., 2017 towards these covariates. The benefit of *integrated* SSFs over regular SSFs is that they provide a means to render two complementary “kernels”. A movement kernel that describes general movement behavior of dispersing AWDs and a habitat kernel that describes preferences of AWDs with regards to environmental conditions (Fieberg et al., 2021). iSSFs also allow interactions among the two kernels and are thus suitable to render that movement behavior may change depending on habitat conditions. A brief summary of the fitted dispersal model is provided in Appendix xx.

## 2.4 Source Areas and Emigration Zones

We simulated dispersing AWDs originating from six distinct source areas located in the vicinity of the Okavango delta (Figure 1). For areas one to six we selected locations at the delta’s periphery that remained dry in both scenarios. At those locations, we generated circular buffers with a radius of 20 km. For source area six, we isolated a polygon covering Chief’s Island, a peninsula located at the OD’s center. Besides source areas, we also generated “zones of emigration” that we used as checkpoints to determine if and where simulated individuals left the delta’s vicinity (Figure 1). We generated emigration zones by first overlaying the OD with an elliptic buffer zone that we dissected using a set of cutlines that originated from the ODs center and spread according to cardinal points (Figure 1).

## 2.5 Dispersal Simulation

For each source area we simulated 1’000 individuals, once assuming a minimum flood, once assuming a maximum flood. This resulted in the simulation of 6’000 individuals for each environmental scenario, hence 12’000 individuals in total. The simulation algorithm was based on the algorithm described in ?? and works as follows. A random location within the source area is chosen as a starting point. Originating from the starting point, a set of 25 random steps is generated by sampling step lengths from a gamma distribution fitted to observed steps (what is a step?) (shape = , scale = ) and turning angles from a uniform distribution ( $-\pi, +\pi$ ). Along each random step the underlying spatial covariates are extracted and relevant movement metrics are computed (i.e.  $\log(sl)$ ,  $\cos(ta)$ ,  $ta$ ). The parametrized dispersal model is used to predict the probability of each step for being chosen given the steps covariate values. One of the steps is sampled based on assigned probabilities and the location of the animal is updated. The procedure is then repeated until the desired number of steps is realized. Here, we simulated each individual for 2’000 steps, which corresponds to the longest dispersal duration recorded in our data. The original model was trained using 4-hourly steps, thus a simulated step also resembled the movement conducted within four hours. Trajectories resulting from such a simulation can be understood as correlated random walks that take into account both habitat and movement preferences of dispersing individuals.

## 2.6 Dispersal Prospects and Connectivity

Based on simulated dispersal trajectories in the two scenarios we quantified dispersal sucess and connectivity using three complementary connectivity metrics as outlined in ?. First, we

generated heatmaps depicting the frequency at which different areas in the landscape were visited by simulated dispersers. Such heatmaps serve to detect dispersal hotspots and areas of intense use. However, they are less suitable for detecting pinchpoints and bottlenecks that are critical in linking distinct patches. Hence, we also computed spatially explicit betweenness scores which are useful to highlight exactly such pinchpoints (Bastille-Rousseau et al., 2018; Bastille-Rousseau and Wittemyer, 2021). To compute betweenness, we overlayed the study area with a regular grid with 2.5 km x 2.5 km grid cells and determined how often simulated individuals transitioned from one grid-cell to another. Note that in case the same individual repeatedly realized the same cell-transition (e.g. repeatedly moved between A-B-A-B...), we only counted a single transition to avoid emphasis on regions where individuals moved in circles. With on the so generated transitions, we generated a network using the centers of all grid-cells as nodes and cell-transitions as weighted connections between the nodes. Based on this network we computed weighted betweenness scores using the R-package `igraph`. As a final connectivity metric and metric of dispersal success, we calculated the number of successful dispersal events between the different source areas as well as towards the emigration zones. We coin this type of connectivity “inter-patch connectivity” as it relates to the movement between distinct patches. Dispersal between two areas was said to be successful whenever a trajectory leaving one area intersected with the target area. To gauge the dispersal duration needed to move between patches (be consistent with “patches”, “source-areas” etc.), we also recorded the minimum number of steps that individuals moved before arriving at the respective patch.

## 3 Results

### 3.1 General

See Figure 3

### 3.2 Heatmaps

Heatmaps produced from simulated dispersal trajectories reveal that the OD acts as a major dispersal barrier during periods of high flood, but reveals viable dispersal corridors during periods of low flood (Figure 4). During minimum flood, the area north-west of Maun appears to serve as vital dispersal habitat. The same area is entirely avoided during maximum flood. Besides striking differences in connectivity for the close vicinity of the delta, the remainder of the study area shows only marginal differences in connectivity between the two scenarios.

For instance, in both scenarios the area south of the Linyanti swamp appears as frequently visited dispersal habitat. Additional heatmaps highlighting differences in connectivity for each source area separately are provided in Appendix SX.

### 3.3 Betweenness

The betweenness maps reveal a similar pattern in that connectivity through the OD is only pronounced during periods of low floods and vanishes entirely during maximum flood (Figure 5). A set of four dispersal corridors meets on the central peninsula (source area 5, Figure 5) at minimum flood but the same corridors are absent when the flood reaches a maximum extent. Instead, a narrow corridor runs north west of Maun, connecting source areas one and two. Again, the remainder of the study area is only marginally affected by flooding patterns. Additional betweenness maps highlighting differences in connectivity for each source area separately are provided in Appendix SX.

### 3.4 Inter-Patch Connectivity

Our analysis of interpatch connectivity demonstrates notable differences in dispersal prospects and duration depending on the extent of the flood (Figure 6). While  $4140 \pm 36.47$  simulated dispersers reach another source area during minimum extent, only  $3626 \pm 36.76$  do so during maximum extent. The differences are particularly pronounced for individuals dispersing from or into the source area located at the OD's center (Figure 7). While the area is reached by  $1325 \pm 32.57$  simulated individuals during minimum flood, only  $298 \pm 17.10$  dispersers arrive there during maximum flood. Furthermore, the dispersal duration into source area six from any other source area increases from  $773 \pm 15.34$  to  $918 \pm 31.84$ . Across all simulations, the average dispersal duration before reaching another source area increases from xx to xx from the minimum to the maximum flood scenario. Nevertheless, connectivity into some areas increases during maximum flooding. Emigration increased slightly from xx to xx

For instance, while dispersers .. Additional maps highlighting differences in inter-patch connectivity for each source area separately are provided in Appendix SX.

## 4 Discussion

According to our simulations, the propensity to move between the eastern and western part of the delta is much lower during maximum extent. This is mainly due to the flood-waters and the city of Maun acting as dispersal barriers. During maximum extent, the floodwaters

of the delta close a gap between the delta and Maun that otherwise would serve as dispersal corridor. Anecdotal evidence supports this hypothesis, for the only dispersing individuals recorded to move from the eastern to the western part of the delta moved at times of low flood. In line with this, it appears that a large flood extent pushes dispersing individuals to move closer to human inhabited areas such as the village of Maun.

