Using step-selection functions to model landscape connectivity for African elephants: accounting for variability across individuals and seasons

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Abstract

Landscape connectivity is an important component of systematic conservation planning. Step-selection functions (SSFs) is a highly promising method for connectivity modeling. However, differences in movement behavior across individuals and seasons are usually not considered in current SSF-based analyses, potentially leading to imprecise connectivity models. Here, our objective was to use SSFs to build functional connectivity models for African elephants *Loxodonta africana* in a seasonal environment to illustrate the temporal variability of functional landscape connectivity. We provide a methodological framework for integrating detected inter-individual variability into resistance surface modeling, for assessing how landscape connectivity changes across seasons, and for evaluating how seasonal connectivity differences affect predictions of movement corridors. Using radio-tracking data from elephants in the Borderland area between Kenya and Tanzania, we applied SSFs to create seasonal landscape resistance surfaces. Based on seasonal models, we predicted movement corridors connecting major protected areas (PAs) using circuit theory and least-cost path analysis. Our findings demonstrate that individual variability and seasonality lead to substantial changes in landscape connectivity and predicted movement corridors. Specifically, we show that the models disregarding seasonal resource fluctuations underestimate connectivity for the wet and transitional seasons, and overestimate connectivity for the dry season. Based on our seasonal models, we predicted a connectivity network between large PAs and highlight seasonal and consistent patterns that are most important for effective management planning. Our findings reveal that elephant movements in the borderland between Kenya and Tanzania are essential for maintaining connectivity in the dry season, and that existing corridors do not protect these movements in full extent.

Introduction

Developing effective management schemes for maintaining landscape connectivity in rapidly changing environments is one of the major tasks in systematic conservation planning (Margules & Pressey, 2000; Rudnick *et al.*, 2012). The concept of landscape connectivity is often the basis for building corridors, which have been widely used in the field of conservation planning (Brooker, Brooker & Cale, 1999; Pelletier *et al.*, 2014). The corridors need to be designed while taking into account actual behaviors and dispersal abilities, because landscape connectivity is both species- and landscape-specific. In contrast to structural connectivity, functional connectivity comprises the response of individuals to landscape features (Brooks, 2003; Benz *et al.*, 2016). For effective conservation planning, models based on functional connectivity have a large potential as they reflect more than just species habitat preferences and can integrate spatial and temporal dynamics (Baguette & Van Dyck, 2007; Goswami & Vasudev, 2017).

Functional connectivity and conservation corridors modeling is commonly achieved using landscape resistance surfaces (Beier, Majka & Spencer, 2008). The resistance surfaces represent spatially explicit probabilities of species movement considering environmental conditions, behavioral states and mortality risk (Zeller, McGarigal & Whiteley, 2012). A variety of datasets and methods can be used to model landscape resistance, including habitat suitability analysis or expert opinion (Keeley, Beier & Gagnon, 2016; Milanesi *et al.*, 2017; Mui *et al.*, 2017). However, connectivity models based on such data may not adequately reflect movement across the landscape and may have a tendency to underestimate functional connectivity (Mateo-Sánchez *et al.*, 2015; Roffler *et al.*, 2016; Ziółkowska *et al.*, 2016).

Hence, connectivity models and underlying landscape resistance surfaces should be based on empirical movement data (Zeller *et al.*, 2012). Step selection functions (SSFs) are a relatively recent but promising approach for analyzing such movement data to calculate resistance surfaces (Richard & Armstrong, 2010; Zeller *et al.*, 2012). SSFs allow estimating the strength of habitat selection by animals moving through a landscape using VHF or GPS data (Fortin, Morales & Boyce, 2005; Thurfjell, Ciuti & Boyce, 2014). Using actual movement steps or paths is more suitable for landscape resistance modeling as this reflects actual movements, rather than the simple presence of a species at a certain location (Zeller *et al.*, 2012, 2015; Keeley *et al.*, 2016). Empirical movement steps or paths have successfully been applied to model functional connectivity and to predict movement corridors in a variety of species (Forester, Im & Rathouz, 2009; Roever, van Aarde & Leggett, 2013; Signer, Fieberg & Avgar, 2017). Nevertheless, several analytical issues remain, particularly with respect to applying SSFs for resistance modeling.

First, it is a common practice in resource selection studies to use mixed effects models with individuals as random terms, or to average individual coefficients for obtaining population level coefficients (Duchesne, Fortin & Courbin, 2010; Fieberg *et al.*, 2010; Killeen *et al.*, 2014). However, with very high individual-level differences and relatively small sample size, this approach could lead to overgeneralization and spatial biases. Observed inter-individual differences in resource selection could be due to individual life history, spatial memory and animal personality, all of which can strongly affect species dispersion and distribution within habitats (Wolf & Weissing, 2012). In theory, individual-based SSF models account for the animals' knowledge of the area because the selection procedure is always restricted to its home range. Randomly distributed individuals with highly overlapping home ranges and a large sample size will have a relatively equal input for a resistance surface modeling, and averaging of individual contributions is a suitable approach in such cases. However, it is rarely the case in telemetry studies, considering equipment costs and employment efforts (Hebblewhite & Haydon, 2010). Small, unequal sample sizes with spatially unevenly distributed animals might impact resource selection functions, including SSFs. Specifically, averaging of SSF coefficients across all individuals may predict lower resistance values where sample size

is larger, that is, selection of well-presented areas for movement will appear stronger, only because more sampled individuals used an area. Indeed, inter-individual variability might also be detected simply because individuals find different environmental conditions to choose from within their home ranges, but would not actually show behavioral variability if they were exposed to the exact same conditions. Because of this, detecting inter-individual variability is particularly likely in cases when individuals were sampled across a large, heterogeneous study area, and when the sampling intensity varies across space. Hence, spatially inhomogeneous distribution of movement data requires a different way for interpolating SSF coefficients to avoid a spatial bias.

Second, disregarding seasonal variations in the environment can be another source of uncertainty when spatially interpolating results from SSFs to landscape resistance. For instance, resources availability is limited during dry seasons, especially in arid and semi-arid areas. Under these conditions, animal movement can be restricted compared to the wet season, simply because individuals only move among the few available resource patches. Consequently, landscape-wide resistance predicted from dry-season movement data will be higher compared to the wet season, and seasonal movement corridors might have different spatial arrangements and predicted intensity of use. Thus, understanding how connectivity changes across seasons and how these changes affect landscape connectivity may comprise vital information for effective conservation planning.

