Integrating habitat suitability modeling with gene flow improves delineation of landscape connections among African savanna elephants

Alida de Flamingh[1,*], Nathan Alexander[2], Tolulope I. N. Perrin-Stowe[3], Cassidy Donnelly[4], Robert A. R. Guldemond[5], Robert L. Schooley[2], Rudi J. van Aarde[5], Alfred L. Roca[1,6]

[1] Center for Indigenous Science, Carl R. Woese Institute for Genomic Biology, University of Illinois, Urbana-Champaign, IL, USA

[2] Department of Natural Resources and Environmental Sciences, University of Illinois, Urbana-Champaign, IL, USA

[3] Technology Transfer Office, Division of Research and Innovation, San Diego State University, San Diego, USA

[4] Peoria Zoo, Peoria, IL, USA

[5] Conservation Ecology Research Unit, Department of Zoology and Entomology, University of Pretoria, Pretoria, Gauteng, South Africa

[6] Department of Animal Sciences, University of Illinois, Urbana-Champaign, IL, USA

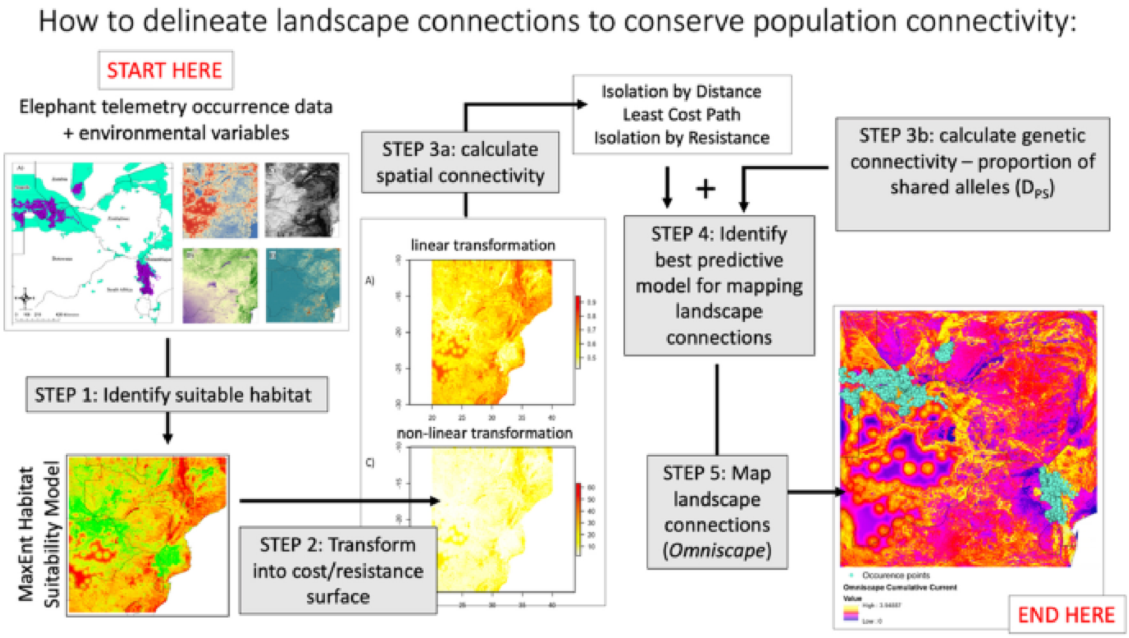
Deceased author: Rudi J. van Aarde

*Correspondence to Alida de Flamingh. Email: adeflamingh@gmail.com

Abstract

Across Africa, space for conservation is sometimes limited to formally protected areas that have become progressively more isolated. There is a need for targeted conservation initiatives such as the demarcation of landscape connections, defined as areas that encompass environmental variables that promote the natural movement of individuals between populations, which can facilitate gene flow. Landscape connections can mitigate genetic isolation, genetic drift, and inbreeding, which can occur in isolated populations in protected areas. Promoting gene flow can reduce the risk of extirpation often associated with isolated populations. Here we develop and test models for identifying landscape connections among African savannah elephant (*Loxodonta africana*) populations by combining habitat suitability modeling with gene flow estimates across a large region including seven countries. We find a pronounced non-linear response to unsuitable habitat, consistent with previous studies showing that non-transformed habitat models are poor predictors of gene flow. We generated a landscape connections map that considers both suitable habitats based on telemetry occurrence data and gene flow estimated as the inverse of individual genetic distance, delineating areas that are important for maintaining elephant population connectivity. Our approach represents a novel framework for developing spatially and genetically informed conservation strategies for elephants and many other taxa distributed across heterogeneous and fragmented landscapes.

Graphical abstract



Keywords: MaxEnt; Circuitscape; Euclidean distance; Least cost path; Molecular ecology; Conservation genetics; Landscape genetics

Introduction

Across much of Africa, space for conservation may be limited to formally protected areas that have become progressively more isolated (Newmark 2008; Ripple et al. 2015). However, despite the compression of African elephants (genus *Loxodonta*) populations into these fragmented protected areas and the resulting potential isolation of elephant populations into discontinuous units, southern African elephant (*Loxodonta africana)* populations do not yet demonstrate characteristics of genetically isolated populations (Garant et al. 2007; Allendorf et al. 2013). Instead, many southern African populations demonstrate genetic diversity that is similar to or higher than populations in east Africa (Lobora et al. 2018; de Flamingh et al. 2023). The genetic diversity of southern African populations has likely been maintained due to the large size of the surviving elephant populations, long elephant generation times, and dispersal and gene flow across the region (de Flamingh et al. 2018). However, there may have been historical connections that are no longer good candidates for connectivity restoration especially with dynamic landscapes or anthropogenic land conversion (Huang et al. 2022). Given the large home range of elephants, connectivity analyses can help identify effective conservation strategies within both protected and unprotected areas to support population persistence by increasing dispersal, gene flow, genetic diversity, and environmental adaptability (Garant et al. 2007).

To understand how gene flow can be maintained despite habitat fragmentation, we focus on landscape connections, or areas that encompass environmental variables that promote the natural movement of individuals between populations. These connections would facilitate gene flow and thereby minimize the genetic isolation and inbreeding that can occur in isolated populations in protected areas. Thus, landscape connections can be instrumental in increasing the genetic health and the persistence of wildlife populations (Allendorf et al. 2013). Landscape connections may be more robust when identified by integrating spatial and genetic data, rather than relying only a single data type. Spatial data may demonstrate habitat suitability and potential routes for dispersal but would not provide evidence of gene flow across populations. By contrast, genetic data may establish that gene flow has occurred among populations but would not identify the specific geographic routes needed to maintain it.

To integrate these data, landscape genetics merges aspects of population genetics with landscape ecology, providing a useful framework to identify gene flow (Manel et al. 2003; Manel and Holderegger 2013). However, methodology and applications vary widely (Riordan-Short et al. 2023). Often expert opinion is used to identify barriers to gene flow, but this method is criticized for non-empiricism (Spear et al. 2010; Milanesi et al. 2017). Habitat suitability models offer a more objective approach (Milanesi et al. 2017), but may be inappropriate for modeling connectivity during specific life events like mating and natal dispersal (Keeley et al. 2017). Furthermore, the spatial scale of habitat suitability models may vary, and landscape genetic studies may use habitat use within a home range (e.g., Shafer et al. 2012; Keeley et al. 2017) or range-wide distribution HSMs to parameterize models (e.g., Shrestha and Kindlmann 2020), which are different orders of habitat selection (Johnson 1980). Species may interact differently with the landscape when within home ranges than during dispersal events (Centeno-Cuadros et al. 2011; Büchi and Vuilleumier 2014; Alexander et al. 2019).

In this study, we create a habitat suitability map, visualize spatial genetic patterns across the study area, and then estimate gene flow and connectivity using a landscape genetic approach. We then delineate landscape connections among African elephant populations in seven southern African countries. We parameterized a commonly used presence-only habitat suitability model, MaxEnt (Philips et al. 2006, 2017). Presence-only models can be expanded to integrate presence-absence data (Renner and Warton 2013; Fletcher et al. 2016; Koshkina et al. 2017), positioning this established HSM framework to be a robust method to empirically identify landscape connections. Next, we created a genetic landscape through a graph-theory network approach (Miller 2005). Finally, we assessed how the top HSM, and logarithmic transformations of the top HSM, correlate to gene flow and identify landscape connections. Overall, we apply this approach to identify suitable habitat patches, spatial genetic structure, and how gene flow is related to habitat suitability for the African savannah elephant, an endangered, wide-ranging mammal (Gobush et al. 2022).

Methods

Although understanding species distributions are important for conservation, it is also critical to understand how landscape features impact gene flow and produce spatial genetic patterns (Manel et al. 2003; Holderegger and Wagner 2008; Richardson et al. 2016). Habitat suitability models can be useful as an empirical approach to understanding which landscape features impact species distribution (Spear et al. 2010; Milanesi et al. 2017). We used the predicted potential species distribution from MaxEnt to create a habitat suitability map (HSM) that we transformed linearly and non-linearly into resistance surfaces (Keeley et al. 2016) (see SI File1: Habitat suitability modelling for information on parameter selection, raster preparation and analysis, selection of MaxEnt background data and model regularization and evaluation). These transformations invert the HSM values so that areas of high suitability have low resistance values (Keeley et al. 2016). We considered nonlinear transformations to investigate possible threshold responses that elephants might have to unsuitable habitats in the resistance surfaces.