Predicting how climate change will impact the dispersal ability of AWDs is challenging for multiple reasons. First of all, predicting the flooding patterns of the OD under climate change is merely impossible due to the complex feedbacks between surface-temperature, soil conditions, precipitation patterns and the associated changes in vegetation. Second, the delta is not only prone to changes in environmental conditions, but also to changes in anthropogenic use of the inflowing water. Finally, it is unclear how AWDs, in fact, how any species, will cope with environmental change due to global warming. Even though some studies predict that AWD populations are likely to decline under increasing temperatures, these studies fail to account for the behavioral plasticity of their focal species. AWDs respiratory system, for instance, has evolved as a perfect adaptation to high temperatures and AWDs may, in fact, profit from a comparative advantage (cite an economist) over their competitors and prey under rising temperatures. Although the theory of comparative advantages is a fundamental concept in economics, it has yet to find its way into ecological studies.

Murray-Hudson et al. (2006) predicted that increased temperatures, additional human abstractions, and reduced river flows might lead to a “Delta dying” and that the impact of climate will be much more pronounced than the impact of anthropogenic water use.

Although local rainfalls in Botswana are expected to increase in terms of intensity, simulations show that the length of the rainy season will decline, more than offsetting the incline in precipitation Akinyemi (2019).

Although dispersal is generally believed to be beneficial for the long term viability of species, it can also lead to the net-loss of individuals in areas where edge effects and anthropogenic mortality are high (Leigh et al., 2012).

We studied a population of African wild dogs that resides in a natural environment with little human influence. This is only representative for a small share of the extant wild dog populations, as most individuals reside in areas that are prone to substantial edge effects. For these populations, the benefit of dispersal is disputed, as dispersal under high anthropogenic mortality may lead to a net-loss of individuals (Leigh et al., 2012).

Dispersal is an important, if not the most important, driver of landscape connectivity

and therefore of major interest to conservation authorities. It has also been demonstrated that dispersal may lead to population declines in areas where anthropogenic mortality is high and dispersal prospects low (Leigh et al., 2012).

Efforts aiming at restoring or improving landscape connectivity should consider and take into account changes in landscape characteristics due to climate change.

We assessed the implications of environmental change on the dispersal prospects, yet we did not consider how changing conditions alter dispersal propensity.

According to our simulations, dispersers are able to cover larger distances during periods of low flood. This finding is little surprising, considering that inundated areas act as dispersal barriers and force dispersers to detour and circumvent water-covered areas. However, it still leads to an interesting hypothesis. Previous studies have shown that the euclidean dispersal distance of female coalitions is larger than that of male coalitions. This has led to ... However, demographic analyses have also revealed that female offspring tend to emigrate from their pack at younger ages and earlier in the year, when floodwaters are still at a relatively low level (Behr). It is thus conceivable that the sex-differences in reported dispersal distances is mainly a consequence of environmental conditions during dispersal, rather than owed to physiological differences between sexes.

While our analysis marks an important step into incorporating environmental change into studies of connectivity, there are several critical additions that should be considered in the future. We studied dispersal and connectivity under two different environmental scenarios, yet our movement model assumed that dispersers had identical habitat and movement preferences in both scenarios. In reality, however, it can be expected that movement and habitat kernels of dispersers differ depending on the season considered (examples).

An additional complication arises when species movement is not solely driven by environmental conditions, but also affected by intra- and inter-specific factors. For instance, ... has shown that dispersers... Rendering such conditions alone is challenging, yet rendering the conditions under changing environmental conditions is merely impossible.

Climate change will not only change species distribution but also community composition (Thuiller et al., 2006).

To address such differences, researchers could model habitat and movement preferences using season-dependent models, or, alternatively, by combining hidden markov models with step-selection functions. (cite papers that fieberg sent)

For the discussion: Through changing environmental conditions, climate change will also impact the distribution of various species with far-reaching consequences on inter- and

intra-specific competition (Abrahms). Due to a lack of data, we omitted any inclusion of social factors in our dispersal model, albeit they are known to be important determinants of dispersal (Armansin). Studying how climate change influences species distribution and their interactions, and ultimately how this alters dispersal, will be challenging but necessary to more realistically simulate dispersal.

Only recently, it has been discovered that AWDs communicate using shared marking sites. The role of such marking sites for dispersing coalitions remains to be investigated, yet it is likely that, akin to resident packs, use SMS as navigation waypoint and demarcation lines. Chemical analyses suggest that the compounds used for communication are highly volatile and may not persist in extreme climate conditions. In result, dispersers may lose their ability to effectively navigate across the landscape and locate potential mates with whom to settle. This would reduce pack-formation prospects and undermine...

Validating predictions from individual-based dispersal models is challenging and requires additional dispersal data, which is inherently scarce anyways. Scitcen science may help to fill this gap by augmenting observed GPS data with occasional sightings of uncollared dispersing coalitions. This is especially critical for species that disperse across borders and beyond confined study areas. The African carnivore wildbook offers ...

Although the OD is arguably the main driver of seasonal change across the studied ecosystem, there are several other factors that undergo seasonal change, including vegetation and the abundance and distribution of prey or predators.

The OD is an important driver of species distribution and it has been found that an expanding flood limits available habitat, thus leading to more inter-specific competition, particularly between AWDs and lions.

Although validating the predictions resulting from our dispersal model is challenging, the simulations enable us to generate several interesting hypotheses...

## 4.1 Conclusion

Our dispersal simulations across two extreme climatic scenarios reveal striking differences in dispersal prospects and landscape connectivity for dispersing AWDs. This implies that (1) climatic variation, be it due to seasonality or climate change, must be included in analyses dealing with dispersal and (2) that projected climate change is likely to have profound impacts on landscape connectivity.

## 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 (?). Access to R-scripts that exemplify the application of the proposed approach using simulated data are provided through Github (<https://github.com/DavidDHofmann/DispersalSimulation>). In addition, all codes required to reproduce the African wild dog case study will be made available through an online repository at the time of publication.

## 7 Acknowledgements

We thank the Ministry of Environment and Tourism of Botswana for granting permission to conduct this research. We thank C. Botes, I. Clavadetscher, and G. Camenisch for assisting with wild dog immobilizations. We also thank B. Abrahms for sharing her data of three dispersing wild dogs. Furthermore, we would like to thank Johannes Signer for assisting with the simulation algorithm. This study was funded by Albert-Heim Foundation, Basler Stiftung für Biologische Forschung, Claraz Foundation, Idea Wild, Jacot Foundation, National Geographic Society, Parrotia Stiftung, Stiftung Temperatio, Wilderness Wildlife Trust Foundation, Forschungskredit der Universität Zürich, and a Swiss National Science Foundation Grant (31003A\_182286) to A. Ozgul.

