

## **Supplementary information:**

### **Supplementary File 1:** Description of habitat suitability modelling (HSM) methodology *Parameter selection*

We considered habitat covariates that are known to influence the distribution of elephants including water availability (Loarie et al., 2009), the slope of the land (Wall et al., 2006), primary productivity (Young et al., 2009a) and human population distribution (Hoare and Du Toit, 1999). Surface-water availability drives the distribution and abundance of elephants (Chamaillé-Jammes et al., 2007). Elephants prefer areas that are close to water, especially during the dry season when access to surface water is limited. Elephants alter their space use to avoid mountainous terrain, as even small hills may present energetic barriers to movement for large-bodied animals (Wall et al., 2006). Primary productivity as a proxy for food availability influences elephant habitat selection and space use (Young et al., 2009b; Roever et al., 2012). In addition, elephants also alter their space use to avoid areas densely populated by humans (Barnes et al., 1991; Hoare and Du Toit, 1999). These four environmental variables included in this study thus directly impact elephant space use and the potential geographic distribution of landscape connections.

We converted the Global Surface Water (GSW) occurrence layer (Pekel et al., 2016) to estimate distance to water across our study range. The GSW occurrence layer represents areas where surface water occurred between 1984 and 2018 and provides information concerning overall water dynamics. This layer captures the frequency with which water was present in a given area. To calculate GSW occurrence, Pekel et al. (2016) respectively summed and then normalized by division the monthly water detections (WD) and valid observations (VO) such that  $\text{GSW occurrence/month} = \sum \text{WD month} / \sum \text{VO month}$ . By averaging the results of all monthly GSW

occurrence calculations, Pekel et al. (2016) were able to provide the long-term overall surface water occurrence.

GSW data were downloaded as 9 individual tiles that covered our study extent and were merged using the “Mosaic to new raster” function in ArcMap V10.7.1 (© ESRI 2011). We transformed the GSW data to represent the geographic distance from an available water source because areas that are further from water sources would represent less suitable habitat, and a gradient layer may therefore be more biologically relevant to elephant space use than a binary presence-absence layer. We reclassified the GSW data so that all points with values  $>0$  were reclassified to represent water occurrence. We used the Euclidean distance tool in ArcMap to calculate, for each cell in our study area, the Euclidean distance to the closest water source (Figure 2B). The GSW dataset was split into subset of four raster layers before executing the Euclidean distance tool to facilitate data processing.

We converted a digital elevation model (Jarvis et al., 2008) to denote slope by calculating the maximum rate of elevation change between pixels using the “Spatial Analyst” toolbox in ArcMap (ESRI © 2011). We use this converted slope layer as our second environmental layer in MaxEnt (Figure 2C).

We used long-term mean Enhanced Vegetation Index (EVI) from Robson et al. (2017), which is an index of primary productivity across our study range (Figure 2D). We use EVI rather than Normalized Difference Vegetation Index (NDVI) because EVI overcomes some of the contamination problems present in NDVI data (e.g., contamination associated with canopy background and residual aerosol influences), and EVI is less likely to become saturated in areas that have high green biomass (Pettorelli et al., 2005).

We used Landscan2016 global population distribution data, which is the finest resolution human population data available. Landscan data represents an “ambient population” (average population distribution over 24 hours; Bright et al., 2017). LandScan data are preferable to other census-based data because they account for differences in spatial data availability, scale and accuracy, and Landscan distribution models are specific to individual countries and regions (Bright et al., 2017). Furthermore, LandScan data as an “ambient population” rather than point density consider both diurnal movements and collective travel habits and integrates these variables into a single measure (Dobson et al., 2000). Other studies have transformed human density data to a gradient-based distance metric that represents geographic distances from densely populated areas (Roever et al., 2013). We assessed both transformed, gradient-based human density and raw LandScan “ambient population” data in our habitat suitability models (Figure 2E). Using raw ambient human population data may better align with a nonlinear relationship in which elephant and human coexistence occurs at a range of human densities, but local absences of elephants are contingent on landscape-dependent thresholds of human density (Hoare and Du Toit, 1999).