Landscape resistance surfaces are grid maps that represent the resistance to traversing the landscape features contained in that grid cell (Milanesi et al. 2017), or the cost of moving through such a landscape. To evaluate alternative quantifications of connectivity across the landscape, we fitted maximum likelihood population effects (MLPE) models (Clarke et al. 2002; Van Strien et al. 2012) between pairwise matrices of genetic distances and matrices of Euclidean, least cost path (LCP) or circuit theory (CT) distances (Shah and McRae 2008). Our MLPE model assessment identified CT distances as the connectivity measure that best explained the estimated gene flow across our landscape. We then used Omniscape to generate connectivity maps across the study region (McRae et al. 2016; Landau et al. 2021). Omniscape estimates connectivity using circuit theory (McRae 2006; McRae and Beier 2007; Shah and McRae 2008) and a moving window approach to generate current maps, or an estimate of the number of random-walks that pass through a location, that are then summed to create a landscape-scale connectivity map. Our final map therefore considered suitable habitats based on spatial data, and also gene flow as the inverse of genetic distance, to delineate landscape connections that should be important for maintaining population connectivity for elephants.

Study area and elephant occurrence data

Our study area spans seven countries across southern Africa, including Angola, Botswana, Mozambique, Namibia, South Africa, Zambia and Zimbabwe (SI Fig. S1), and includes a range of different vegetation classes (SI Fig. S2). Together these countries contain > 70% of the elephants of Africa and > 42% of the total range of elephants in Africa (Thouless et al. 2016). Elephants occur across landscapes that have a range of precipitation and vegetation characteristics (Loarie et al. 2009a; Roever et al. 2013). These include, but are not limited to, areas of very low precipitation such as desert landscapes in Namibia (Ishida et al. 2016), to areas with intermediate precipitation such as wetland landscapes in the Okavango Delta of Botswana (Songhurst et al. 2015), to high precipitation areas such as the mesic savannas of Malawi and Zambia (Ott 2008) and the forest and Futi floodplains of Maputo Special Reserve in Mozambique (Ntumi et al. 2005).

The Conservation Ecology Research Unit (University of Pretoria, South Africa) has an extensive database of elephant telemetry (GPS collar) data (SI Fig. S1—Elephant occurrence data; Fig. 1A). We used quality filtering criteria similar to Roever et al. (2013) to select reliable telemetry locations. To decrease temporal and spatial autocorrelation, we filtered the data so that only a single point per day per elephant was retained. Our final occurrence dataset comprised 80 elephants (15 male and 65 female) and 53,954 location points. These elephants fall within three regional population clusters that include the Chobe, Kafue, and Limpopo clusters (SI Fig. S3).

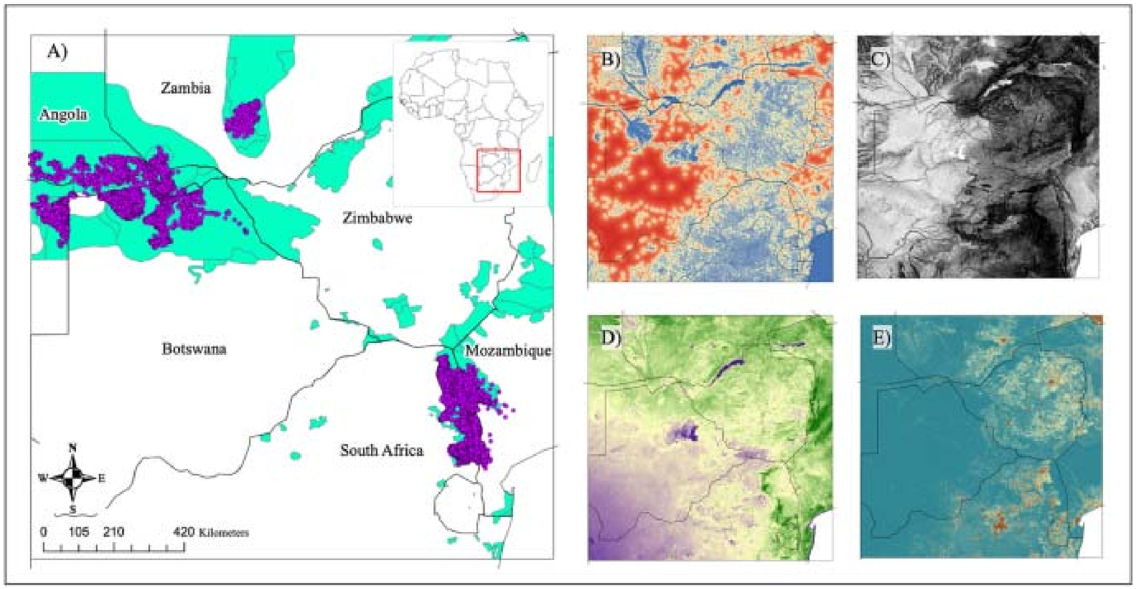


Fig. 1. The top MaxEnt habitat suitability model was based on elephant occurrence points that correspond with areas of known elephant range (**A** purple dots represent occurrence data and green areas represent the current elephant range as demarcated by the IUCN Red List of Threatened Species; Blanc 2008). MaxEnt environmental variables included habitat covariates that are known to influence elephant space use: water availability as represented by distance to the closest water source (**B** blue areas are close to water, red areas are far from water), the slope of the land (**C** dark areas represent steep slopes), primary productivity indexed by long-term mean Enhanced Vegetation Index (EVI; **D** green areas indicate high primary productivity, brown and purple areas indicate low primary productivity), and ambient human population density (**E** red indicates areas with high ambient population density, blue indicates areas with low ambient population density)

Elephant genetic data

Fresh elephant fecal samples were collected from six southern African countries from 2010 to 2014 (SI Fig. S1—Elephant genetic samples). A total of 142 samples were collected and genotyped for 9 highly variable nuclear DNA microsatellite loci (de Flamingh et al., (2018); SI Table S1). Sample collection, DNA extraction procedures, and microsatellite amplification are detailed in de Flamingh et al. (2018), and genotype errors were quantified as described in de Flamingh et al. (2014). Heterozygous genotypes were replicated at least four times, and homozygous genotypes were replicated at least three times. Diversity indices for individual microsatellite loci were calculated in Arlequin (Excoffier and Lischer 2010). We found low population differentiation (Rst = 0.04; 95% of variation observed within populations) and high gene flow through an analysis of molecular variance (AMOVA) of the complete dataset of 142 samples across 17 sampling locations (SI Table S2). These results are in accordance with previous genetic studies of elephants from southern Africa that reported low nuclear genetic differentiation (de Flamingh et al. 2018).

Spatial visualization of gene flow

To visualize gene flow across the landscape, we interpolated genetic distances to form a landscape shape in the program *Alleles In Space* (AIS; Miller 2005). AIS creates a connectivity network across all sample locations and places genetic distances as midpoints of each pairwise connection. The program then interpolates genetic distances across the extent of the study area and produces a 3-dimensional surface plot in which surface heights represent interpolated genetic distances, and where higher peaks in the surface plot indicate greater genetic distances. We tested for correlation between genetic and geographic distances, and calculated genetic distance in AIS as in Nei et al. (1983). We used a distance weighting parameter (*a*) of 1 to interpolate genetic distance across the landscape (Miller 2005). We exported the interpolated output using the highest possible resolution of 500 × 500 bins for the X and Y geographic axes, and plotted for each of the bin coordinates the peak heights using ArcMap V10.7.1 (© ESRI 2011).

Landscape genetics

We transformed the top HSM, linearly and nonlinearly, through a negative exponential function into resistance surfaces (Keeley et al. 2016). Resistance is usually assumed to be a negative linear function of suitability (Hunter et al. 2003; Larkin et al. 2004; Pullinger and Johnson 2010). However, in addition to a negative linear transformation, we also tested slight and pronounced nonlinear transformations to investigate potential threshold responses by elephants to unsuitable habitats in the resistance surfaces. A linear transformation assumes that cost (R_{lin}) is inversely related to habitat suitability, where less suitable habitat would be costlier to move through (Eq. 1).

$$\mathrm{R_{lin}} = 1 - \mathrm{HSM} \tag{1}$$

R_{lin} is the landscape resistance based on a linear transformation of habitat suitability (HSM) (Fig. 2A). A nonlinear response would be, for example, when elephant movement across the landscape is only substantially impacted by highly unsuitable habitats (e.g., very high cost areas), but where medium- and low-cost areas do not impact movement. We used a negative exponential function to nonlinearly transform HSM to cost, R (Eq. 2).

$$\mathrm{R} = 100 - 99 * ((1 - \exp(-\mathrm{c} * \mathrm{H})) / (1 - \exp(-\mathrm{c}))) \tag{2}$$

where R is resistance, H is suitability, and the factor c determines the shape of the curves. We generated resistance surfaces for c = 2 (slight nonlinear transformation) and c = 8 (pronounced nonlinear transformation) to allow for variable strengths of nonlinear responses (Fig. 2B).