## References

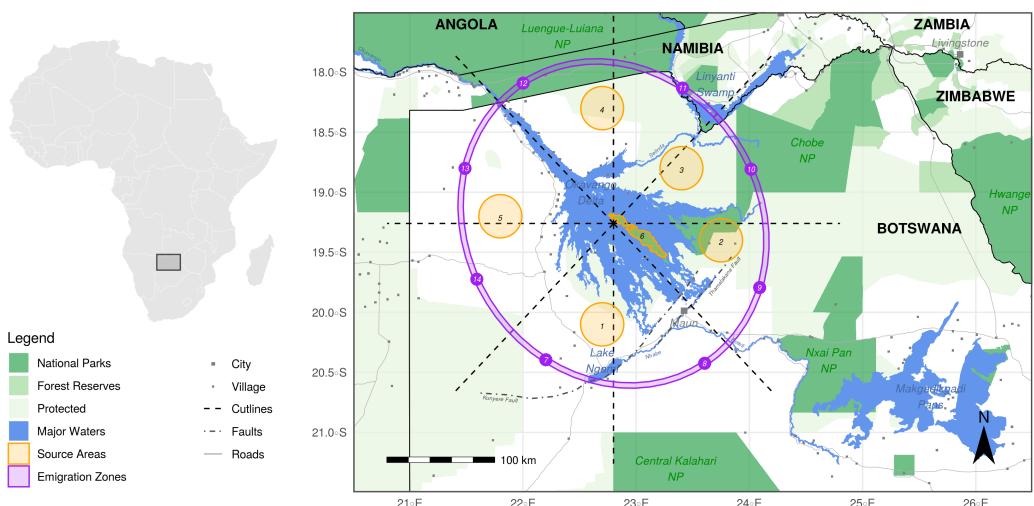
- Adriaensen, F., Chardon, J., De Blust, G., Swinnen, E., Villalba, S., Gulinck, H., and Matthysen, E. (2003). The Application of ‘Least-Cost’ Modelling as a Functional Landscape Model. *Landscape and Urban Planning*, 64(4):233–247.
- Akinyemi, F. O. (2019). Potential Impacts of Global Warming Levels 1.5 C and Above on Climate Extremes in Botswana. *Climatic Change*, page 14.
- Allen, C. H., Parrott, L., and Kyle, C. (2016). An Individual-Based Modelling Approach to Estimate Landscape Connectivity for Bighorn Sheep (*ovis Canadensis*). *PeerJ*, 4:e2001.
- Anderson, A. S., Reside, A. E., VanDerWal, J. J., Shoo, L. P., Pearson, R. G., and Williams, S. E. (2012). Immigrants and refugees: The importance of dispersal in mediating biotic attrition under climate change. *Global Change Biology*, 18(7):2126–2134.
- Ashrafzadeh, M. R., Naghipour, A. A., Haidarian, M., Kusza, S., and Pilliod, D. S. (2019). Effects of climate change on habitat and connectivity for populations of a vulnerable, endemic salamander in Iran. *Global Ecology and Conservation*, 19:e00637.
- Avgar, T., Lele, S. R., Keim, J. L., and Boyce, M. S. (2017). Relative Selection Strength: Quantifying Effect Size in Habitat- and Step-Selection Inference. *Ecology and Evolution*, 7(14):5322–5330.
- Avgar, T., Potts, J. R., Lewis, M. A., and Boyce, M. S. (2016). Integrated Step Selection Analysis: Bridging the Gap Between Resource Selection and Animal Movement. *Methods in Ecology and Evolution*, 7(5):619–630.
- Baddeley, A., Rubak, E., and Turner, R. (2015). *Spatial Point Patterns: Methodology and Applications with R*. Chapman and Hall/CRC Press, London.
- Baguette, M., Blanchet, S., Legrand, D., Stevens, V. M., and Turlure, C. (2013). Individual Dispersal, Landscape Connectivity and Ecological Networks: Dispersal, Connectivity and Networks. *Biological Reviews*, 88(2):310–326.
- Bastille-Rousseau, G., Douglas-Hamilton, I., Blake, S., Northrup, J. M., and Wittemyer, G. (2018). Applying Network Theory to Animal Movements to Identify Properties of Landscape Space Use. *Ecological Applications*, 28(3):854–864.
- Bastille-Rousseau, G. and Wittemyer, G. (2021). Characterizing the Landscape of Movement to Identify Critical Wildlife Habitat and Corridors. *Conservation Biology*, 35(1):14.
- Behr, D. M. (2020). Dispersal and Its Demographic Consequences in the Endangered African Wild Dog (*Lycaon pictus*). page 14.
- Benz, R. A., Boyce, M. S., Thurfjell, H., Paton, D. G., Musiani, M., Dormann, C. F., and Ciuti, S. (2016). Dispersal Ecology Informs Design of Large-Scale Wildlife Corridors. *PLoS ONE*, 11(9):e0162989.
- Boyce, M. S., Vernier, P. R., Nielsen, S. E., and Schmiegelow, F. K. (2002). Evaluating Resource Selection Functions. *Ecological Modelling*, 157(2-3):281–300.
- Brennan, A., Beytell, P., Aschenborn, O., Du Preez, P., Funston, P., Hanssen, L., Kilian, J., Stuart-Hill, G., Taylor, R., and Naidoo, R. (2020). Characterizing Multispecies Connectivity Across a Transfrontier Conservation Landscape. *Journal of Applied Ecology*, 57:1700–1710.
- Briatte, F. (2021). *Gnetwork: Geometries to Plot Networks with 'Ggplot2'*.
- Brown, J. H. and Kodric-Brown, A. (1977). Turnover Rates in Insular Biogeography: Effect of Immigration on Extinction. *Ecology*, 58(2):445–449.
- Chetkiewicz, C.-L. B. and Boyce, M. S. (2009). Use of Resource Selection Functions to Identify Conservation Corridors. *Journal of Applied Ecology*, 46(5):1036–1047.

- Chetkiewicz, C.-L. B., St. Clair, C. C., and Boyce, M. S. (2006). Corridors for Conservation: Integrating Pattern and Process. *Annual Review of Ecology, Evolution, and Systematics*, 37(1):317–342.
- Clobert, J., Baguette, M., Benton, T. G., and Bullock, J. M. (2012). *Dispersal Ecology and Evolution*. Oxford University Press.
- Cozzi, G., Behr, D. M., Webster, H. S., Claase, M., Bryce, C. M., Modise, B., Mcnutt, J. W., and Ozgul, A. (2020). African Wild Dog Dispersal and Implications for Management. *The Journal of Wildlife Management*, pages 614–621.
- Csardi, G. and Nepusz, T. (2006). The igraph software package for complex network research. *InterJournal, Complex Systems*:1695.
- Cushman, S. A. and Lewis, J. S. (2010). Movement Behavior Explains Genetic Differentiation in American Black Bears. *Landscape Ecology*, 25(10):1613–1625.
- Davies-Mostert, H. T., Kamler, J. F., Mills, M. G. L., Jackson, C. R., Rasmussen, G. S. A., Groom, R. J., and Macdonald, D. W. (2012). Long-Distance Transboundary Dispersal of African Wild Dogs Among Protected Areas in Southern Africa. *African Journal of Ecology*, 50(4):500–506.
- Diniz, M. F., Cushman, S. A., Machado, R. B., and De Marco Júnior, P. (2019). Landscape Connectivity Modeling from the Perspective of Animal Dispersal. *Landscape Ecology*, 35:41–58.
- Doerr, V. A. J., Barrett, T., and Doerr, E. D. (2011). Connectivity, Dispersal Behaviour and Conservation Under Climate Change: A Response to Hodgson Et Al.: Connectivity and Dispersal Behaviour. *Journal of Applied Ecology*, 48(1):143–147.
- Durant, J., Hjermann, D., Ottersen, G., and Stenseth, N. (2007). Climate and the Match or Mismatch Between Predator Requirements and Resource Availability. *Climate Research*, 33:271–283.
- Eddelbuettel, D. and François, R. (2011). Rcpp: Seamless R and C++ integration. *Journal of Statistical Software*, 40(8):1–18.
- Elliot, N. B., Cushman, S. A., Macdonald, D. W., and Loveridge, A. J. (2014). The Devil Is in the Dispersers: Predictions of Landscape Connectivity Change with Demography. *Journal of Applied Ecology*, 51(5):1169–1178.
- Engelbrecht, F., Adegoke, J., Bopape, M.-J., Naidoo, M., Garland, R., Thatcher, M., McGregor, J., Katzfey, J., Werner, M., Ichoku, C., and Gatebe, C. (2015). Projections of rapidly rising surface temperatures over Africa under low mitigation. *Environmental Research Letters*, 10(8):085004.
- Etherington, T. R. (2016). Least-Cost Modelling and Landscape Ecology: Concepts, Applications, and Opportunities. *Current Landscape Ecology Reports*, 1(1):40–53.
- Fahrig, L. (2003). Effects of Habitat Fragmentation on Biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, 34(1):487–515.
- Fieberg, J., Signer, J., Smith, B., and Avgar, T. (2021). A ‘How to’ Guide for Interpreting Parameters in Habitat-Selection Analyses. *Journal of Animal Ecology*, 90(5):1027–1043.
- Fortin, D., Beyer, H. L., Boyce, M. S., Smith, D. W., Duchesne, T., and Mao, J. S. (2005). Wolves Influence Elk Movements: Behavior Shapes a Trophic Cascade in Yellowstone National Park. *Ecology*, 86(5):1320–1330.
- Fortin, D., Fortin, M.-E., Beyer, H. L., Duchesne, T., Courant, S., and Dancose, K. (2009). Group-Size-Mediated Habitat Selection and Group Fusion–Fission Dynamics of Bison Under Predation Risk. *Ecology*, 90(9):2480–2490.