In this study, we used GPS movement data obtained from collared elephants from the Greater Amboseli Ecosystem (GAE) in Eastern Africa to illustrate that accounting for seasonality can strongly impact our understanding of functional connectivity and alters predicted movement corridors. We chose the African elephant *Loxodonta africana* as the focal species for representing landscape connectivity in this region, as this species is a keystone megafauna that substantially impacts the vegetation and wildlife distributions in their environments and are likely a good umbrella species of connectivity across the landscape (Western, 1989; Epps *et al.*, 2011).

Using the elephant data, we applied SSFs to estimate resistance to movement in wet, dry and transitional seasons. As elephants have a good spatial memory and strong individual habitat preferences (Polansky, Kilian & Wittemyer, 2015), we offer an analytical approach for dealing with spatial sampling bias where unequal amounts of movement data are available for different parts of the study area (i.e. different number of collared individuals and different number of fixes per individual). Using movement data simulations, we demonstrate that resistance surfaces modeled using our approach have higher predictive power compared to the common method of simply averaging coefficients equally across individuals. We compared seasonal connectivity and predicted movement corridors using morphological spatial pattern analysis (MSPA) and graph theoretic analysis (Vogt *et al.*, 2006; McRae *et al.*, 2008). We verified that the model that not accounting for seasonal changes overestimates overall landscape connectivity for the dry season, and

underestimates it for the wet season. Based on seasonal resistance surfaces, we predicted movement corridors connecting large protected areas (PAs) and compared their relative importance for maintaining connectivity in each season.

Materials and methods

Study area

The study area covers approximately 50 000 km^2 and is located in the Borderland between Kenya and Tanzania. The Borderland encompasses the GAE and extends to the South Rift valley (Fig. 1). The region encloses 36 nationally protected lands and large segments of non-PAs belong to group ranches that play an important role in local wildlife conservation initiatives (Ntiati, 2002; Browne-Nuñez, Jacobson & Vaske, 2013). Intensive agricultural development, including fencing, in non-protected lands together with rapid human population growth increases the potential for fragmentation, connectivity loss, and human–wildlife conflict (Western, 1975, 2007; Okello & D'amour, 2008).

Telemetry data

We obtained GPS telemetry data from 14 elephants collared within the area of Amboseli-West Kilimanjaro and South-Rift-Magadi Ecosystems. Information on collars types and collaring operation is available in Ngene *et al.* (2014). Fix rates, sample sizes and collaring locations are presented in Appendix S1 in Supporting Information (Table S1). The movement data were regularized to 4 h intervals. In cases where collars failed to receive the signal in more than 8 h, the trajectories were burstified, and the bursts with <10 steps were excluded from further analysis.

Environmental layers

Environmental data were collected from publicly available Geographic Information System (GIS) datasets and derivatives from remote sensing data (Table S2, Appendix S1).

GIS layers

The GIS raster and vector data used in the analysis are presented in Table S2, Appendix S1. All vector layers were reprojected to the Cartesian coordinate system (UTM) and rasterized to a cell size of 250. Final surfaces were transformed to continuous surfaces where each pixel represents the Euclidean distance to the nearest target features.

Remote-sensing analysis

We acquired satellite data from three global remote sensing missions: Terra, SRTM and Landsat (Table S2, Appendix S1). The normalized difference vegetation index (NDVI) derived from MODIS has been shown in previous studies as a reliable proxy of forage quality for large mammals, including African elephant (Ryan *et al.*, 2012; Wall, 2015). Using the NDVI time series allows reproduction of vegetation productivity dynamics corresponding to the real seasonal vegetation changes (Ngene, 2010; Bohrer *et al.*, 2014). We created a time series on the monthly NDVI imagery corresponding to the entire time frame of available elephant GPS movement data (2007–2015).

We used multispectral Landsat 8 satellite imagery for land cover classification. The workflow of the supervised classification, post classification analysis and accuracy assessment are provided in the Appendix S2. We included in the model the proportional coverage of three major land cover classes (grassland, bushland and woodland). The proportion of each class was calculated by applying a circular buffer to each pixel of a raster surface with the radius of the average step length pooled over all elephants (1337 m).

## Resistance to movement modeling

Step-selection function

SSFs require information on habitat crossed by an animal during movement, that is habitat values are quantified along a line connecting two consecutive animal locations. This 'used' habitat is then compared to 'available' habitat, which means that habitat variables are collected along alternative steps where an animal could potentially have moved given the step lengths and angle distributions (Fortin *et al.*, 2005; Forester *et al.*, 2009). Each used step is compared to the set of available steps using conditional logistic regression (Manly *et al.*, 2002; Johnson *et al.*, 2006). SSFs take the form:

$$\widehat{w}(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \cdots \beta_p x_p)$$

where $\widehat{w}(x)$ is an exponential function given the sample of used and available habitat variables; $\beta_1 \ldots \beta_p$ are estimated regression coefficients; and $x_1 \ldots x_p$ are predictor covariates (Fortin *et al.*, 2005; Thurfjell *et al.*, 2014).

We simulated 10 'control' (available) steps to each 'case' (used) step, and used step lengths drawn from a Gamma distribution with rate and shape parameters estimated from the empirical data (step lengths distribution for all collared elephants) using maximum likelihood (*rhr* R package) (Signer & Balkenhol, 2015). Turning angles for the control steps were drawn from a uniform distribution between $-\pi$ and π. We collected environmental values crossed by a spatial line representing an animal's step. The average of these values characterizes the habitats choices (used and available). The methodological framework with data analysis steps is presented in Fig. 2.

For NDVI, we sampled movement data according to the exact date (year/month) in the time series and extracted NDVI values for each corresponding stratum. For the seasonal models, we subset movement paths for the wet, dry and early dry seasons. Seasonality was estimated from the results of the long-term annual field monitoring based on vegetation productivity conducted by the African Conservation Center (see Table S3).