#### *Raster preparation for habitat suitability modeling*

MaxEnt requires all environmental layers to have the same resolution and spatial extent. We resampled environmental layers to 900m X 900m (0.0083 x 0.0083 decimal degrees; standardized across environmental data layers) so that resolution represented a biologically relevant scale in view of elephant space use and distribution. The spatial resolution of our layers is informative for a highly mobile species such as elephants (Young et al., 2009b) but is still much smaller than average home range size of elephants (~628km<sup>2</sup> on average for southern African populations; Roever et al., 2012). We used a bilinear interpolation approach that is suitable for continuous data to resample our environmental layers using the “Data management” toolbox in ArcMap (ESRI ©

2011). Bilinear interpolation calculates the value of each pixel by averaging the values of surrounding pixels. We standardized the coordinate system and datum to WGS\_1984 for all input layers and tested for correlation among our environmental variables by calculating Pearson's correlation coefficient in the R package "virtualspecies" (Leroy et al., 2016; R Core Team, 2019)

### *Habitat suitability analysis*

We predicted the potential distribution of elephants using a maximum-entropy (MaxEnt) species distribution modeling approach (Phillips et al., 2006, 2017). MaxEnt has been used extensively to predict the potential distribution of animals and is a widely used software for distribution modeling in conservation studies (Fourcade et al., 2014). MaxEnt moves beyond classical regression methods such as resource selection functions (Boyce and McDonald, 1999; Chetkiewicz and Boyce, 2009) and generalized linear models (Guisan et al., 2002) and employs an algorithmic modeling approach that is based on machine learning (Fourcade et al., 2014). MaxEnt estimates the potential distribution of animals by finding the spatial distribution of maximum entropy (the distribution that is closest to being uniform) when comparing the expected value of each environmental variable under this estimated distribution to the empirical average that has been calculated from the occurrence or telemetry data (Merow et al., 2013). MaxEnt is especially efficient when there is a complex relationship between response and predictor variables (Elith et al., 2011), and MaxEnt has outperformed other modeling approaches to predict animal distribution (Hernandez et al., 2006; Wisz et al., 2008; Shabani et al., 2016).

We used MaxEnt to determine which environments represented suitable habitats for elephants. MaxEnt requires presence-only data to model species distribution and predict habitat suitability (Elith et al., 2011). MaxEnt uses occurrence data points (presences; SI Figure 4A) in combination with a set of environmental predictor variables (e.g., distance to water, slope,

vegetation index, human presence), and compares these presences and their associated environmental constraints to a set of random background points (Merow et al., 2013). MaxEnt then predicts the relative occurrence rate (ROR) for each cell in the landscape grid, where ROR is the relative probability that the cell is contained in the presence data, and where ROR is contingent on selecting the “raw” output option in MaxEnt (Elith et al., 2011).

MaxEnt can also be used to estimate the probability of presence by using a logistic transformation of the ROR that allows for large differences in output values to translate to large differences in suitability. Logistic probability of presences may improve model calibration and are contingent on selecting the “logistic” output option in MaxEnt (Phillips and Dudík, 2008). We only compare map predictions that were generated using the same assumptions to estimate the probability of presence (Merow et al., 2013).

#### *MaxEnt background data*

Choosing relevant background location data for comparison to presence data is critical when the MaxEnt model will be used to predict or extrapolate to novel environments (Elith et al., 2011; Webber et al., 2011). Background data should be chosen to reflect the environmental conditions that are relevant to the species for which the model is generated, and they should be based on the spatial scale of the ecological questions of interest (Saupe et al., 2012; Merow et al., 2013; SI Figure 4). Model fit metrics can be inflated by increasing the number of background points, and by selecting background data that may not be ecologically informative for species distribution modeling (Lobo et al., 2008; Anderson, 2012).

We aimed to delineate landscape connections within and across areas where elephants are known to occur. We were also interested in delineating connections that may not currently fall within the known elephant range, but where future initiatives may aim to conserve these corridors

to re-establish connectivity between isolated populations. We therefore tested two different background datasets: range-based background data generated for areas of known elephant range as demarcated by the IUCN Red List of Threatened Species (SI Figure 4B, Blanc, 2008); and use-based background data from areas included in an 80% convex hull of the presence points (SI Figure 4C). For each of these datasets, we generated 10,000 random points to compare to the presence data.

#### *MaxEnt model regularization*

Model regularization can reduce model complexity and over-fitting (Merow et al., 2013). Regularization may allow for less precise fitting of the empirical constraints from environmental features in the MaxEnt model, and it simplifies models by incorporating a penalty that is proportional to the magnitude of the regularization coefficient (Merow et al 2013). Therefore, using explicit regularization parameters may prevent model complexity from increasing beyond what is supported by the empirical dataset (Phillips and Dudík, 2008). We tested four regularization beta parameters in Maxent ( $\beta = 1, 2, 3, 4$ ), and compared the area under the receiver-operator curve (AUC) values for cross-validated models as a measure of model fit to determine the most suitable beta parameter for our dataset. Regularization parameters were tested for both background datasets (SI Table 4).