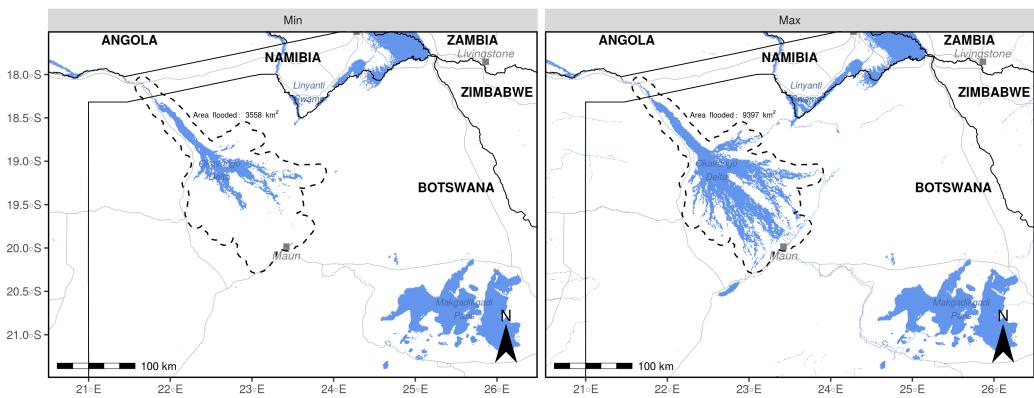
- Frankham, R., Briscoe, D. A., and Ballou, J. D. (2002). *Introduction to Conservation Genetics*. Cambridge university press.
- Fuller, A., Mitchell, D., Maloney, S. K., and Hetem, R. S. (2016). Towards a Mechanistic Understanding of the Responses of Large Terrestrial Mammals to Heat and Aridity Associated with Climate Change. *Climate Change Responses*, 3(1):10.
- Graves, T., Chandler, R. B., Royle, J. A., Beier, P., and Kendall, K. C. (2014). Estimating Landscape Resistance to Dispersal. *Landscape Ecology*, 29(7):1201–1211.
- Gustafson, E. J. and Gardner, R. H. (1996). The Effect of Landscape Heterogeneity on the Probability of Patch Colonization. *Ecology*, 77(1):94–107.
- Hanski, I. (1999). Habitat Connectivity, Habitat Continuity, and Metapopulations in Dynamic Landscapes. *Oikos*, 87(2):209.
- Hauenstein, S., Fattebert, J., Grüebler, M. U., Naef-Daenzer, B., Pe'er, G., and Hartig, F. (2019). Calibrating an Individual-Based Movement Model to Predict Functional Connectivity for Little Owls. *Ecological Applications*, 29(4):e01873.
- Heller, N. E. and Zavaleta, E. S. (2009). Biodiversity Management in the Face of Climate Change: A Review of 22 Years of Recommendations. *Biological conservation*, 142(1):14–32.
- Hijmans, R. J. (2022). *Terra: Spatial Data Analysis*.
- Hodgson, J. A., Thomas, C. D., Wintle, B. A., and Moilanen, A. (2009). Climate Change, Connectivity and Conservation Decision Making: Back to Basics. *Journal of Applied Ecology*, 46(5):964–969.
- IPCC (2022). Summary for Policymakers. In Shukla, P., Skea, J., Slade, R., Khoardajie, A. A., van Diemen, R., McCollum, D., Pathak, M., Some, S., Vyas, P., Fradera, R., Belkacemi, M., Hasija, A., Lisboa, G., Luz, S., and Malley, J., editors, *Climate Change 2022: Mitigation of Climate Change. Contribution of Working Group III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK and New York, NY, USA.
- Kanagaraj, R., Wiegand, T., Kramer-Schadt, S., and Goyal, S. P. (2013). Using Individual-Based Movement Models to Assess Inter-Patch Connectivity for Large Carnivores in Fragmented Landscapes. *Biological Conservation*, 167:298–309.
- Kaszta, Ż., Cushman, S. A., and Slotow, R. (2021). Temporal Non-Stationarity of Path-Selection Movement Models and Connectivity: An Example of African Elephants in Kruger National Park. *Frontiers in Ecology and Evolution*, 9:553263.
- Killeen, J., Thurfjell, H., Ciuti, S., Paton, D., Musiani, M., and Boyce, M. S. (2014). Habitat Selection During Ungulate Dispersal and Exploratory Movement at Broad and Fine Scale with Implications for Conservation Management. *Movement Ecology*, page 13.
- Kokko, H. (2006). From Individual Dispersal to Species Ranges: Perspectives for a Changing World. *Science*, 313(5788):789–791.
- Leigh, K. A., Zenger, K. R., Tammen, I., and Raadsma, H. W. (2012). Loss of Genetic Diversity in an Outbreeding Species: Small Population Effects in the African Wild Dog (*Lycaon pictus*). *Conservation Genetics*, 13(3):767–777.
- Lines, R., Bormpoudakis, D., Xofis, P., and Tzanopoulos, J. (2021). Modelling Multi-Species Connectivity at the Kafue-Zambezi Interface: Implications for Transboundary Carnivore Conservation. *Sustainability*, 13(22):12886.
- Littlefield, C. E., Crosby, M., Michalak, J. L., and Lawler, J. J. (2019). Connectivity for Species on the Move: Supporting Climate-Driven Range Shifts. *Frontiers in Ecology and the Environment*, 17(5):270–278.