Greater Amboseli Ecosystem
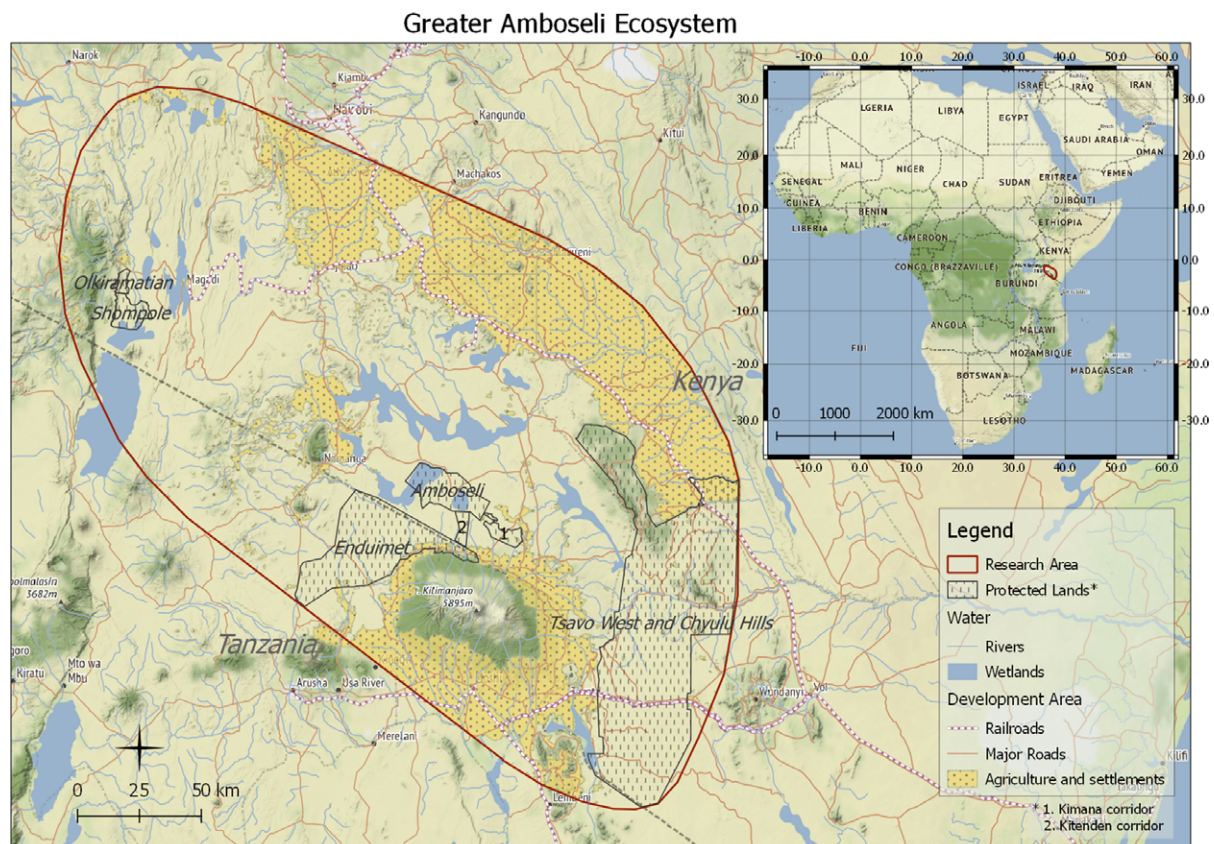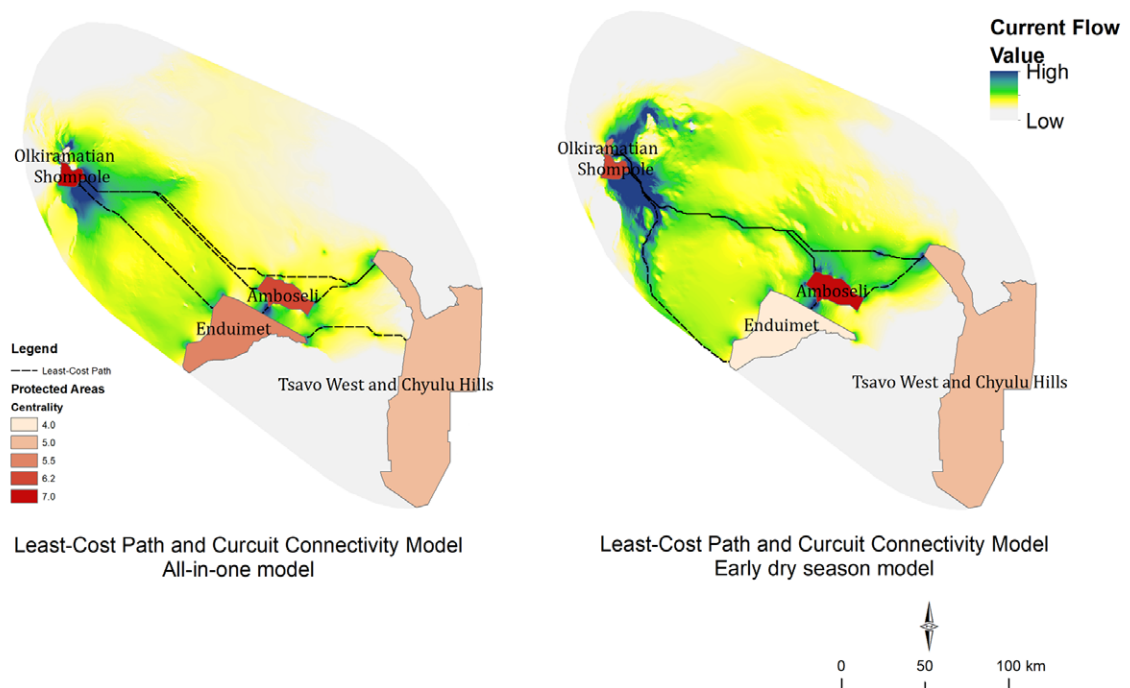