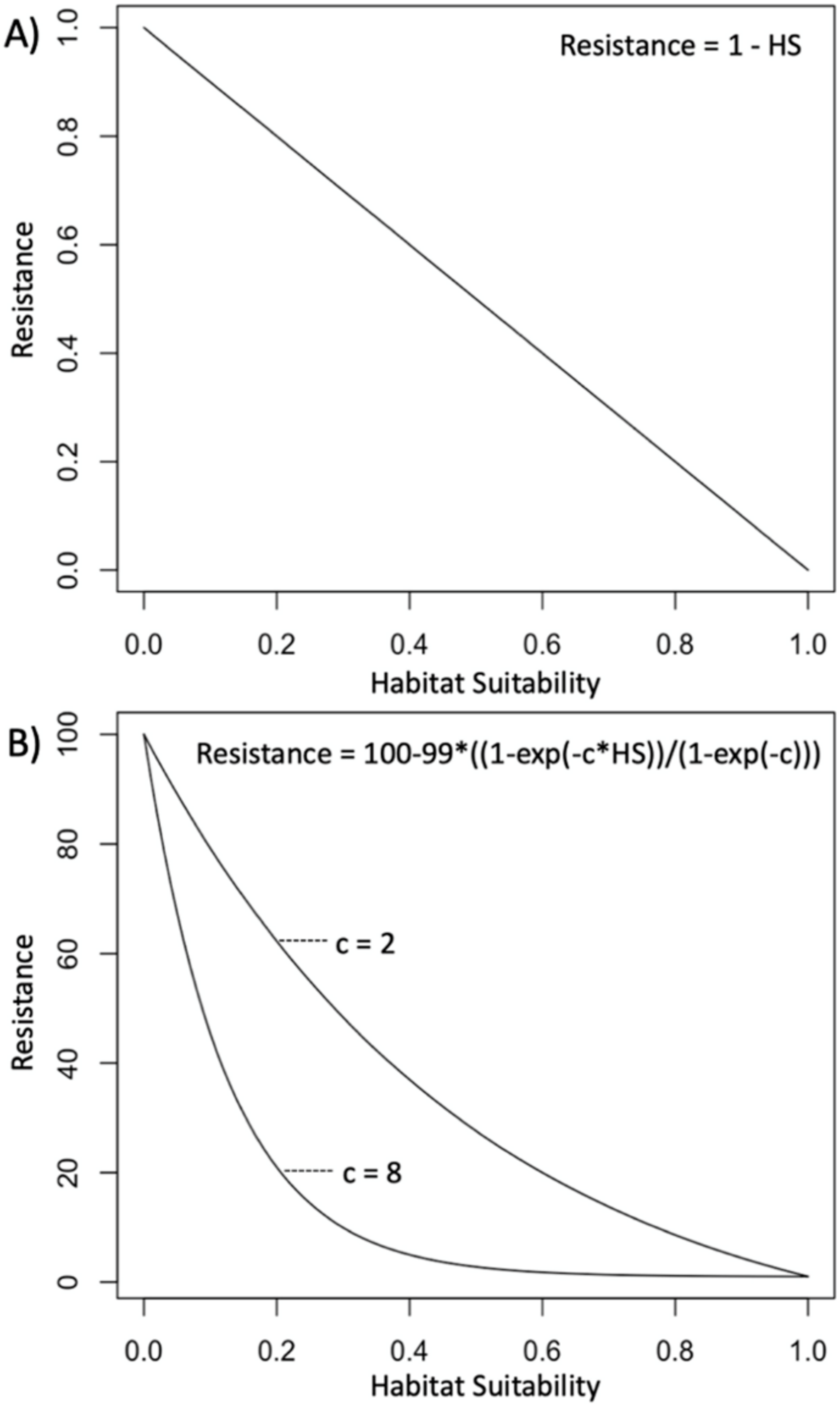


Fig. 2. The single best habitat suitability model was transformed linearly (**A**) and nonlinearly (**B**) into resistance surfaces. A linear transformation assumes that resistance is inversely related to habitat suitability, where less suitable habitat would be costlier to move through. A transformation by means of a negative exponential function allowed for the possibility of nonlinear responses that elephants might have to unsuitable habitats. We generated resistance surfaces for transformations using $c = 2$ and $c = 8$ to respectively generate slight and pronounced nonlinear responses. Equations for linear and nonlinear transformations are provided in the upper right corner of each graph

For each of the transformed resistance surfaces, we calculated three commonly used measures of landscape connectivity (McRae and Beier 2007) in a pairwise fashion for 142 elephant sample locations for which we had microsatellite data for 9 nuclear DNA loci (SI Table 3). These connectivity measures included standard geographic Euclidean distance, Least-Cost Path (LCP; Adriaensen et al. 2003; Cushman et al. 2006), and resistance distance based on circuit theory (CT; McRae and Beier 2007).

To validate connectivity models, cost distance is compared to genetic distance. We assumed an inverse relationship between gene flow and genetic distance (GD), where areas of high gene flow would result in low genetic distances among individuals and vice versa. Different estimates of GD vary in their ability to capture variation at the landscape scale (Shirk et al. 2012, 2017). We therefore quantified pairwise GD using four alternative GD estimates previously used in landscape genetic studies (Shirk et al. 2012; Kamvar et al. 2014; Milanesi et al. 2017; Tang et al. 2019) using the program R (R Core Team 2019). Some GD estimates rely on the same data variables (e.g., allele presence and frequency) to quantify GD. The GD measures presented in this study are therefore not independent and there may be overlap between GD quantifications and model outcomes when GD estimates with highly similar data variables are used as response variables for model fitting. To represent response variables in our MLPE models, we calculated GD as (1) a value of 1 minus the proportion of shared alleles (D_{PS}) using the "propShared" function in the R package "adegenet" (Jombart 2008); (2) the number of allelic differences between two individuals using the "diss.dist" function in the R package "poppr" (Kamvar et al. 2014); (3) the Euclidean distance among a vector of allele frequencies using the "dist" function in the R package "adegenet"; (4) Reynolds's distance with the "Reynolds.dist" function in the R package "poppr".

Euclidean, LCP and CT distances represent the fixed effects in each model while the four quantifications of pairwise genetic distances among individuals represent the response variables. Using the "base" package in R (R Core Team 2019), we scaled our response variables prior to fitting MLPE models to allow for the comparison with predictor variable values. The scale function in "base" centers and scales the columns of a numeric matrix (Becker et al. 1988). For each of three cost surface and four genetic distance response variables, we fitted MLPE models that considered as fixed effects Euclidean distance only, LCP and Euclidean distance, and CT and Euclidean distance, resulting in a comparison of 36 MLPE models in total. We include Euclidean distance as a fixed effect to our LCP and CT MLPE models to parse out geographic distance effects that are inherently included in LCP and CT (Row et al. 2017).

Model selection and fit was identified using Akaike's information criterion, marginal R^2 and conditional R^2 values calculated for maximum likelihood population effects (MLPE) models where genetic distance is the response variable, resistance distances of connectivity models are fixed effects, and individual identification is used as random effects to account for pseudo-replication (Clarke et al. 2002; Van Strien et al. 2012). We fitted MLPE models between pairwise matrices of genetic distances and matrices of Euclidean, LCP or CT distances.

Akaike's information criterion (AIC) was calculated in the "lme4" package in R (Burnham and Anderson 2004; Bates et al. 2015), and marginal and conditional R^2 were calculated in the R package "MuMIn" (Barton 2009). The lowest AIC values indicate the MLPE model with the best balance between model fit and complexity (Burnham and Anderson 2004), higher marginal R^2 values represent higher predictive power of the fixed effects, whereas higher conditional R^2 value represent higher total variance explained by the combined fixed and random effects (Edwards et al. 2008). Compared to traditional R^2 values, marginal and conditional R^2 values are favorable model selection criteria (Van Strien et al. 2012) because they do not necessarily increase with the addition of model parameters (Orelien and Edwards 2008). Restricted maximum likelihood (REML) estimation of MLPE models has been recommended for determining accurate estimates of R^2 (Verbeke and Molenberghs 2000; Gurka 2006), so we calculated conditional and marginal R^2 values using REML. However, REML should not be used when comparing information criteria for MLPE models with different fixed effects, and we therefore did not include REML when we calculated AIC.

Landscape connections

Out of the 36 MLPE models, we identified a single model that had the lowest AIC and the highest conditional and marginal R^2. We independently compared AIC values per individual response variable since AIC values should not be compared across models that use different response variables. For each of our response variables, we identified the model with the lowest AIC.

Our final landscape connections map thus considers suitable habitats based on spatial data, validated by estimating gene flow as the inverse of genetic distance, to delineate areas in the landscape that may be important for maintaining population connectivity as part of elephant conservation initiatives. To create a summary map that considers both spatial and genetic data, we used Omniscape (McRae et al. 2016; Landau et al. 2021) to visualize habitat suitability using the top MaxEnt model (i.e., lowest AIC). Omniscape uses a moving window to estimate connectivity of surrounding cells in relation to one central cell using a CT approach, reducing the spatial bias introduced by genetic sampling locations (McRae et al. 2016; Landau et al. 2021) in the program Julia (Bezanson et al. 2017). The radius was set to 334 pixels (~300 km) to allow for connectivity mapping using a geographic scale relevant to both elephant space use (Loarie et al. 2009b; Roever et al. 2013; Huang et al. 2022) and gene flow (de Flamingh et al. 2018). We evaluated the Omniscape map by comparing Normalized Cumulative Current values at 10,000 locations where elephants were present (occurrence points) to 10,000 random locations (SI Fig. S5A). The Normalized Cumulative Current represents only the impacts of the HSM on gene flow by accounting for the effects of geographic distances from the raw cumulative current map. We limited our evaluation extent so that it overlapped broadly with our genetic sampling extent, but excluded obvious unsuitable areas (e.g., the Indian Ocean; see SI Fig. S5 for the evaluation extent boundaries). A two-sample z-test (Kitchens 2002) was used to compare location points and random points using a custom script in R after confirming that the data were normally distributed.

Results

Elephant occurrence data

From the Conservation Ecology Research Unit, occurrence data from 80 elephants were used, of which 65 were from elephant breeding herds and 15 were male elephants. Our spatial database included a total of 53,954 location points. The temporal scale of data varied per individual since GPS collars were deployed in different years, but overall, the elephant monitoring occurred from 2002 to 2015 across all seasons.

Elephant genetic data

We genotyped 142 elephant fecal samples for 9 nuclear DNA microsatellite loci developed in elephants (SI Table S1; Comstock et al. 2000; Eggert et al. 2000; Archie et al. 2003). Across the elephants used in this study, the loci were highly variable, with the number of alleles ranging between six and thirteen per locus (mean = 8.89). The observed heterozygosity was slightly lower than the expected heterozygosity (SI Table S1), likely reflecting a limited degree of population differentiation among populations across Southern Africa.

Habitat suitability

We found no significant correlation (Pearson's $R < 0.5$, $p > 0.5$) between our MaxEnt environmental layers when including "ambient population" distribution as a measure of human pressure (SI Fig. S6). In contrast, the transformed gradient-based human distance metric was correlated with our GSW environmental variable ($r > 0.60$; Fig. 1). Also, the gradient-based distance from high human densities performed poorly compared to ambient population (SI Table S4). We therefore used raw ambient human population data (Fig. 1E) rather than transformed gradient-based distance data to represent human population distribution in our MaxEnt models.