- Luo, Z., Wang, X., Yang, S., Cheng, X., Liu, Y., and Hu, J. (2021). Combining the Responses of Habitat Suitability and Connectivity to Climate Change for an East Asian Endemic Frog. *Frontiers in Zoology*, 18(1):14.
- MacArthur, R. H. and Wilson, E. O. (2001). *The Theory of Island Biogeography*, volume 1. Princeton university press.
- Masenga, E. H., Jackson, C. R., Mjingo, E. E., Jacobson, A., Riggio, J., Lyamuya, R. D., Fyumagwa, R. D., Borner, M., and Røskift, E. (2016). Insights into Long-Distance Dispersal by African Wild Dogs in East Africa. *African Journal of Ecology*, 54(1):95–98.
- McNutt, J. (1996). Sex-Biased Dispersal in African Wild Dogs, *Lycaon pictus*. *Animal Behaviour*, 52(6):1067–1077.
- McRae, B. H., Dickson, B. G., Keitt, T. H., and Shah, V. B. (2008). Using Circuit Theory to Model Connectivity in Ecology, Evolution, and Conservation. *Ecology*, 89(10):2712–2724.
- Melbourne, B. A. and Hastings, A. (2008). Extinction Risk Depends Strongly on Factors Contributing to Stochasticity. *Nature*, 454(7200):100–103.
- Muff, S., Signer, J., and Fieberg, J. (2020). Accounting for Individual-Specific Variation in Habitat-Selection Studies: Efficient Estimation of Mixed-Effects Models Using Bayesian or Frequentist Computation. *Journal of Animal Ecology*, 89(1):80–92.
- Mui, A. B., Caverhill, B., Johnson, B., Fortin, M.-J., and He, Y. (2017). Using Multiple Metrics to Estimate Seasonal Landscape Connectivity for Blanding's Turtles (*Emydoidea blandingii*) in a Fragmented Landscape. *Landscape Ecology*, 32(3):531–546.
- Murray-Hudson, M., Wolski, P., and Ringrose, S. (2006). Scenarios of the Impact of Local and Upstream Changes in Climate and Water Use on Hydro-Ecology in the Okavango Delta, Botswana. *Journal of Hydrology*, 331(1):73–84.
- Osipova, L., Okello, M. M., Njumbi, S. J., Ngene, S., Western, D., Hayward, M. W., and Balkenhol, N. (2019). Using Step-Selection Functions to Model Landscape Connectivity for African Elephants: Accounting for Variability Across Individuals and Seasons. *Animal Conservation*, 22(1):35–48.
- Ozgul, A., Childs, D. Z., Oli, M. K., Armitage, K. B., Blumstein, D. T., Olson, L. E., Tuljapurkar, S., and Coulson, T. (2010). Coupled Dynamics of Body Mass and Population Growth in Response to Environmental Change. *Nature*, 466(7305):482–485.
- Paniw, M., James, T. D., Ruth Archer, C., Römer, G., Levin, S., Compagnoni, A., Che-Castaldo, J., Bennett, J. M., Mooney, A., Childs, D. Z., Ozgul, A., Jones, O. R., Burns, J. H., Beckerman, A. P., Patwary, A., Sanchez-Gassen, N., Knight, T. M., and Salguero-Gómez, R. (2021). The myriad of complex demographic responses of terrestrial mammals to climate change and gaps of knowledge: A global analysis. *Journal of Animal Ecology*, 90(6):1398–1407.
- R Core Team (2022). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Radchuk, V., Reed, T., Teplitsky, C., van de Pol, M., Charmantier, A., Hassall, C., Adamík, P., Adriaensen, F., Ahola, M. P., Arcese, P., Miguel Avilés, J., Balbontin, J., Berg, K. S., Borras, A., Burthe, S., Clobert, J., Dehnhard, N., de Lope, F., Dhondt, A. A., Dingemanse, N. J., Doi, H., Eeva, T., Fickel, J., Filella, I., Fossøy, F., Goodenough, A. E., Hall, S. J. G., Hansson, B., Harris, M., Hasselquist, D., Hickler, T., Joshi, J., Kharouba, H., Martínez, J. G., Mihoub, J.-B., Mills, J. A., Molina-Morales, M., Moksnes, A., Ozgul, A., Parejo, D., Pilard, P., Poisbleau, M., Rousset, F., Rödel, M.-O., Scott, D., Senar, J. C., Stefanescu, C., Stokke, B. G., Kusano, T., Tarka, M., Tarwater, C. E., Thonicke, K., Thorley, J., Wilting, A., Tryjanowski, P., Merilä, J., Sheldon, B. C., Pape Møller, A., Matthysen, E., Janzen, F., Dobson, F. S., Visser, M. E., Beissinger, S. R., Courtiol, A., and Kramer-Schadt, S. (2019). Adaptive responses of animals to climate change are most likely insufficient. *Nature Communications*, 10(1):3109.