Functional Landscape Connectivity Maps

Figure 1 Study area and functional connectivity maps for all-in-one and transitional seasonal models.
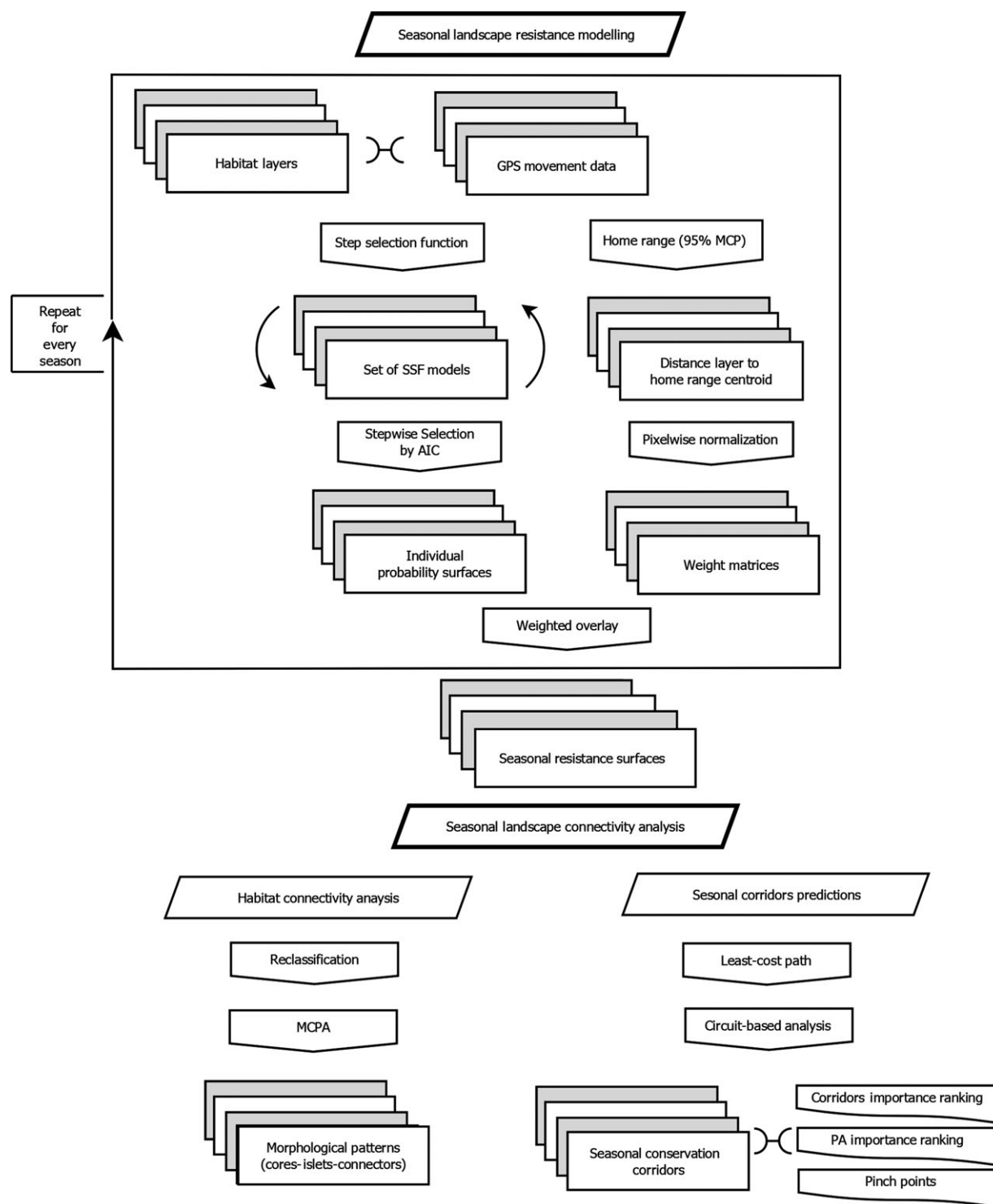
Figure 2 Workflow chart of the SSF modeling and functional connectivity assessment. SSF, step selection function; MSPA, morphological spatial patterns analysis; PA, protected areas; AIC, Akaike information criterion; MCP, minimum convex polygon.

We tested environmental variables for collinearity using pairwise scatterplots and Pearson correlation. Each pair had a correlation coefficient <0.7, so all variables were retained for further analysis (Zuur, Ieno & Elphick, 2010).

Conditional multiple logistic regression models were built for each individual by including all possible permutations of explanatory variables including full (all environmental variables are included) and null (no environmental variables

included) models. We applied both-way stepwise selection using Akaike information criterion (AIC) and choose the model with the lowest AIC score (Akaike, 1974; Zar, 1996; Venables & Ripley, 2013).

To evaluate variability in individual step-selection, we compared the relative contribution of environmental covariates among seasons using Jaccard index of similarity. We assigned a value of 1 ('present') to a variable when its coefficient was included in the best model (lowest AIC score), and 0 when it was excluded from the best model ('absent').

Landscape resistance modeling

We spatially interpolated the results from SSFs by calculating the relative selection strength (Avgar *et al.*, 2017) for each point of the raster image and then applying pixel-wise logit transformations for obtaining the 0–1 scaled probability values. The inverse values of these probabilities represent landscape resistance to movement surface. To adequately reflect all individuals with their potential variability in step-selection (due either to actual behavioral differences or due to sampling bias), we calculated a spatial weight matrix based on the inverse distance of each pixel to the individual's home-range center. For this, we estimated home ranges using 95% minimum convex polygon (Anderson, 1982), and normalized distance values across all individuals so that the sum of inverse distances for each cell in the landscape ranged from 0 to 1 and summed to 1 across individuals for each cell. See Appendix S3 in Supporting Information for details and an example. We then applied a weighted overlay, where we summed the movement probability layers of all individuals after weighting them by the corresponding distance-to-home-range-center layer. The inverse of these movement probability surfaces represents landscape resistance surfaces, which we used for functional connectivity modeling (see next section). All analyses were performed using the *raster* package in R (Hijmans 2016).

For validating the predictive power of the applied framework, we modeled resistance surfaces using two different methods: distance-to-home-range-center overlay (weighted overlay) and by averaging individual regression coefficients (averaging) (Fieberg *et al.*, 2010). We followed a leave-one-out validation procedure, and excluded the movement data of each individual for constructing resistance surfaces using both approaches, so that we created 28 resistance surfaces in total (14 using weighted overlay, and 14 for using averaging). We then simulated movements for each left-out individual based on the respective resistance surfaces using the starting point and number of steps of the excluded individual (Quaglietta & Porto, 2018). In these simulations, the choice of steps of each individual was defined by the values of the underlying resistance surface: the lower the predicted resistance, the higher the probability that the next step will transit this area. Finally, we calculated utilization distributions (UD) for empirical and simulated movement data to compare actual movement patterns with those predicted from the two different methods (weighted overlay vs. simple averaging). Specifically, we used 90% kernel density estimators to quantify UDs reflecting individual movement behavior and estimated the overlap between the UD derived from actual movement data and simulated tracks. The overlap index takes values from 0 to 1 with larger values indicating greater overlap between the two UDs (Fieberg & Kochanny, 2005). We repeated the movement simulations and overlapped calculations 100 times per individual. Finally, we compared the overlap between the weighted overlay versus averaging approach. We can expect a higher overlap between real and simulated movements for the approach that leads to resistance surfaces that better capture actual movements of individuals.