We tested four regularization beta parameters in Maxent ($\beta = 1, 2, 3, 4$) for each of the background datasets (range-based and use-based background). The range-based background dataset resulted in slightly higher AUC than use-based background dataset and we therefore selected the range-based dataset. We found that $\beta = 1$ had the highest regularization gain and AUC, and we therefore selected the MaxEnt model calculated using range-based background data and $\beta = 1$ as the top habitat suitability model (SI Fig. S7).

We investigated how each of the environmental variables contributed to the predicted habitat suitability model and found that human density as "ambient population" distribution, distance to water, and slope contributed in a non-linear fashion. All three of these environmental variables decreased in their habitat suitability until they reach a threshold beyond which they were not suitable for elephants (SI Fig. S8). The habitat suitability model indicated elephants occur in areas of low human density, close to water, and with no or low slopes. Intermediate values of primary productivity contributed the most to our predictive habitat suitability model, which is congruent with the distribution of elephants in our study area that mostly occurs in landscapes with intermediate productivity (e.g., savanna or non-woody habitats; Mapaure and Campbell 2002; Young et al. 2009a).

Spatial visualization of gene flow

Using GD calculated in AIS, we found no correlation between genetic and geographic distances (partial Mantel test $r = -0.035$, probability of observing a $\geq$ correlation $P = 0.9$, probability of observing a $\leq$ correlation $P = 0.06$). To visualize genetic patterns across the landscape, we interpolated genetic distances to form a landscape shape in the program AIS. The interpolated GD surface is a relative representation of gene flow across the study area because the GD estimates are relative to genetic variation captured by the microsatellite marker system. Our GD surface indicated there was less constrained gene flow in the south-eastern region of the study area than in the north-western region (Fig. 3).

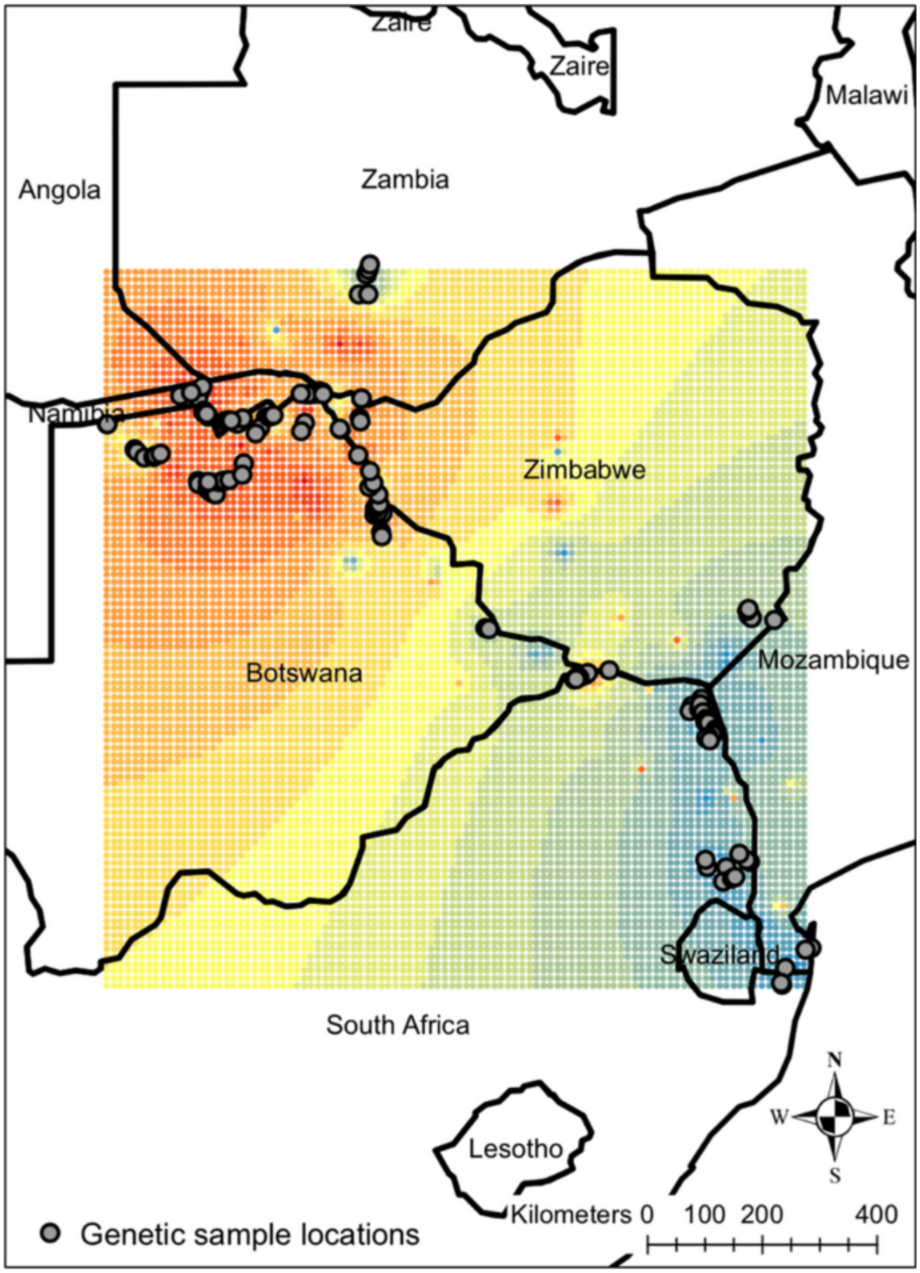


Fig. 3. Visual representation of genetic patterns across the study extent, showing that areas in South Africa (e.g., Kruger National Park) were genetically similar (low interpolated genetic distances) relative to elsewhere. The interpolated genetic distance surface is a relative representation of gene flow across the study area and is dependent on the genetic variation captured by the marker system. Areas in blue indicate higher relative gene flow (lower genetic distance) and areas in red indicate lower relative gene flow (higher genetic distance) among 142 elephant genetic samples (grey circles)

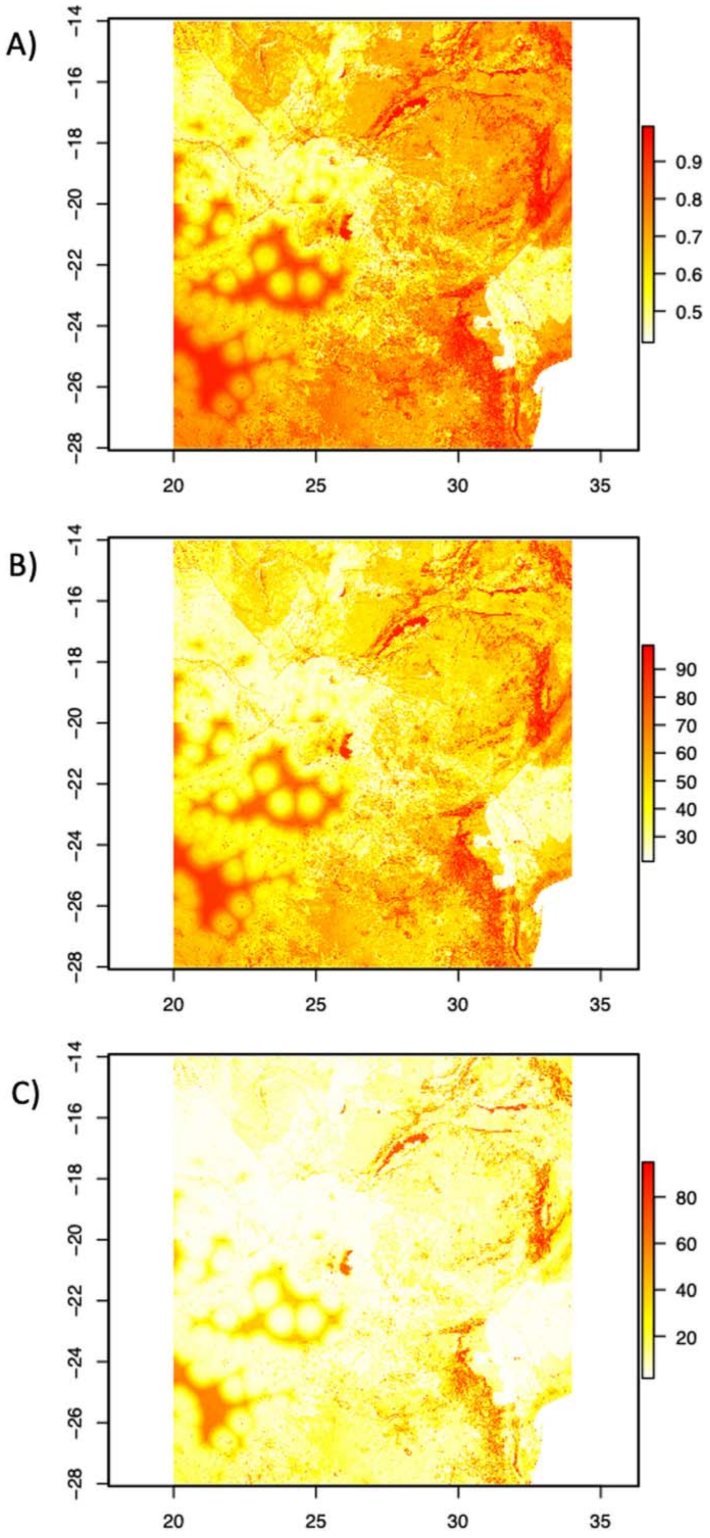


Fig. 4. Transformation of the MaxEnt habitat suitability model into three alternative representations of landscape resistance. The linear transformation (**A**) assumes that resistance is inversely related to habitat suitability, while the nonlinear transformations allowed for slight nonlinear responses (**B**) and pronounced nonlinear responses (**C**) to unsuitable habitats. The X and Y axes indicate longitude and latitude, and map colors indicate areas in the landscape that are very costly (red) to less costly (white) for elephants to move through

Landscape genetics

We linearly and nonlinearly transformed the top MaxEnt HSM (range-based background points, $\beta = 1$) into three alternative representations of landscape resistance (Fig. 4). The MLPE model assessment consistently identified CT distances calculated for the pronounced nonlinear transformation ($c = 8$) as the connectivity measure that best explained the observed gene flow for all four genetic metrics across the landscape (Table SI 2). These genetic metrics are not independent and will likely result in similar delineation and visualization of landscape connections. However, to limit replicate analyses we focused on one genetic metric, D_{PS}, which has often been used in landscape genetic studies (e.g., see Hazlitt et al. (2004) and Milanesi et al. (2017) for examples of usage of D_{PS} for model evaluation and Waits and Storfer (2015) for a general overview of D_{PS} as a genetic metric).