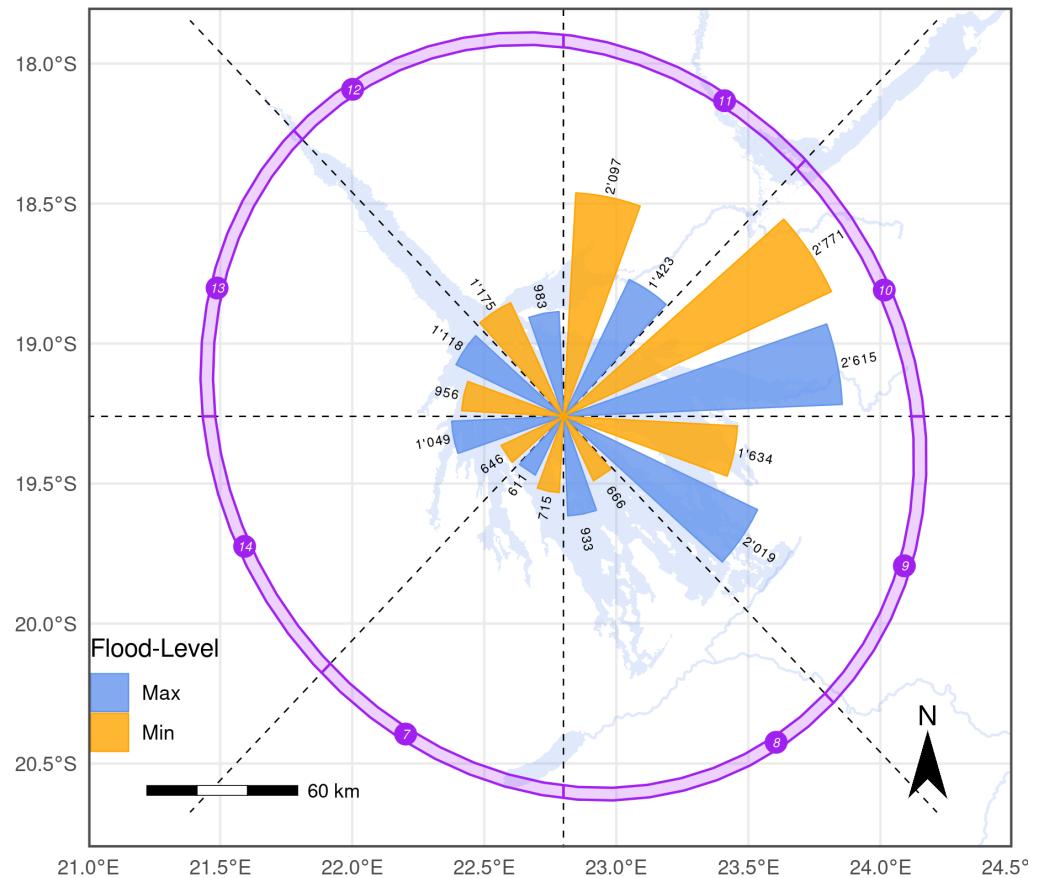
- Raia, P., Passaro, F., Fulgione, D., and Carotenuto, F. (2012). Habitat tracking, stasis and survival in Neogene large mammals. *Biology Letters*, 8(1):64–66.
- Sawyer, S. C., Epps, C. W., and Brashares, J. S. (2011). Placing Linkages Among Fragmented Habitats: Do Least-Cost Models Reflect How Animals Use Landscapes?: Least-Cost Modelling for Habitat Linkage Design. *Journal of Applied Ecology*, 48(3):668–678.
- Squires, J. R., DeCesare, N. J., Olson, L. E., Kolbe, J. A., Hebblewhite, M., and Parks, S. A. (2013). Combining Resource Selection and Movement Behavior to Predict Corridors for Canada Lynx at Their Southern Range Periphery. *Biological Conservation*, 157:187–195.
- Taylor, P. D., Fahrig, L., Henein, K., and Merriam, G. (1993). Connectivity Is a Vital Element of Landscape Structure. *Oikos*, 68(3):571–573.
- Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., Erasmus, B. F. N., de Siqueira, M. F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A. S., Midgley, G. F., Miles, L., Ortega-Huerta, M. A., Peterson, A. T., Phillips, O. L., and Williams, S. E. (2004). Extinction Risk from Climate Change. 427.
- Thuiller, W., Broennimann, O., Hughes, G., Alkemade, J. R. M., Midgley, G. F., and Corsi, F. (2006). Vulnerability of African Mammals to Anthropogenic Climate Change Under Conservative Land Transformation Assumptions. *Global Change Biology*, 12(3):424–440.
- Thurfjell, H., Ciuti, S., and Boyce, M. S. (2014). Applications of Step-Selection Functions in Ecology and Conservation. *Movement Ecology*, 2(4).
- Tischendorf, L. and Fahrig, L. (2000). On the Usage and Measurement of Landscape Connectivity. *Oikos*, 90(1):7–19.
- Travis, J. M. J., Delgado, M., Boedi, G., Baguette, M., Bartoń, K., Bonte, D., Boulangeat, I., Hodgson, J. A., Kubisch, A., Penteriani, V., Saastamoinen, M., Stevens, V. M., and Bullock, J. M. (2013). Dispersal and Species' Responses to Climate Change. *Oikos*, 122(11):1532–1540.
- Turchin, P. (1998). *Quantitative Analysis of Movement: Measuring and Modeling Population Redistribution in Plants and Animals*. Sinauer Associates, Sunderland, MA.
- Unnithan Kumar, S., Kaszta, Ź., and Cushman, S. A. (2022a). Pathwalker: A New Individual-Based Movement Model for Conservation Science and Connectivity Modelling. *ISPRS International Journal of Geo-Information*, 11(6):329.
- Unnithan Kumar, S., Turnbull, J., Hartman Davies, O., Hodgetts, T., and Cushman, S. A. (2022b). Moving Beyond Landscape Resistance: Considerations for the Future of Connectivity Modelling and Conservation Science. *Landscape Ecology*, 37(10):2465–2480.
- Vasudev, D., Fletcher, R. J., Goswami, V. R., and Krishnadas, M. (2015). From Dispersal Constraints to Landscape Connectivity: Lessons from Species Distribution Modeling. *Ecography*, 38(10):967–978.
- Wickham, H. (2016). *Ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York.
- Wilson, R. R., Gilbert-Norton, L., and Gese, E. M. (2012). Beyond Use Versus Availability: Behaviour-Explicit Resource Selection. *Wildlife Biology*, 18(4):424–430.
- Wolski, P., Murray-Hudson, M., Thito, K., and Cassidy, L. (2017). Keeping It Simple: Monitoring Flood Extent in Large Data-Poor Wetlands Using MODIS SWIR Data. *International Journal of Applied Earth Observation and Geoinformation*, 57:224–234.
- Zeller, K. A., McGarigal, K., and Whiteley, A. R. (2012). Estimating Landscape Resistance to Movement: A Review. *Landscape Ecology*, 27(6):777–797.
- Zeller, K. A., Wattles, D. W., Bauder, J. M., and DeStefano, S. (2020). Forecasting Seasonal Habitat Connectivity in a Developing Landscape. *Land*, 9(7):233.



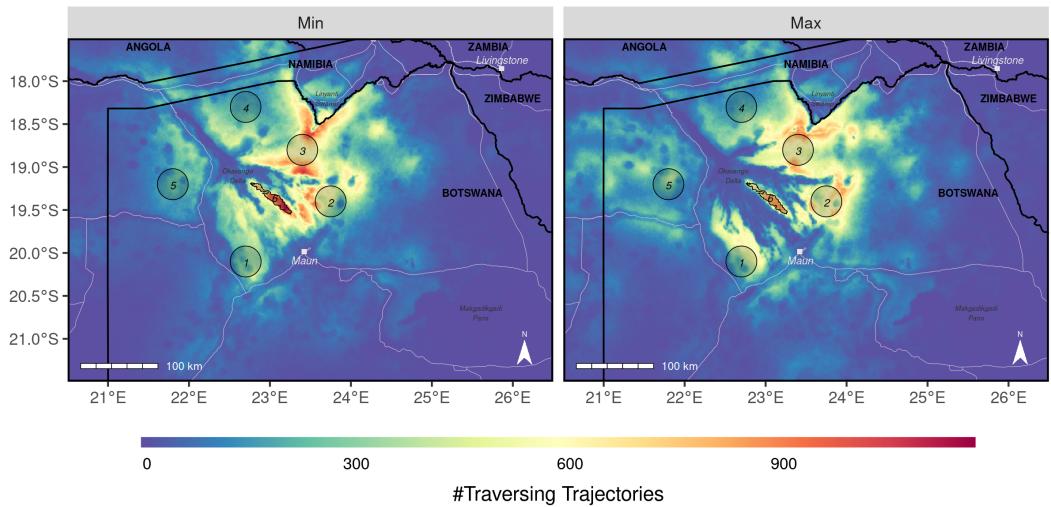
**Figure 1:** Study area across which we simulated dispersal. Simulated dispersers were released at random locations within the orange source areas distributed across the delta. Emigration zones (purple) served as checkpoints and enabled us to identify if and where simulated dispersers left the close surroundings of the Okavango delta. These zones were generated using a set of cutlines originating from the center of the delta and roughly cutting an elliptical buffer zone into sections of equal size.