Functional landscape connectivity model

MSPA

We compared landscape permeability (the proportion of landscape that most likely provides connectivity) of the all-in-one (the surface calculated for all dataset disregarding the seasons) and seasonal resistance maps through morphological spatial pattern analysis (MSPA) (Soille & Vogt, 2009). We used three descriptive categories: *cores* represent non-fragmented patches highly suitable for movements, *islets* represent fragmented smaller patches and *connectors* represent corridors connecting cores and islets (Vogt *et al.*, 2006, 2007; Soille & Vogt, 2009).

We reclassified the resistance maps to Boolean images by applying a set of successive classification thresholds starting from 0.5 with increases of 0.02. The MSPA classification was conducted through Guidos Toolbox (Vogt *et al.*, 2006) and iteratively applied to each set of binary images until increasing the threshold was equal to one. For estimating overall accuracy and potential pitfalls of the all-in-one model, we built a confusion matrix where the all-in-one model's number of elements (cores, islets and connectors) was compared to the number of the same elements in seasonal models.

Least-cost path and circuit theory

We built seasonal functional connectivity networks among the core areas (largest national parks and conservancies) using circuit theory and least-cost path (LCP) methods (Fig. 1). The LCP approach estimates the shortest distance between target nodes (i.e. PAs) while accounting for resistance to movement (Adriaensen *et al.*, 2003). Circuit-theoretic connectivity can be assessed using graph-theoretic metrics that can be directly interpreted in landscape connectivity terms (McRae *et al.*, 2008). The amount of current running through the nodes reflects the likelihood of random walks along graph edges (Shah & McRae, 2008; Carroll, McRae & Brookes, 2012). Estimated effective resistance values (connectivity measure within a least-cost corridor) enables the calculation of current flow centrality across the network (centrality score). The centrality score represents how important a link or core area is for overall network connectivity (McRae *et al.*, 2008). We calculated, normalized and

mosaicked the cost-weighted distance (CWD) surfaces for building a single composite corridor map. We estimated current flow, effective resistances, cores and corridors centrality scores (Carroll *et al.*, 2012). Finally, we predicted LCPs for each pair of the PAs in the study area. The analysis was implemented in Linkage Mapper (ArcGIS 10.3.1) (McRae & Kavanagh, 2011).

Results

SSF models

The all-in-one SSF model revealed high inter-individual variability in habitat preferences (Table S3, Appendix S1). The number of explanatory variables selected in the final model ranged from 12 (one individual) to five (two individuals), with an average of 7.86 ± 2.07 dependent variables affecting individual movement choices. NDVI and distance to PA were significant explanatory variables for most individuals (11 and nine individuals respectively). Anthropogenic factors, such as distance to developments area and distance to roads, were significant for 9 out of 14 individuals. Distance to large water surfaces and distances to towns were important only for half the individuals (7 out of 14).

Overall, seasonal models retained less dependent variables than the all-in-one model. The average number of habitat variables selected was 6.14 ± 2.0, 6.71 ± 2.16 and 5.88 ± 2.31 for wet, dry and early dry seasons, respectively. NDVI was included in the models for almost all individuals in the wet season (12 out of 14), but was less important for the dry (10 out of 14) and early dry season (4 out of 8). Distance to PAs in the seasonal models was less important than in the all-in-one model (6 out of 14 for the wet season, 7 out of 14 for dry seasons, and 3 out of 8 models for the early dry season; Table S3, Appendix S1). Jaccard indices calculated for coefficients across the seasons are less or equal to 0.5, which indicates low similarity between the data clusters (mean index values are below 0.5 for all compared pairs; Fig. 4).

Resistance to movement surface interpolation

Accounting for individual variability

The results of our simulation-based validation confirmed that the weighted overlay produces more accurate predictions for animal movements compared to the averaging method. The surface modeled using averaging coefficients is sensitive to the spatial sampling distribution: it produced very low resistance values in the area where numerous individuals were collared, and high resistance values in the areas with a smaller sample size (Appendix S4). Tests with simulations confirmed the lower predictive power of the first method. All 14 resistance surfaces modeled with weighted overlay led to simulated UDs that have a higher overlap with the actual movements of the animal excluded from the resistance interpolation (Fig. 3). Individual movement predictions based on

weighted overlay surfaces were consistently better for all surfaces despite the spatial affiliation or home-range size of tested individuals (Fig. S3, Appendix S4).

Accounting for seasonal patterns

Seasonal resistance to movement surfaces reflect the differences in habitat preferences between the seasons (Appendix S5). In the all-in-one surface, the proportion of pixels with lower resistance values (<0.5) is 0.34, and the values increase to 0.5 in both the wet and early dry seasons. In the dry season, the proportion of lower resistance pixels is 0.27. The Pearson correlation coefficients for all pairs of resistance surfaces had values <0.7, except for all-in-one and dry season surfaces ($r = 0.75$).

Morphological spatial pattern analysis

The proportion of elements changes within the three morphological categories (cores, islets and connectors) for 23 classification thresholds (Fig. 4). The overall accuracy of the seasonal models ranged from 0 to 30% across all classification thresholds (Table 1). The dry seasonal model tended to overestimate the number of elements (61%, 39% and 73% of elements are overestimated for the cores, islets and connectors accordingly); while for the wet season it tends to underestimate element numbers (70%, 57% and 83% are underestimated). The number of elements for islets and connectors are underestimated for the early dry season (61% and 57% accordingly), but the number of elements for cores are either underestimated or overestimated (48% of underestimates, and 52% of overestimates) (Table 1; Fig. 5).

Circuit-based and LCP analysis

Using circuit-based analysis and LCP, we modeled eight wide-ranging corridors maintaining overall functional connectivity between five large PAs (Tables S3 and S4, Appendix S5). Connectivity parameters support the results of the morphological spatial pattern analysis. The five most prominent corridors modeled based on the all-in-one resistance surface have higher effective resistance values compared to the wet season, and lower resistance values for the dry season. The lowest resistance values and CWD/path ratios were assigned to wet and early dry seasons, and the values decreased in the dry season (Table 3).