Landscape connections

Because we identified CT distances as the connectivity measure that best explained the gene flow across our landscape, we used CT distances in Omniscape (Shah and McRae 2008) to delineate and visualize areas that represent landscape connections for elephants (Fig. 5A). We found areas in our landscape connections map where the impact of different environmental determinants was noticeable; primary productivity (Fig. 5B) and "ambient human population" distribution (Fig. 5C) seem to be the primary drivers of connectivity in parts of the landscape. The mean Normalized Cumulative Current at elephant occurrence points was higher than the mean at random points ($z = -78.952$, $p < 0.001$), indicating the connectivity map generated using Omniscape was a good predictor of where elephants occur (SI Fig. S5B).

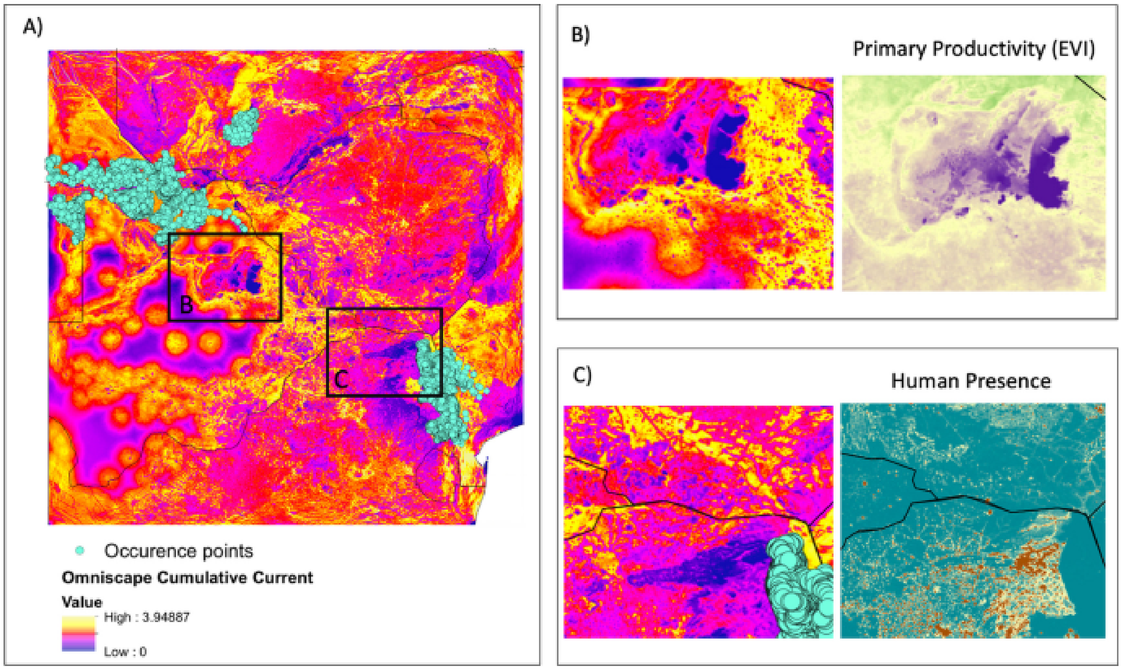


Fig. 5. Delineation by Omniscape of regions of high connectivity and low resistance, i.e., landscape connections. The Normalized Cumulative Current map of landscape connections (**A**) considers suitable habitats based on spatial data, and also gene flow as the inverse of genetic distance, to delineate areas in the landscape (yellow) that may be important for maintaining or restoring population connectivity. Connectivity across our landscape was associated with different environmental determinants, e.g., primary productivity (**B**) and "ambient human population" distribution (**C**)

Discussion

Here we provide a new framework for empirically delineating landscape connections for species by integrating habitat suitability and gene flow. We found a pronounced nonlinear response to habitat suitability that suggests elephant movement and gene flow are mostly impacted by very unsuitable habitats, and that moderately unsuitable habitat impedes connectivity between elephant populations to a lesser degree. This nonlinear response agrees with space use described for some elephant populations in our study region; for example, elephants in Botswana are known to range across populated areas to access food and water (Hoare and Du Toit 1999; Jackson et al. 2008). Despite this, we identified ambient human population as a likely a barrier to elephant habitat suitability and there is likely a population threshold that eventually prevents gene flow. However, the challenges faced by elephants in moving across a landscape may vary for different populations (Huang et al. 2022), requiring consideration of different factors when analyzing paths of connectivity for different sets of populations.

The pronounced nonlinear response to habitat suitability agrees with criticisms of typical habitat suitability models used in gene flow analyses (Keeley et al. 2017) as the linear model performed poorly. However, the performance of the pronounced non-linear transformation of habitat suitability to resistance indicates that habitat suitability models can still provide insight to gene flow across complex landscapes. Specifically, the resistance map using transformed suitability identified areas with different limiting factors (ambient human population and vegetation) to gene flow. Through this method, empirical models can be created and used to determine gene flow (but see section “Caveats and future directions”).

The analyses also indicated that landscape representations that consider multiple paths of connectivity (isolation by resistance based on circuit theory; IBR) perform better at predicting gene flow across the landscape than singular paths (LCP) or geographic distance alone. Similar IBR frameworks have been more effective at explaining gene flow for black bears (Ursus americanus, Cushman et al. 2006), hedgehogs (Erinaceus europaeus, Braaker et al. 2017), and other plant and animal species (McRae and Beier 2007).

Our landscape connections map in Omniscape (Fig. 5) shows that gene flow and connectivity appear to be influenced by different environmental variables across the landscape, where connectivity in some areas is clearly driven by a single variable. For example, primary productivity as a proxy of food availability was the primary driver of connectivity in regions surrounding the Makgadikgadi pans in Botswana (Fig. 5B). The low primary productivity associated with the pans is reflected as low predicted connectivity or suitability of this area as a landscape connection. We found human density as the primary driver of connectivity in the landscape that links elephants from Botswana with elephants in South Africa in the areas adjacent to northern parts of Kruger National Park (Fig. 5C), which is also consistent with the results of Huang et al., (2022) using a more extensive spatial dataset. Although not highlighted in Fig. 5, examples of the impacts of other environmental variables include slope as the primary driver of landscape connectivity for regions that overlap with the Lebombo mountain range (du Toit 1929; Saggerson and Bristow 1983) that separates elephants in southern Kruger National Park (South Africa) and Maputo Special Reserve (Mozambique). Similarly, distance to water was the primary driver of connectivity in the Caprivi region of Namibia.

When demarcating landscape connections for conservation, researchers and conservation stakeholders should therefore consider that landscape connections may be dependent on the specific geographic area and environmental variables under consideration, and that a "one-map-fits-all" approach should be avoided. Huang et al. (2022) provide case studies of different elephant populations that each have unique conservation challenges, and also describe ways to assess whether landscape connectivity could be restored if challenges are negated, or whether such efforts would be futile. We therefore urge researchers and conservation stakeholders to consider additional factors other than landscape connectivity and gene flow when demarcating landscape connections for conservation. Factors such as land ownership (Pinter-Wollman 2012), human-elephant conflict mitigation (Jackson et al. 2008; Pinter-Wollman 2012), the direct and indirect impact of creating landscape connections on local indigenous communities (Baldus et al. 2007), landscape connections overlapping with poaching hotspots (Zafra-Calvo et al. 2018; Schlossberg et al. 2019), and other sociopolitical factors need to be integrated into conservation decisions.

Caveats and future directions

Our goal was to test and validate a general methodology that could be replicated across systems. However, elephant space use and habitat suitability modeling may be influenced by factors that were not considered in this study. For example, the pronounced nonlinear response to occurrence-based habitat suitability models suggests that alternative or expert-based quantifications of habitat use might be needed to accurately establish elephant connectivity requirements. Researchers could, for example, separate elephant movements into different behavioral states using hidden Markov models fitted in a Bayesian framework (Leos-Barajas and Michelot 2018; Wang 2019; Vogel et al. 2020), and identify from those states the environmental variables that are important for establishing or maintaining connectivity. For example, Keeley et al., (2017) showed that habitat suitability is a poor proxy for landscape connectivity during dispersal and mating movements in kinkajous (*Potos flavus*), where tolerance for unsuitable habitat during dispersal seems common. Mateo-Sánchez et al., (2015) showed that dispersing Cantabrian brown bears (*Ursus arctos*) might be more flexible in their dispersal movement behavior than they are in their habitat use behavior. Determining behavioral states may be especially relevant to elephant landscape connections because exploratory movements within corridors may be fast and directional compared to encamped foraging movements that are slow and meandering (Vogel et al. 2020). It may therefore be beneficial for future studies to consider both behavior and space use when delineating landscape connections for African elephants.

In addition to behavior, other aspects not considered here could also impact the accurate delineation of landscape connections. Mashintonio et al., (2014) showed elephants select habitat based on environmental qualities at multiple spatial scales, and it may therefore be informative to incorporate habitat suitability modeling at different scales. Researchers could, for example, use a Gaussian pixel smoothing algorithm approach, which can be effective for determining the scale at which elephants select resources (Mashintonio et al. 2014).