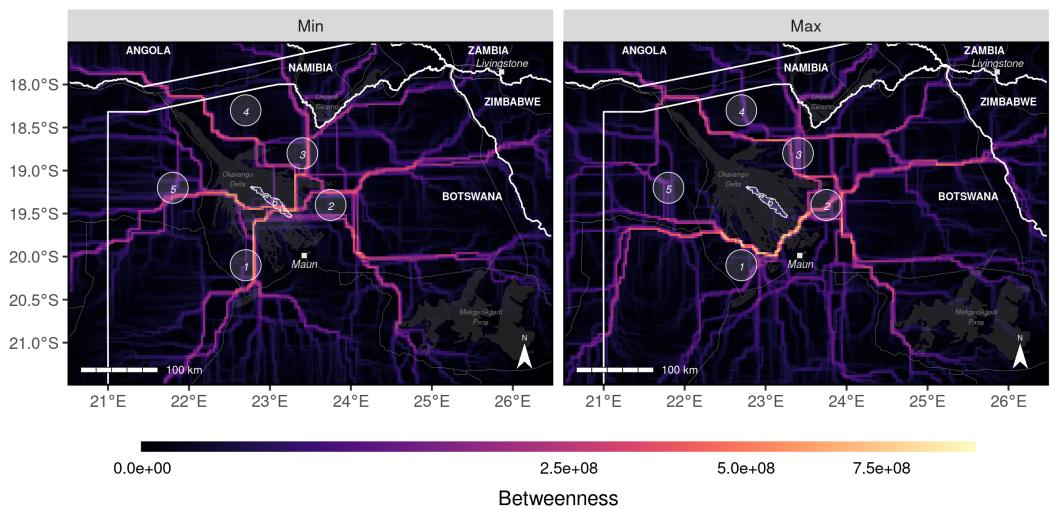
**Figure 2:** Flood extent in the two scenarios considered. In the left panel, the flood is at an extremely low level, stretching across  $3'558 \text{ km}^2$ , whereas in the right panel the flood is at an extremely high level and covers  $9'397 \text{ km}^2$ . The two maps were generated using 700 remote sensed MODIS MCD43A4 satellite images spanning the years 2000 to 2019.



**Figure 3:** Caption



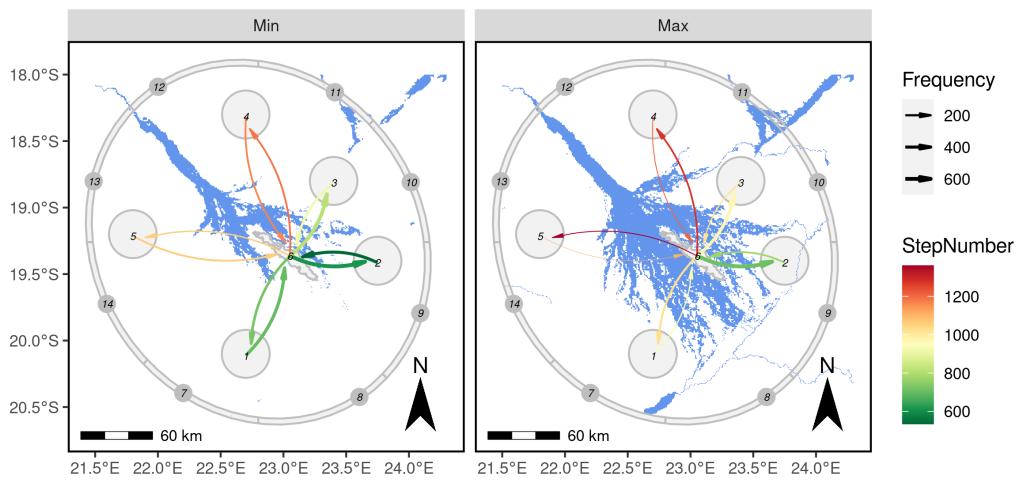
**Figure 4:** Heatmaps depicting the number of simulated dispersal trajectories traversing each grid-cell in the study area. The left panel shows results for the minimum flood scenario, whereas the right panel shows results for the maximum flood scenario. Source areas (numbered 1-6) from which dispersers were released, and emigration zones (numbered 7-14) are shaded in dark gray.



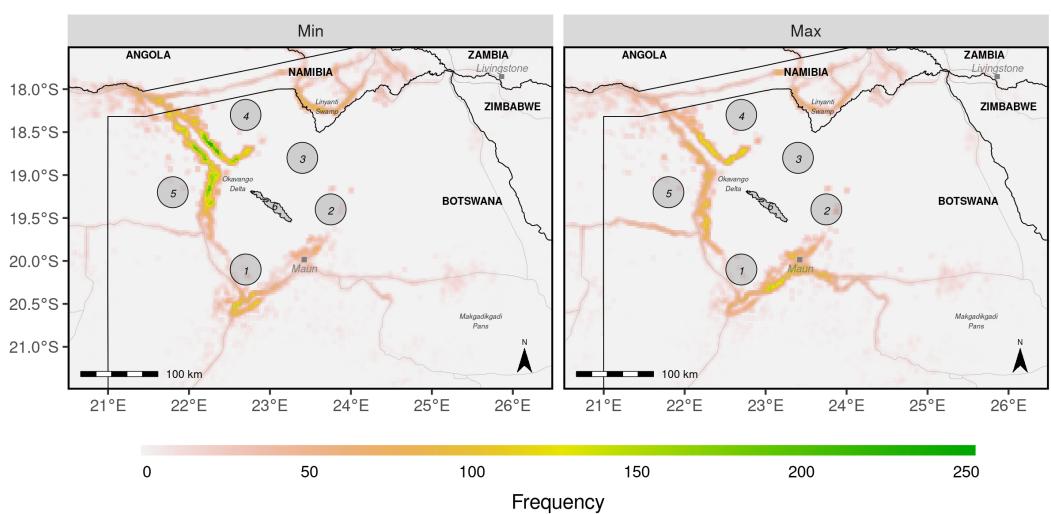
**Figure 5:** Betweenness scores highlighting potential dispersal corridors for both the minimum and maximum flood scenario. Areas with high betweenness scores (bright yellow) are used by many simulated individuals to move into adjacent regions and can thus be understood as critical pinch-points. Source areas (numbered 1-6) from which dispersers were released, and emigration zones (numbered 7-14) are shaded in light gray.