Amboseli National Park (NP), Enduimet and Shompole Conservancy have the highest current-flow centrality score and are always ranked among the top three despite seasonal differences (Table 2). The most important cumulative corridors were predicted for Amboseli and Enduimet; Amboseli and Tsavo West (including Chyulu Hills); Enduimet and Shompole. These three linkages are in the top three based on centrality ranking and have the lowest effective resistance values (Table S3, Appendix S5).

LCPs calculated for the wet season have a tendency to converge in the center of the study area connecting the west
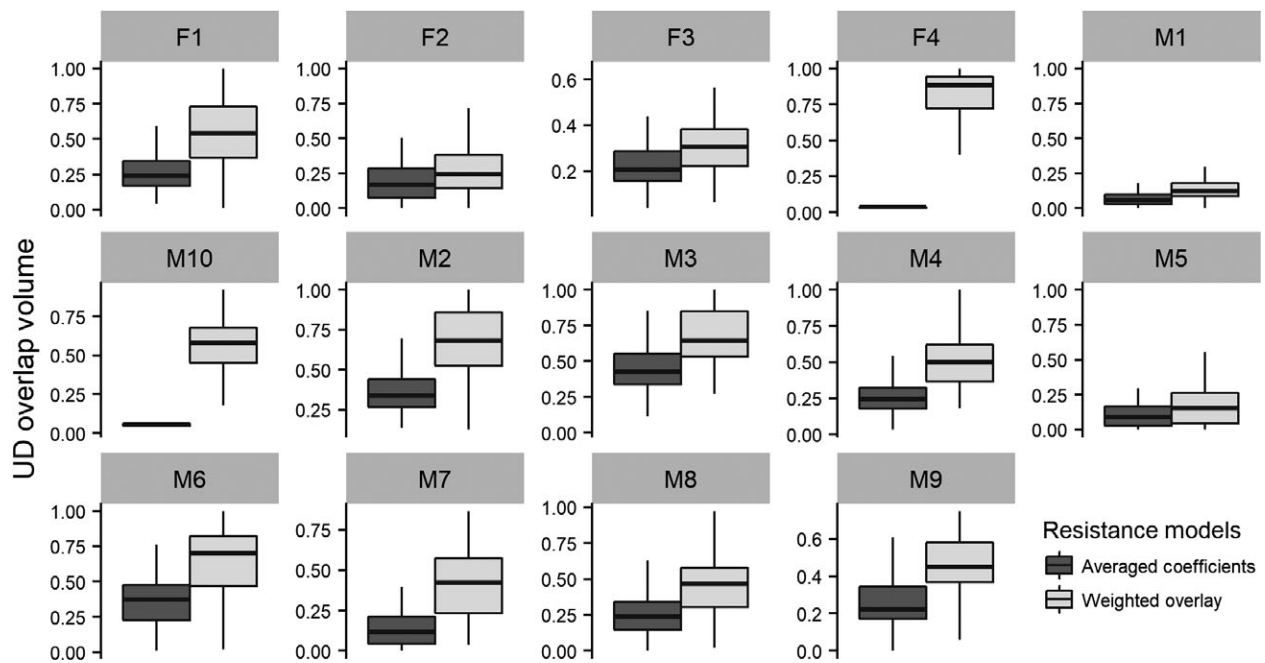
Figure 3 Overlap volumes calculated between utilization distributions (UD overlap volume] of collared elephants and simulated movement tracks (90% kernel density estimation). Each facet represents one individual excluded from resistance surface interpolation, and simulations (*N* = 100) based on this resistance surface. The data were simulated using two interpolation techniques: averaging regression coefficients (dark gray boxes) and weighted overlay using a distance to home-range center matrix (light gray boxes).
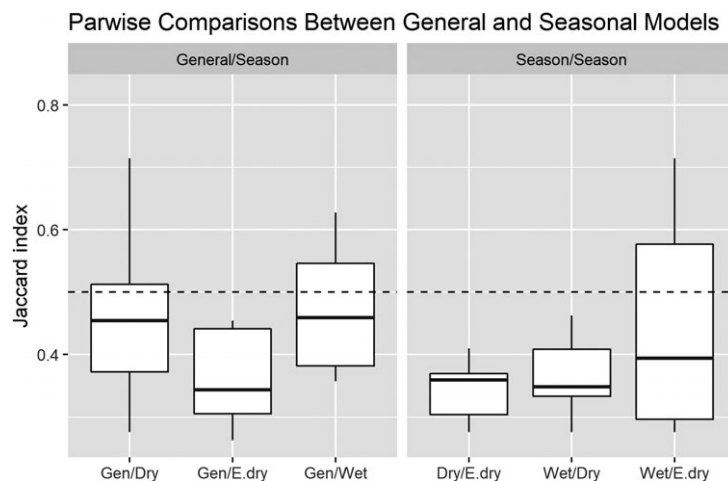

Figure 4 Jaccard index estimated for each pair of general and seasonal model. Gen, general model; Wet, wet season model; E.dry, early dry season model; Dry, dry season model.

and east (Fig. S6 in Appendix S5). Wet and early dry seasons have a larger potential for providing connectivity in the north-western direction. Early dry season provides an alternative path between Chyulu Hills and Olkiramatian that does not exist for other seasons. Furthermore, early dry and dry seasons demonstrate increasing permeability of the Tanzania's side (Appendix S5).

Discussion

Using an empirical movement dataset of elephants, our study shows substantial variability in landscape connectivity and predicted movement corridors across seasons. Furthermore, our study also shows that accounting for observed inter-individual variability, which is either caused by actual behavioral

Table 1 Confusion matrix

	Cores (%)		
	Dry season	Wet season	Early dry season
Accuracy	30.43	21.74	0.00
Underestimates	8.70	69.57	47.83
Overestimates	60.87	8.70	52.17
Islets (%)			
Accuracy	30.43	26.09	4.35
Underestimates	30.43	56.52	60.87
Overestimates	39.13	17.39	34.78
Connectors (bridges and loops) (%)			
Accuracy	21.74	17.39	8.70
Underestimates	4.35	82.61	56.52
Overestimates	73.91	0.00	34.78

All-in-one model accuracy assessment using morphological spatial patterns analysis categories. Accuracy: Proportion of cases with equal number of elements (i.e. cores, islets, or connectors) predicted for all-in-one and seasonal model. Underestimates: Proportion of cases with smaller number of elements predicted for all-in-one compared to the seasonal model. Overestimates: Proportion of cases with larger number of elements predicted for all-in-one compared to the seasonal model.

differences in movement preferences, or by spatial sampling bias, significantly improves the ability to accurately predict movements from the modeled resistance surfaces. Hence, it is fundamental that corridor design accounts for seasonal differences and inter-individual variability. Indeed, integrating dynamic changes is among the most important factors for effective conservation applications, and one of the best approaches for conservation planning is to focus on preserving connectivity rather than large protected lands (Margules & Pressey, 2000; Pressey *et al.*, 2007).