In addition to scale and resolution, seasonality and sex are crucial drivers of elephant dispersal and land use patterns (Young et al. 2009b). Future studies could consider seasonal and sex-specific differences when predicting gene flow across the landscape by generating individually modeled landscape connections maps for males and females, and for wet and dry seasons (Young et al. 2009a; Purdon et al. 2018). Sex- and season-based landscape connections maps may be especially important for elephant connectivity mapping since dispersal is predominantly male-mediated (Nyakaana and Arctander 1999; Roca et al. 2005), and males typically have larger home ranges and disperse farther than females with young calves (Mole et al. 2016). For conservation, protecting dispersal and movement of males may be a critical component for maintaining adequate gene flow across the region.

Despite these limitations, the conservation genetic approach developed and applied here integrates multidisciplinary datasets and methods in an innovative way and may therefore be a useful framework for future studies on elephant and other taxa that aim to develop spatially and genetically informed conservation strategies. In particular, an habitat suitability models robust to integrating data types. Although we applied these methods to a robust dataset, MaxEnt and AIS are effective even with small sample sizes, and this approach should be applicable to a range of taxa, especially taxa with depauperate occurrence data.

Broader context and application

The defragmentation of conservation areas through the development and maintenance of landscape connections could induce regional demographic stability in elephant numbers, increase available areas to roam thus allowing for space use that may change seasonally, reduce local impact that elephants have on the landscape (van Aarde and Jackson 2007; Huang et al. 2022), and mitigate the consequences of genetic isolation by promoting gene glow and increasing genetic diversity (Allendorf and Luikart 2009; Burkart et al. 2016; Orton et al. 2020). Integrating multifaceted landscape habitat modeling with genetic analyses has been proposed and applied as a conservation tool, and it is an expedient method through which landscape connections hypotheses can be tested. For example, the integration of spatial and genetic analyses was used to detect and evaluate landscape connectivity and movement corridors for wolves (Canis lupus, Kabir et al. 2017), Cantabrian brown bears (Mateo-Sánchez et al. 2015), rodents (Wang et al. 2008) and birds (Klinga et al. 2019). In this study, we show that the integration of spatial landscape modeling and genetic analyses can also be used to delineate landscape connections for African elephant conservation planning.

Acknowledgements

We dedicate this paper to the memory of Rudi van Aarde whose life-long passion and dedication to conservation was and continues to be a driving force for the protection of Africa’s elephants. We thank Camilla Nørgaard for permission to include the late Rudi van Aarde as co-author. For facilitating sample collection, we thank Elephant Without Borders (Botswana) and the CERU team. The Zambian Wildlife Authority, the Department of Wildlife and National Parks (Botswana), South African National Parks (SANParks) and the Department of Agriculture, Forestry and Fisheries (South Africa) sanctioned the research. We acknowledge technical support provided by the University of Pretoria’s Sequencing Facility; the High-Throughput Sequencing and Genotyping Unit of the University of Illinois at Urbana-Champaign (UIUC); and the Illinois Campus Cluster, a computing resource that is operated by the Illinois Campus Cluster Program (ICCP) in conjunction with the National Center for Supercomputing Applications (NCSA) and which is supported by funds from UIUC.

Funding

For funding we thank the International Fund for Animal Welfare; the Conservation Ecology Research Unit (CERU) of the University of Pretoria; the Conservation Foundation (Zambia); the US Fish and Wildlife Service African Elephant Conservation Fund. In addition to support from these sources, AdF received a Francis M. and Harlie M. Clark Research Support Grant, a Harley J. Van Cleave Research Award, a University of Illinois Graduate College Dissertation

Project Travel Grant, and support from the Cooperative State Research, Education, and Extension Service, US Department of Agriculture under project number ILLU 875–952.

Contributions

AdF, RLS, RJvA and ALR conceived and developed the methodological analysis approach. AdF, TINPS and CD completed the molecular work, and AdF and NA conducted the computational analyses. AdF wrote the original draft of the manuscript, all authors provided critical feedback throughout the process of interpretation of the data and of manuscript preparation, and approved of the final version of the manuscript.

Competing interests

The authors have no relevant financial or non-financial interests to disclose.

Ethical approval

The Animal Ethics Committee of the University of Pretoria (AUCC-040611-013) and the Botswana Ministry of Environment, Wildlife, & Tourism (OP 46/1 LXXXV 89) reviewed and approved the telemetry collaring of the elephants. Collection and export/import of elephant dung was sanctioned by appropriate authorities prior to collection, including South African National Parks, the Department of Agriculture, Forestry and Fisheries in South Africa and the United States Department of Agriculture in the United States of America.

Data availability

All bioinformatic code associated with this manuscript may be found at https://github.com/adeflamingh/de_Flamingh_et_al_Landscape_Connectivity and genetic data is available on DRYAD: https://doi.org/10.5061/dryad.qnk98sfp5.

References

Adriaensen F, Chardon JP, De Blust G, Swinnen E, Villalba S, Gulinck H et al (2003) The application of 'least-cost' modelling as a functional landscape model. Landsc Urban Plan 64:233–247. https://doi.org/10.1016/S0169-2046(02)00242-6

Alexander NB, Statham MJ, Sacks BN, Bean WT (2019) Generalist dispersal and gene flow of an endangered keystone specialist (*Dipodomys ingens*). J Mammal 100:1533–1545

Allendorf FW, Luikart G (2009) Conservation and the genetics of populations. Blackwell Publishing, Wiley & Sons, West Sussex

Allendorf FW, Luikart G, Aitken SN (2013) Conservation and the genetics of populations, 2nd edn. Blackwell Publishing, Wiley and Sons, West Sussex

Anderson RP (2012) Harnessing the world's biodiversity data: promise and peril in ecological niche modeling of species distributions. Ann N Y Acad Sci 1260:66–80. https://doi.org/10.1111/J.1749-6632.2011.06440.X

Archie EA, Moss CJ, Alberts SC (2003) Characterization of tetranucleotide microsatellite loci in the African Savannah Elephant (*Loxodonta africana africana*). Mol Ecol Notes 3:244–246. https://doi.org/10.1046/J.1471-8286.2003.00412.X

Baldus RD, Hahn R, Ellis C, DeLeon SD (2007) Connecting the world's largest elephant ranges: the Selous-Niassa corridor. Peace Parks. https://doi.org/10.7551/mitpress/7433.003.0013

Barnes RFW, Barnes KL, Alers MPT, Blom A (1991) Man determines the distribution of elephants in the rain forests of northeastern Gabon. Afr J Ecol 29:54–63

Barton K (2009) MuMIn: multi-model inference. R package version 1. 0. 0. http://r-forge.r-project.org/projects/mumin/.

Bates D, Maechler M, Bolker B, Walker S, Christensen RHB, Singmann H et al. (2015) Package 'lme4.' *Convergence* 12.

Becker RA, Chambers JM, Wilks AR (1988) The New S Language. Wadsworth & Brooks/Cole, Pacific Grove

Bezanson J, Edelman A, Karpinski S, Shah VB (2017) Julia: a fresh approach to numerical computing. SIAM Rev 59:65–98

Blanc J (2008) *Loxodonta africana*. The IUCN Red List of Threatened Species 2008: e. T12392A3339343.

Boyce MS, McDonald LL (1999) Relating populations to habitats using resource selection functions. Trends Ecol Evol 14:268–272

Braaker S, Kormann U, Bontadina F, Obrist MK (2017) Prediction of genetic connectivity in urban ecosystems by combining detailed movement data, genetic data and multi-path modelling. Landsc Urban Plan 160:107–114

Bright EA, Rose AN, Urban ML and McKee JJ (2017) LandScan 2016.

Büchi L, Vuilleumier S (2014) Coexistence of specialist and generalist species is shaped by dispersal and environmental factors. Am Nat 183:612–624

Burkart S, Gugerli F, Senn J, Kuehn R, Bolliger J (2016) Evaluating the functionality of expert-assessed wildlife corridors with genetic data from roe deer. Basic Appl Ecol 17:52–60

Burnham KP, Anderson DR (2004) Multimodel inference: understanding AIC and BIC in model selection. Soc Methods Res 33:261–304

Centeno-Cuadros A, Roman J, Delibes M, Godoy JA (2011) Prisoners in their habitat? Generalist dispersal by habitat specialists: a case study in southern water vole (*Arvicola sapidus*). PLoS ONE 6:e24613

Chamaillé-Jammes S, Valeix M, Fritz H (2007) Managing heterogeneity in elephant distribution: interactions between elephant population density and surface-water availability. J Appl Ecol 44:625–633

Chetkiewicz CLB, Boyce MS (2009) Use of resource selection functions to identify conservation corridors. J Appl Ecol 46:1036–1047. https://doi.org/10.1111/j.1365-2664.2009.01686.x

Clarke RT, Rothery P, Raybould AF (2002) Confidence limits for regression relationships between distance matrices: estimating gene flow with distance. J Agric Biol Environ Stat 7:361

Comstock KE, Wasser SK, Ostrander EA (2000) Polymorphic microsatellite DNA loci identified in the African elephant (*Loxodonta africana*). Mol Ecol 9:1004–1006. https://doi.org/10.1046/J.1365-294X.2000.00939-8.X

Cushman SA, McKelvey KS, Hayden J, Schwartz MK (2006) Gene flow in complex landscapes: testing multiple hypotheses with causal modeling. Am Nat 168:486–499

de Flamingh A, Sole CL, van Aarde RJ (2014) Microsatellite repeat motif and amplicon length affect amplification success of degraded faecal DNA. Conserv Genet Resour. https://doi.org/10.1007/s12686-014-0160-5

de Flamingh A, Roca AL, van Aarde RJ (2018) Origin and phylogeography of African savannah elephants (*Loxodonta africana*) in Kruger and nearby parks in southern Africa. Conserv Genet. https://doi.org/10.1007/s10592-017-1005-z

de Flamingh A, Ishida Y, Pečnerová P, Vilchis S, Siegismund HR, van Aarde RJ et al (2023) Combining methods for non-invasive fecal DNA enables whole genome and metagenomic analyses in wildlife biology. Front Genet. https://doi.org/10.3389/fgene.2022.1021004