		From								From					
		1	2	3	4	5	6		1	2	3	4	5	6	
1	Min	1000 ± 0	129 ± 10.13	58 ± 7.02	30 ± 5.4	131 ± 10.37	284 ± 14.54		1 ± 0	1055 ± 45.68	1122 ± 62.33	1471 ± 57.13	1025 ± 45.95	721 ± 27.23	
	Max	1000 ± 0	64 ± 7.54	27 ± 5.05	7 ± 2.6	137 ± 10.84	174 ± 12.13		1 ± 0.45	1003 ± 60.72	1332 ± 81.53	1401 ± 128.82	950 ± 44.82	1026 ± 33.55	
2	Min	328 ± 14.67	1000 ± 0	516 ± 15.42	319 ± 14.37	92 ± 8.99	637 ± 15.33		959 ± 28.17	1 ± 0.01	688 ± 23.57	1121 ± 27.2	1378 ± 42.62	611 ± 19.32	
	Max	160 ± 11.56	1000 ± 0	515 ± 15.57	276 ± 13.71	18 ± 4.05	631 ± 15.93		1130 ± 38.76	1 ± 0	721 ± 24.19	1086 ± 29.72	1503 ± 104.25	708 ± 18.23	
3	Min	251 ± 13.8	672 ± 14.69	1000 ± 0	616 ± 15.05	103 ± 9.56	549 ± 16.39		1125 ± 31.86	558 ± 19.42	1 ± 0	630 ± 19.02	1320 ± 33.21	814 ± 21.68	
	Max	61 ± 7.34	545 ± 15.29	1000 ± 0	666 ± 14.71	32 ± 5.3	418 ± 15.26		1335 ± 50.98	657 ± 22.44	1 ± 0.4	564 ± 19.47	1260 ± 82.97	971 ± 23.77	
4	Min	66 ± 7.71	167 ± 11.94	317 ± 14.5	1000 ± 0	126 ± 10.58	139 ± 11.13		1367 ± 44.61	1088 ± 37.22	809 ± 32.17	1 ± 0.01	1159 ± 42.5	1189 ± 41.06	
	Max	15 ± 3.87	135 ± 10.82	369 ± 14.64	1000 ± 0	45 ± 6.51	128 ± 10.67		1566 ± 86.69	1153 ± 43.76	704 ± 28.5	1 ± 0	1141 ± 67.52	1276 ± 36.25	
5	Min	114 ± 10.44	29 ± 5.27	24 ± 4.83	50 ± 6.76	1000 ± 0	78 ± 8.55		992 ± 43.38	1463 ± 66.87	1268 ± 104.1	1159 ± 67.73	1 ± 0.09	1060 ± 60.11	
	Max	190 ± 12.17	7 ± 2.64	10 ± 3.07	64 ± 7.51	1000 ± 0	32 ± 5.56		1083 ± 38.32	1524 ± 172.02	1211 ± 164.09	1265 ± 54.3	1 ± 0.01	1361 ± 73.93	
6	Min	437 ± 15.96	391 ± 15.71	221 ± 13.05	139 ± 10.88	139 ± 10.91	1000 ± 0		694 ± 22.63	534 ± 24.5	919 ± 38.5	1166 ± 40.34	1061 ± 43.03	1 ± 0.09	
	Max	65 ± 7.69	127 ± 11.04	64 ± 7.72	34 ± 5.71	8 ± 2.75	1000 ± 0		926 ± 61.33	772 ± 49.47	1023 ± 62.79	1206 ± 86.47	1106 ± 163.4	1 ± 0.05	
7	Min	413 ± 15.92	38 ± 5.74	20 ± 4.22	10 ± 3.16	105 ± 9.67	130 ± 10.55		483 ± 23.49	1286 ± 67.05	1366 ± 93.58	1465 ± 103.63	1010 ± 49.42	995 ± 36.92	
	Max	369 ± 15.8	36 ± 5.77	10 ± 3.08	4 ± 1.96	124 ± 10.56	68 ± 7.64		734 ± 25.64	1182 ± 68.29	1073 ± 83.2	1479 ± 216.38	1044 ± 46.49	1252 ± 50.72	
8	Min	379 ± 15.48	67 ± 7.9	33 ± 5.72	13 ± 3.53	38 ± 6.3	138 ± 11.11		543 ± 25.11	1185 ± 56.28	1324 ± 79.58	1620 ± 80.28	1315 ± 76.69	954 ± 40.21	
	Max	443 ± 16.08	168 ± 11.45	72 ± 8.41	28 ± 5.26	53 ± 7.22	169 ± 11.81		689 ± 24.3	909 ± 41.5	1174 ± 58.57	1355 ± 84.7	1332 ± 60.79	1166 ± 36.17	
9	Min	177 ± 12.28	552 ± 15.3	346 ± 15.52	175 ± 12.33	40 ± 6.3	344 ± 15.4		1143 ± 39.19	461 ± 22.61	804 ± 27.84	1226 ± 33.79	1467 ± 57.83	952 ± 27.35	
	Max	187 ± 12.44	746 ± 14.04	408 ± 15.33	210 ± 12.29	20 ± 4.36	446 ± 16.37		1110 ± 35.85	372 ± 16.0	871 ± 25.22	1180 ± 34.08	1373 ± 91.93	921 ± 21.81	
10	Min	221 ± 12.74	725 ± 13.86	771 ± 13.03	498 ± 16.23	73 ± 8.16	482 ± 15.88		1215 ± 30.84	468 ± 18.43	470 ± 17.32	873 ± 21.86	1489 ± 38.33	947 ± 22.47	
	Max	105 ± 9.86	768 ± 13.42	750 ± 13.75	490 ± 15.49	21 ± 4.43	473 ± 16.1		1295 ± 45.35	413 ± 15.54	487 ± 16.31	887 ± 23.63	1456 ± 93.47	1012 ± 21.72	
11	Min	123 ± 10.6	374 ± 14.92	616 ± 14.73	625 ± 15.12	75 ± 8.18	276 ± 14.52		1344 ± 38.5	958 ± 26.2	593 ± 21.7	493 ± 19.78	1464 ± 44.43	1182 ± 28.29	
	Max	12 ± 3.49	204 ± 12.65	458 ± 15.39	576 ± 15.68	32 ± 5.56	141 ± 10.82		1428 ± 95.5	1109 ± 37.92	680 ± 25.1	572 ± 21.8	1347 ± 87.04	1258 ± 35.32	
12	Min	50 ± 6.66	92 ± 9.07	192 ± 12.22	502 ± 15.2	259 ± 13.56	83 ± 8.63		1352 ± 59.94	1330 ± 41.14	1068 ± 35.35	493 ± 21.6	936 ± 31.04	1381 ± 43.78	
	Max	14 ± 3.82	62 ± 7.42	214 ± 13.01	543 ± 15.82	99 ± 9.47	51 ± 6.99		1640 ± 77.33	1293 ± 48.93	981 ± 36.72	477 ± 22.65	1006 ± 54.61	1449 ± 58.7	
13	Min	50 ± 6.96	25 ± 4.84	46 ± 6.48	125 ± 10.49	665 ± 14.89	45 ± 6.6		1158 ± 66.47	1484 ± 75.32	1304 ± 67.35	928 ± 48.03	399 ± 14.97	1297 ± 60.06	
	Max	150 ± 11.29	8 ± 2.79	37 ± 6.06	117 ± 10.07	780 ± 13.15	26 ± 4.93		1216 ± 39.35	1154 ± 151.4	1289 ± 76.11	975 ± 44.66	318 ± 14.11	1451 ± 75.68	
14	Min	115 ± 9.99	15 ± 3.93	7 ± 2.69	19 ± 4.26	445 ± 15.73	46 ± 6.44		892 ± 49.38	1379 ± 75.81	1698 ± 114.09	1310 ± 108.91	480 ± 22.47	1288 ± 61.95	
	Max	287 ± 14.11	9 ± 2.93	7 ± 2.52	33 ± 5.52	676 ± 14.72	38 ± 6.14		953 ± 29.81	1288 ± 128.49	1570 ± 168.96	1434 ± 71.05	509 ± 19.88	1344 ± 63.92	

**Figure 6:** Dispersal frequency (a) and duration (b) (in steps) between source areas and emigration zones during minimum and maximum flood.



**Figure 7:** Inter-patch connectivity into and from source area number six. This patch experienced the most drastic reduction in connectivity in result to a high flood level. During minimum flood there is ample connectivity from and into source areas 1-3. During maximum flood, connectivity is lower and mainly limited to source area 2.



**Figure 8:** Caption