Accounting for individual variability

Individual differences and their effects on species ecology have been much debated (Bolnick *et al.*, 2011; Maiorano *et al.*, 2017). Individual variability is an influential factor for resistance surface modeling, particularly when collaring of individuals was unevenly distributed across the study area. Here, we suggest a framework using a weight matrix for modeling the overall resistance surface. Each resistance value obtained for an individual is weighted by the distance to the home-range center and our validation confirmed that the typically used averaging method produces spatial biases caused by relatively small sample size and uneven distribution of collared animals. Simple coefficient averaging predicts an overly simplistic resistance surface with extremely low resistance values in the area with larger sample size, and high resistance where only few animals were collared (Appendix S4). In contrary, the weighted overlay produces a smoother distribution of resistance values and balance-out the data discrepancy. This problem is particularly apparent for the South Rift region in the study area, where only two individuals were collared (F4 and M10, Fig. 3). These animals' home ranges are relatively small and isolated from the rest of collared animals (Shompole and Olkiramatian Conservancies, Appendix S4). As expected, the simulation predictions are very poor for the averaged model, while weighted overlay produced a very strong prediction (e.g. F4 overlapping indices are 0.03 ± 0.003 and 0.82 ± 0.160 for first and second methods accordingly, Fig. 3).

We conclude that the weighted overlay method outperforms coefficient averaging for studies implemented on relatively small datasets of species that show strong individual variability. The offered approach allows to adjust the resistance interpolation according to the proximity to the sampling domains (each individual), and avoid spatial biases. Nevertheless, coefficient averaging might have an adequate
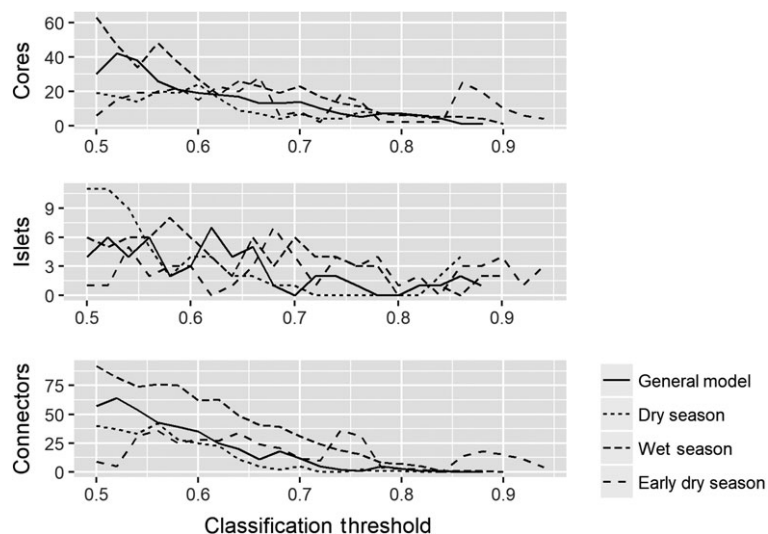

Figure 5 Number of elements in each morphological class (cores, islets and connectors) calculated from the resistance surfaces and plotted against different classification thresholds.

Table 2 Protection areas (PA) centrality and ranking estimated using circuit theory

PA	All-in-one model		Wet season		Dry season		Early dry season	
	Core centrality	Rank	Core centrality	Rank	Core centrality	Rank	Core centrality	Rank
Amboseli	6.20	2	6.56	3	6.50	3	7.26	1
Tsavo West and Chyulu Hills	5.02	4	4.19	4	4.23	4	4.96	4
Enduimet	6.09	3	6.56	2	6.54	2	4.91	5
Shompole	7.13	1	7.03	1	7.03	1	6.29	2
Olkiramatian	4.00	5	4.00	5	4.00	5	5.43	3

A higher centrality value indicates greater importance of the PA for providing landscape-wide connectivity.

predictive power for studies with a larger sample size, where study animals are evenly distributed within the area.

Comparing seasonal connectivity models

To compare the all-in-one connectivity model to the seasonal models, we applied two conceptually distinct methods: MSPA and circuit theory analysis. The first method allows the estimation of patch-based metrics and is based on a patch-corridor-matrix concept (Forman, 1995; Zeller *et al.*, 2017). The approach requires a binary classification and treats the area with low potential connectivity as a non-permeable matrix. However, a number of studies have shown that matrix quality can be heterogeneous and be responsible for different level of patches isolation (Vandermeer & Carvajal, 2001; Revilla *et al.*, 2004). In contrast, circuit analysis simulates random walkers across a continuous surface, and, therefore, uses the full permeability potential for predicting corridors.

The results of our research confirmed the assumption that the all-in-one model underestimated connectivity for the wet season and overestimated connectivity for the dry season. We used seasonal changes of NDVI values as a surrogate for resource availability, and large herbivores are known to travel with the seasonal 'wave of green-up' to provide themselves enough food and water (Birkett *et al.*, 2012; Merkle *et al.*, 2016). We assume that these changes are captured by the seasonal connectivity models. Results of MSPA supported our conclusion of decreasing connectivity from wet to dry seasons. Overall, the accuracy of the all-in-one model was small compared to the seasonal models (<30%, Table 1). The wet season provides the highest number of corridors and patches; while the dry season has a lower number of core areas, thus, the landscape is less variable and provides fewer possible connectors between habitat patches.