Dobson JE, Bright EA, Coleman PR, Durfee RC, Worley BA (2000) LandScan: a global population database for estimating populations at risk. Photogramm Eng Remote Sensing 66:849–857

du Toit AL (1929) The volcanic belt of the Lebombo—a region of tension. Trans Royal Soc South Africa 18:189–217

Edwards LJ, Muller KE, Wolfinger RD, Qaqish BF, Schabenberger O (2008) An R2 statistic for fixed effects in the linear mixed model. Stat Med 27:6137–6157

Eggert LS, Ramakrishnan U, Mundy NI, Woodruff DS (2000) Polymorphic microsatellite DNA markers in the African elephant (*Loxodonta africana*) and their use in the Asian elephant (*Elephas maximus*). Mol Ecol 9:2223–2225

Elith J, Phillips SJ, Hastie T, Dudík M, Chee YE, Yates CJ (2011) A statistical explanation of MaxEnt for ecologists. Divers Distrib 17:43–57

Excoffier L, Lischer HEL (2010) Arlequin suite ver 3.5: a new series of programs to perform population genetics analyses under Linux and Windows. Mol Ecol Resour 10:564–567

Fletcher RJ, McCleery RA, Greene DU, Tye CA (2016) Integrated models that unite local and regional data reveal larger-scale environmental relationships and improve predictions of species distributions. Landsc Ecol 31:1369–1382. https://doi.org/10.1007/S10980-015-0327-9/FIGURES/4

Fourcade Y, Engler JO, Rödder D, Secondi J (2014) Mapping species distributions with MAXENT using a geographically biased sample of presence data: a performance assessment of methods for correcting sampling bias. PLoS ONE 9:e97122

Garant D, Forde SE, Hendry AP (2007) The multifarious effects of dispersal and gene flow on contemporary adaptation. Funct Ecol 21:434–443

Gobush KS, Edwards CTT, Balfour D, Wittemyer G, Maisels F and Taylor RD (2022) *Loxodonta africana* (amended version of 2021 assessment)(The IUCN Red List of Threatened Species, 2021). *The IUCN Red List of Threatened Species*.

Grainger M, Van Aarde R, Whyte I (2005) Landscape heterogeneity and the use of space by elephants in the Kruger National Park, South Africa. Afr J Ecol 43:369–375

Guisan A, Edwards TC Jr, Hastie T (2002) Generalized linear and generalized additive models in studies of species distributions: setting the scene. Ecol Modell 157:89–100

Gurka MJ (2006) Selecting the best linear mixed model under REML. Am Stat 60:19–26

Hazlitt SL, Eldridge MDB, Goldizen AW (2004) Fine-scale spatial genetic correlation analyses reveal strong female philopatry within a brush-tailed rock-wallaby colony in southeast Queensland. Mol Ecol 13:3621–3632. https://doi.org/10.1111/J.1365-294X.2004.02342.X

Hernandez PA, Graham CH, Master LL, Albert DL (2006) The effect of sample size and species characteristics on performance of different species distribution modeling methods. Ecography 29:773–785

Hoare RE, Du Toit JT (1999) Coexistence between people and elephants in African savannas. Conserv Biol 13:633–639

Holderegger R, Wagner HH (2008) Landscape genetics. Bioscience 58:199–207

Huang RM, van Aarde RJ, Pimm SL, Chase MJ, Leggett K (2022) Mapping potential connections between Southern Africa's elephant populations. PLoS ONE. https://doi.org/10.1371/JOURNAL.PONE.0275791

Huang RM, Maré C, Guldemond RAR, Pimm SL, Van Aarde RJ (2024) Protecting and connecting landscapes stabilizes populations of the Endangered savannah elephant. Sci Adv 10:eadk2896

Hunter RD, Fisher RN, Crooks KR (2003) Landscape-level connectivity in coastal southern California, USA, as assessed through carnivore habitat suitability. Nat Areas J 23:302–314

Ishida Y, Coeverden V, de Groot PJ, Leggett KEA, Putnam AS, Fox VE, Lai J et al (2016) Genetic connectivity across marginal habitats: the elephants of the Namib Desert. Ecol Evol 6:6189–6201

Jackson TP, Mosojane S, Ferreira SM, van Aarde RJ (2008) Solutions for elephant Loxodonta africana crop raiding in northern Botswana: moving away from symptomatic approaches. Oryx 42:83–91

Jarvis A, Reuter HI, Nelson A and Guevara E (2008) Hole-filled SRTM for the globe Version 4. *available from the CGIAR-CSI SRTM 90m Database (*http://srtm.csi.cgiar.org*).*

Johnson DH (1980) The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71

Jombart T (2008) adegenet: a R package for the multivariate analysis of genetic markers. Bioinformatics 24:1403–1405

Kabir M, Shoaib Hameed HA, Bosso L, Din JU, Bischof R, Redpath S et al (2017) Habitat suitability and movement corridors of grey wolf (*Canis lupus*) in Northern Pakistan. PLoS ONE. https://doi.org/10.1371/journal.pone.0187027

Kamvar ZN, Tabima JF, Grünwald NJ (2014) Poppr: an R package for genetic analysis of populations with clonal, partially clonal, and/or sexual reproduction. PeerJ 2:e281

Keeley ATH, Beier P, Gagnon JW (2016) Estimating landscape resistance from habitat suitability: effects of data source and nonlinearities. Landsc Ecol 31:2151–2162. https://doi.org/10.1007/s10980-016-0387-5

Keeley ATH, Beier P, Keeley BW, Fagan ME (2017) Habitat suitability is a poor proxy for landscape connectivity during dispersal and mating movements. Landsc Urban Plan 161:90–102

Kitchens, L. J. (2002). *Basic Statistics and Data Analysis*. Thomson/Brooks/Cole.

Klinga P, Mikoláš M, Smolko P, Tejkal M, Höglund J, Paule L (2019) Considering landscape connectivity and gene flow in the Anthropocene using complementary landscape genetics and habitat modelling approaches. Landsc Ecol 34:521–536

Koshkina V, Wang Y, Gordon A, Dorazio RM, White M, Stone L (2017) Integrated species distribution models: combining presence-background data and site-occupancy data with imperfect detection. Methods Ecol Evol 8:420–430. https://doi.org/10.1111/2041-210X.12738

Landau VA, Shah VB, Anantharaman R, Hall KR (2021) Omniscape. jl: Software to compute omnidirectional landscape connectivity. J Open Source Softw 6:2829

Larkin JL, Maehr DS, Hoctor TS, Orlando MA, Whitney K (2004) Landscape linkages and conservation planning for the black bear in west-central Florida. Animal Conservation forum. Cambridge University Press, Cambridge, pp 23–34

Leos-Barajas, V., and Michelot, T. (2018). An Introduction to Animal Movement Modeling with Hidden Markov Models using Stan for Bayesian Inference. *arXiv preprint* arXiv:1806.10639.

Leroy B, Meynard CN, Bellard C, Courchamp F (2016) virtualspecies, an R package to generate virtual species distributions. Ecography 39:599–607

Loarie SR, van Aarde RJ, Pimm SL (2009a) Elephant seasonal vegetation preferences across dry and wet savannas. Biol Conserv 142:3099–3107

Loarie SR, van Aarde RJ, Pimm SL (2009b) Fences and artificial water affect African savannah elephant movement patterns. Biol Conserv 142:3086–3098

Lobo JM, Jiménez-Valverde A, Real R (2008) AUC: a misleading measure of the performance of predictive distribution models. Glob Ecol Biogeogr 17:145–151

Lobora AL, Nahonyo CL, Munishi LK, Caro T, Foley C, Prunier JG et al (2018) Incipient signs of genetic differentiation among African elephant populations in fragmenting Miombo ecosystems in South-Western Tanzania. Afr J Ecol 56:993–1002

Manel S, Holderegger R (2013) Ten years of landscape genetics. Trends Ecol Evol 28:614–621

Manel S, Schwartz MK, Luikart G (2003) Landscape genetics: combining landscape ecology and population genetics. Ecol Evol 18:189–198

Mapaure IN, Campbell BM (2002) Changes in Miombo woodland cover in and around Sengwa Wildlife Research Area, Zimbabwe, in relation to elephants and fire. Afr J Ecol 40:212–219

Mashintonio AF, Pimm SL, Harris GM, Van Aarde RJ, Russell GJ (2014) Data-driven discovery of the spatial scales of habitat choice by elephants. PeerJ 2:e504

Mateo-Sánchez MC, Balkenhol N, Cushman S, Pérez T, Domínguez A, Saura S (2015) Estimating effective landscape distances and movement corridors: comparison of habitat and genetic data. Ecosphere 6:1–16

McRae BH (2006) Isolation by resistance. Evolution 60:1551–1561

McRae BH, Beier P (2007) Circuit theory predicts gene flow in plant and animal populations. Proc Natl Acad Sci. https://doi.org/10.1073/pnas.0706568104

McRae BH, Popper K, Jones A, Schindel M, Buttrick S, Hall K et al (2016) Conserving nature's stage: mapping omnidirectional connectivity for resilient terrestrial landscapes in the pacific northwest. The Nature Conservancy, Portland

Merow C, Smith MJ, Silander JA Jr (2013) A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. Ecography 36:1058–1069

Milanesi P, Holderegger R, Caniglia R, Fabbri E, Galaverni M, Randi E (2017) Expert-based versus habitat-suitability models to develop resistance surfaces in landscape genetics. Oecologia 183:67–79

Miller MP (2005) Alleles in space (AIS): computer software for the joint analysis of interindividual spatial and genetic information. J Hered 96:722–724

Mole MA, Rodrigues DÁraujo S, Van Aarde RJ, Mitchell D, Fuller A (2016) Coping with heat: behavioural and physiological responses of savanna elephants in their natural habitat. Conserv Physiol. https://doi.org/10.1093/conphys/cow044

Nei M, Tajima F, Tateno Y (1983) Accuracy of estimated phylogenetic trees from molecular data. J Mol Evol 19:153–170

Newmark WD (2008) Isolation of African protected areas. Front Ecol Environ 6:321–328

Ntumi CP, Van Aarde RJ, Fairall N, De Boer WF (2005) Use of space and habitat by elephants (*Loxodonta africana*) in the Maputo Elephant Reserve, Mozambique. South African J Wildlife Re 35:139–146

Nyakaana S, Arctander P (1999) Population genetic structure of the African elephant in Uganda based on variation at mitochondrial and nuclear loci: evidence for male-biased gene flow. Mol Ecol 8:1105–1115

Orelien JG, Edwards LJ (2008) Fixed-effect variable selection in linear mixed models using R2 statistics. Comput Stat Data Anal 52:1896–1907

Orton RW, Tucker DB, Harrison JS, McBrayer LD (2020) Spatial and temporal patterns of genetic diversity in a fragmented and transient landscape. Evol Ecol. https://doi.org/10.1007/s10682-019-10030-3

Ott, T. (2008). Landscape heterogeneity as a determinant of range utilization by African elephants (*Loxodonta africana*) in mesic savannas.

Pekel J-F, Cottam A, Gorelick N, Belward AS (2016) High-resolution mapping of global surface water and its long-term changes. Nature 540:418–422

Pettorelli N, Vik JO, Mysterud A, Gaillard J-M, Tucker CJ, Stenseth NC (2005) Using the satellite-derived NDVI to assess ecological responses to environmental change. Trends Ecol Evol 20:503–510

Phillips SJ, Dudík M (2008) Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography 31:161–175

Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. Ecol Modell 190:231–259

Phillips, S. J., Dudík, M., and Schapire, R. E. (2017). Maxent software for modeling species niches and distributions (Version 3.4. 1). *Biodiversity Informatics*.

Pinter-Wollman N (2012) Human–elephant conflict in Africa: the legal and political viability of translocations, wildlife corridors, and transfrontier parks for large mammal conservation. J Int Wildlife Law Policy 15:152–166

Pullinger MG, Johnson CJ (2010) Maintaining or restoring connectivity of modified landscapes: evaluating the least-cost path model with multiple sources of ecological information. Landsc Ecol 25:1547–1560

Purdon A, Mole MA, Chase MJ, Van Aarde RJ (2018) Partial migration in savanna elephant populations distributed across southern Africa. Sci Rep 8:1–11

R Core Team (2019) R Core Team (2019). R: A language and environment for statistical computing. *R Found. Stat. Comput. Vienna, Austria. URL* http://www.R-project.org/*., page R Foundation for Statistical Computing.*

Renner IW, Warton DI (2013) Equivalence of MAXENT and poisson point process models for species distribution modeling in ecology. Biometrics 69:274–281. https://doi.org/10.1111/J.1541-0420.2012.01824.X

Richardson JL, Brady SP, Wang IJ, Spear SF (2016) Navigating the pitfalls and promise of landscape genetics. Mol Ecol. https://doi.org/10.1111/mec.13527

Riordan-Short E, Pither R, Pither J (2023) Four steps to strengthen connectivity modeling. Ecography. https://doi.org/10.1111/ECOG.06766

Ripple WJ, Newsome TM, Wolf C, Dirzo R, Everatt KT, Galetti M et al (2015) Collapse of the world’s largest herbivores. Sci Adv 1:e1400103

Robson AS, Trimble MJ, Purdon A, Young-Overton KD, Pimm SL, van Aarde RJ (2017) Savanna elephant numbers are only a quarter of their expected values. PLoS ONE 12:e0175942

Roca AL, Georgiadis N, O’Brien SJ (2005) Cytonuclear genomic dissociation in African elephant species. Nat Genet 37:96–100

Roever CL, Van Aarde RJ, Leggett K (2012) Functional responses in the habitat selection of a generalist mega-herbivore, the African savannah elephant. Ecography 35:972–982

Roever CL, van Aarde RJ, Leggett K (2013) Functional connectivity within conservation networks: delineating corridors for African elephants. Biol Conserv 157:128–135

Row JR, Knick ST, Oyler-McCance SJ, Lougheed SC, Fedy BC (2017) Developing approaches for linear mixed modeling in landscape genetics through landscape-directed dispersal simulations. Ecol Evol 7:3751–3761

Saggerson EP, Bristow JW (1983) The geology and structural relationships of the southern Lebombo volcanic and intrusive rocks. South Africa Bulletin Volcanologique 46:161

Saupe EE, Barve V, Myers CE, Soberón J, Barve N, Hensz CM et al (2012) Variation in niche and distribution model performance: the need for a priori assessment of key causal factors. Ecol Modell 237:11–22

Schlossberg S, Chase M, Biology RSC (2019) Evidence of a growing elephant poaching problem in Botswana. *cell.comS Schlossberg, MJ Chase, R SutcliffeCurrent Biology, 2019•cell.com*, 2017–2018. https://doi.org/10.1016/j.cub.2019.05.061

Shabani F, Kumar L, Ahmadi M (2016) A comparison of absolute performance of different correlative and mechanistic species distribution models in an independent area. Ecol Evol 6:5973–5986

Shafer ABA, Northrup JM, White KS, Boyce MS, Côté SD, Coltman DW (2012) Habitat selection predicts genetic relatedness in an alpine ungulate. Ecology 93:1317–1329

Shah VB, and McRae BH (2008) Circuitscape: a tool for landscape ecology. In: Proceedings of the 7th Python in Science Conference, (SciPy 2008, Pasadena, California, USA), pp. 62–66.

Shirk AJ, Cushman SA, Landguth EL (2012) Simulating pattern-process relationships to validate landscape genetic models. Int J Ecol. https://doi.org/10.1155/2012/539109

Shirk AJ, Landguth EL, Cushman SA (2017) A comparison of individual-based genetic distance metrics for landscape genetics. Mol Ecol Resour 17:1308–1317. https://doi.org/10.1111/1755-0998.12684

Shrestha B, Kindlmann P (2020) Implications of landscape genetics and connectivity of snow leopard in the Nepalese Himalayas for its conservation. Sci Rep 10:19853

Songhurst A, Chase M, Coulson T (2015) Using simulations of past and present elephant (*Loxodonta africana*) population numbers in the Okavango Delta Panhandle, Botswana to improve future population estimates. Wetl Ecol Manag 23:583–602

Spear SF, Balkenhol N, Fortin M, McRae BH, Scribner KIM (2010) Use of resistance surfaces for landscape genetic studies: considerations for parameterization and analysis. Mol Ecol 19:3576–3591

Tang Q, Fung T, Rheindt FE (2019) ResDisMapper: An r package for fine-scale mapping of resistance to dispersal. Mol Ecol Resour. https://doi.org/10.1111/1755-0998.13127

Thouless C, Dublin HT, Blanc JJ, Skinner DP, Daniel TE, Taylor RD et al (2016) African elephant status report 2016. Occasional Paper Series of the IUCN Species Survival Commission 60.

van Aarde RJ, Jackson TP (2007) Megaparks for metapopulations: addressing the causes of locally high elephant numbers in southern Africa. Biol Conserv 134:289–297

Van Strien MJ, Keller D, Holderegger R (2012) A new analytical approach to landscape genetic modelling: least-cost transect analysis and linear mixed models. Mol Ecol 21:4010–4023

Verbeke G, Molenberghs G (2000) Linear mixed models for longitudinal data. Springer, Cham

Vogel SM, Lambert B, Songhurst AC, McCulloch GP, Lee Stronza A, Coulson T (2020) Exploring movement decisions: can Bayesian movement-state models explain crop consumption behaviour in elephants (*Loxodonta africana*)? J Animal Ecol 89(4):1055–1068

Waits LP, Storfer A (2015) Basics of population genetics: quantifying neutral and adaptive genetic variation for landscape genetic studies. Landsc Genet. https://doi.org/10.1002/9781118525258.CH03

Wall J, Douglas-Hamilton I, Vollrath F (2006) Elephants avoid costly mountaineering. Curr Biol 16:R527–R529

Wang G (2019) Machine learning for inferring animal behavior from location and movement data. Ecol Inform 49:69–76

Wang Y-H, Yang K-C, Bridgman CL, Lin L-K (2008) Habitat suitability modelling to correlate gene flow with landscape connectivity. Landsc Ecol 23:989–1000

Webber BL, Yates CJ, Le Maitre DC, Scott JK, Kriticos DJ, Ota N et al (2011) Modelling horses for novel climate courses: insights from projecting potential distributions of native and alien Australian acacias with correlative and mechanistic models. Divers Distrib 17:978–1000

Wisz MS, Hijmans RJ, Li J, Peterson AT, Graham CH, Guisan A et al (2008) Effects of sample size on the performance of species distribution models. Divers Distrib 14:763–773

Young KD, Ferreira SM, Van Aarde RJ (2009a) Elephant spatial use in wet and dry savannas of southern Africa. J Zool 278:189–205

Young KD, Ferreira SM, van Aarde RJ (2009b) The influence of increasing population size and vegetation productivity on elephant distribution in the Kruger National Park. Austral Ecol 34:329–342

Zafra-Calvo N, Lobo JM, Prada C, Nielsen MR, Burgess ND (2018) Predictors of elephant poaching in a wildlife crime hotspot: the Ruvuma landscape of southern Tanzania and northern Mozambique. J Nat Conserv 41:79–87. https://doi.org/10.1016/J.JNC.2017.11.006