Identifying stable connectivity patterns across seasons

The seasonally stable connectivity patterns discovered in this research are particularly interesting as they complement hypotheses about population structure and distribution of elephants in the GAE (Kikoti, 2009; Moss, Croze & Lee, 2011). The results suggest that connectivity in the north-south direction via the Kenya-Tanzania border is higher than connectivity in the east-west direction for all seasons. This highlights the importance of Borderland movements for maintaining overall landscape connectivity. Previous studies suggested that the Amboseli elephant population extents only to the Chyulu Hills and Tsavo West (Moss *et al.*, 2011). Indeed, the predicted corridor connecting Amboseli NP and Chyulu Hills was always ranked high in centrality score for all seasons. However, distinctive transboundary movements indicate that the elephants of southern Kenya and northern Tanzania are part of a single, contiguous population (Western, 2007; Kikoti, 2009). The Amboseli NP and the corridor between Amboseli and Enduimet PAs had the highest current-flow centrality scores and the lowest resistance for all seasonal connectivity models. A relatively short corridor connecting Kenya and Tanzania appears to be essential for elephant movements; aerial surveys confirm high concentrations of family groups within the same corridor in both the wet and dry seasons (KWS/TAWIRI report, unpubl. data, 2015).

Despite higher connectivity between the southern and northern ends of the study area, the high connectivity potential between the Amboseli Ecosystem and the South Rift Valley remains stable across all seasons (Table 3). Even though it is not certain whether elephant families from the South Rift and Amboseli form one single population, genetic studies showed independent colonization of the South Rift area between Amboseli and Maasai Mara NP (Ahlering *et al.*, 2012a). Shompole Conservancy has slowly been recolonized by elephants over the past decade since the establishment of community conservancies in this area (Ahlering *et al.*, 2012b). Elephant population growth, extensive agriculture developments and new electric fencing around Amboseli NP might push elephants out of the commonly used area to the safe conditions (Western, 2007; Okello & D'amour, 2008; Okello *et al.*, 2015). Our results suggest that in addition to preserving the undoubtedly important Borderland corridor, special attention should be given to the corridors connecting Amboseli and the South Rift.

Implications for conservation

Here, we modeled movement corridors connecting large PAs and assessed their relative contribution in conserving landscape connectivity for the elephants. Preserving connectivity across non-protected lands is a critical issue for fragmented populations of African elephants as the PAs are not large enough to maintain viable population sizes (Armbruster & Lande, 1993).

Table 3 Quantitative comparison of movement corridors predicted with least-cost and circuit-theory models

No.	1	2	3	4	5	6	7	8
CWD/path[a]								
All-in-one model	0.29	0.34	0.50	0.26	0.44	0.42	0.53	–
Wet season	0.21	0.26	0.34	0.20	0.28	0.28	0.34	–
Early dry season	0.30	0.48	0.27	0.25	0.29	0.26	0.24	0.02
Dry season	0.30	0.47	0.61	0.26	0.48	0.48	0.63	–
Eff. resist[b]								
All-in-one model	22.20	7.44	75.00	24.84	87.13	–	68.44	–
Wet season	17.93	5.32	66.43	20.57	–	–	61.03	–
Early dry season	25.41	10.02	45.90	46.81	–	59.31	60.18	0.15
Dry season	45.45	9.61	257.76	49.57	–	–	152.97	–
Centrality[c]								
All-in-one model	2.41	3.82	2.18	1.96	1.68	–	2.40	–
Wet season	2.45	3.90	2.77	1.93	–	–	3.30	–
Early dry season	3.42	4.12	1.50	1.48	–	1.26	1.25	4.14
Dry season	2.40	3.78	2.82	2.07	–	–	3.24	–
Rank								
All-in-one model	2	1	4	5	6	–	3	–
Wet season	2	1	4	5	–	–	3	–
Early dry season	3	2	4	5	–	6	7	1
Dry season	4	1	3	5	–	–	2	–

Corridors as they appears in the table above: (1) Amboseli/Tsavo West and Chyulu Hills; (2) Amboseli/Enduimet; (3) Amboseli/Shompole; (4) Tsavo West and Chyulu Hills/Enduimet; (5) Tsavo West and Chyulu Hills/Shompole; (6) Tsavo West and Chyulu Hills/Olkiramatian; (7) Enduimet/Shompole; (8) Amboseli/Olkiramatian.

[a]CWD/Path: ratio of cost-weighted distance to the unweighted length of the least-cost path (the distance traveled moving along the path).
[b]Eff. resist: corridor's effective resistance, a measure of connectivity that complements least-cost path.
[c]Centrality: calculated using circuit analysis; the parameter explains a contribution of each link to overall landscape connectivity.

Our study confirms that Amboseli NP is a stepping stone in preserving cross-border connectivity, while Shompole Conservancy is crucial for linking western and eastern parts of the research area. The wetlands adjacent to the eastern part of Shompole play a critical role in connectivity as all LCPs connect through this area.

Furthermore, we verified the importance of existing protected historical corridors for preserving functional landscape connectivity. The GAE contains two historically PAs, Kimana and Kitenden, established by signing a lease between conservation organizations [Africal Wildlife Foundation and International Fund for Animal Welfare (IFAW)] and local communities (Appendix S6). Our analysis indicates that the Kimana corridor together with the Chyulu Hills PA play a crucial role in preserving connectivity in the eastern part of the study area, and its value is especially high in the dry season. The Kimana corridor encompasses a part of the swamps *en route* to the Chyulu Hills in an area suffering from rapid agricultural expansion (98% increase between 2010 and 2014; Space For Giants Report, 2015). The Kitenden corridor connecting Amboseli NP with Tanzania has a high potential for connectivity, but the corridor with the highest current-flow centrality score and lowest resistance predicted for all seasons was predicted to the west of Kitenden (Appendix S6). Aerial count data support the importance of this area (Amboseli/Enduimet corridor), so it is highly recommended for consideration in any prioritization scheme in management plans (KWS, TAWIR Report, 2013).

We conclude that it is highly desirable to incorporate seasonal changes into functional connectivity models whenever it is feasible. This is especially relevant for systems with pronounced seasonal spatial variation in forage and water availability. Extreme environmental conditions, such as low rainfall or droughts, may significantly decrease landscape permeability and should be considered with special care in conservation prioritization and corridors planning.

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Authors' contribution

Liudmila Osipova, Niko Balkenhol and David Western conceived the ideas and designed methodology; Moses M.Okello, Stephen J. Njumbi and Shadrack Ngene collected the data; Liudmila Osipova analyzed the data; Niko Balkenhol and Matt Hayward led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Telemetry data and seasonality specification.
Appendix S2. Remote sensing analytical workflow.
Appendix S3. Probability surfaces weighted overlay based on the proximity to the home-range center.
Appendix S4. Resistance to movement models estimated using averaging coefficients and weighted overlay methods.
Appendix S5. Functional landscape connectivity models.
Appendix S6. Historical corridors performance.