#### *Model evaluation*

We evaluated the Maxent models using a 5 k-fold cross validation. We withheld a random sample of 20% of the presence data for testing and trained our model with the remaining 80% of the data. We assessed the evaluated models by investigating the AUC. AUC calculates the probability that a presence location ranks higher than a random background point in the predicted model (Merow et al., 2013). We compared AUC values for both types of background data, where

each type of background data was fitted using  $\beta = 1, 2, 3, 4$  (8 models in total). We selected the best scoring combination of background type and regularization parameter to generate our HSM.

### Supplementary Tables

**SI Table 1.** Marker names, profiles and characteristics<sup>4</sup> of nine microsatellite loci used in this study.

<b>Marker Name</b>	<b>Locus Name</b>	<b>Repeat Motif</b>	<b>Size (bp)</b>	<b>Ta- °C</b>	<b>No of alleles</b>	<b>HO</b>	<b>HE</b>
<b>LaT08<sup>2</sup></b>	1	(TAGA)16	166–234	56	13	0.81955	0.86347
<b>Lat13<sup>1</sup></b>	2	(CATC)21	173–262	56	10	0.62963	0.76649
<b>Lat17<sup>1</sup></b>	3	(GGAT)15... (GGAT)	324–352	56	8	0.71212	0.80626
<b>Lat24<sup>1</sup></b>	4	(GGAT)22	203–231	56	8	0.77953	0.84075
<b>FH1<sup>2</sup></b>	5	(CA)12	81–89	55	6	0.56522	0.61660
<b>FH39<sup>2</sup></b>	6	(CA)18	232–256	60	12	0.63704	0.78441
<b>FH102<sup>2</sup></b>	7	(CT)11(CA)14	175–187	60	6	0.51773	0.49862
<b>LA5<sup>3</sup></b>	8	(CA)13	139–153	52	8	0.56028	0.55996
<b>Lat25<sup>1</sup></b>	9	(CCAT)15	287–321	52	9	0.66923	0.83710
<b>Mean</b>					8.889	0.65448	0.73041
<b>s.d.</b>					2.421	0.10179	0.13554

<sup>1</sup> Comstock et al., 2000

<sup>2</sup> Archie et al., 2003

<sup>3</sup> Eggert et al., 2000

<sup>4</sup> Number of alleles per locus, observed heterozygosity (HO) and expected heterozygosity (HE)

**SI Table 2.** Analysis of molecular variance (AMOVA) of 9 nuclear microsatellites for 142 elephants showed low population differentiation ( $R_{st} = 0.04$ ), where most of the variation (95%) was explained by differences within populations.

<b>SOURCE OF VARIATION</b>	<b>DF</b>	<b>SUM OF SQUARES</b>	<b>ESTIMATED VARIANCE</b>	<b>PERCENTAGE OF VARIATION</b>
<b>AMONG POPULATIONS</b>	16	14132.372	24.196	5%
<b>Within populations</b>	267	133858.051	501.341	95%
<b>Total</b>	283	147990.423	525.537	100%
<b>R<sub>st</sub></b>	0.046			

**SI Table 3.** Calculated MLPE models for three resistance surfaces (linear, slight nonlinear, and pronounced nonlinear transformation of HSM) and four genetic distance response variables ( $D_{PS}$  = 1 minus the proportion of shared alleles;  $GD\_Aldiff$  = genetic distance as the number of allelic differences between two individuals;  $GD\_euc$  = genetic distance as the Euclidean distance among a vector of allele frequencies;  $GD\_TotGD$  = Reynold's genetic distance measure). For each of these resistance surface and genetic distance combinations, we fitted MLPE models that considered as fixed effects geographic Euclidean distance (Geo ED) only, Least-cost path distance (LCP) and Geo ED, and resistance distance (Circuit Theory) and Geo ED, resulting in a comparison of 36 MLPE models in total. Based on AIC, conditional and marginal  $R^2$ , that the model with CT and Geo ED calculated using the pronounced nonlinear HSM transformation is the best predictor across genetic markers.  $D_{PS}$  was used for visualization of gene flow and landscape connections across the landscape (indicated in **boldface**).

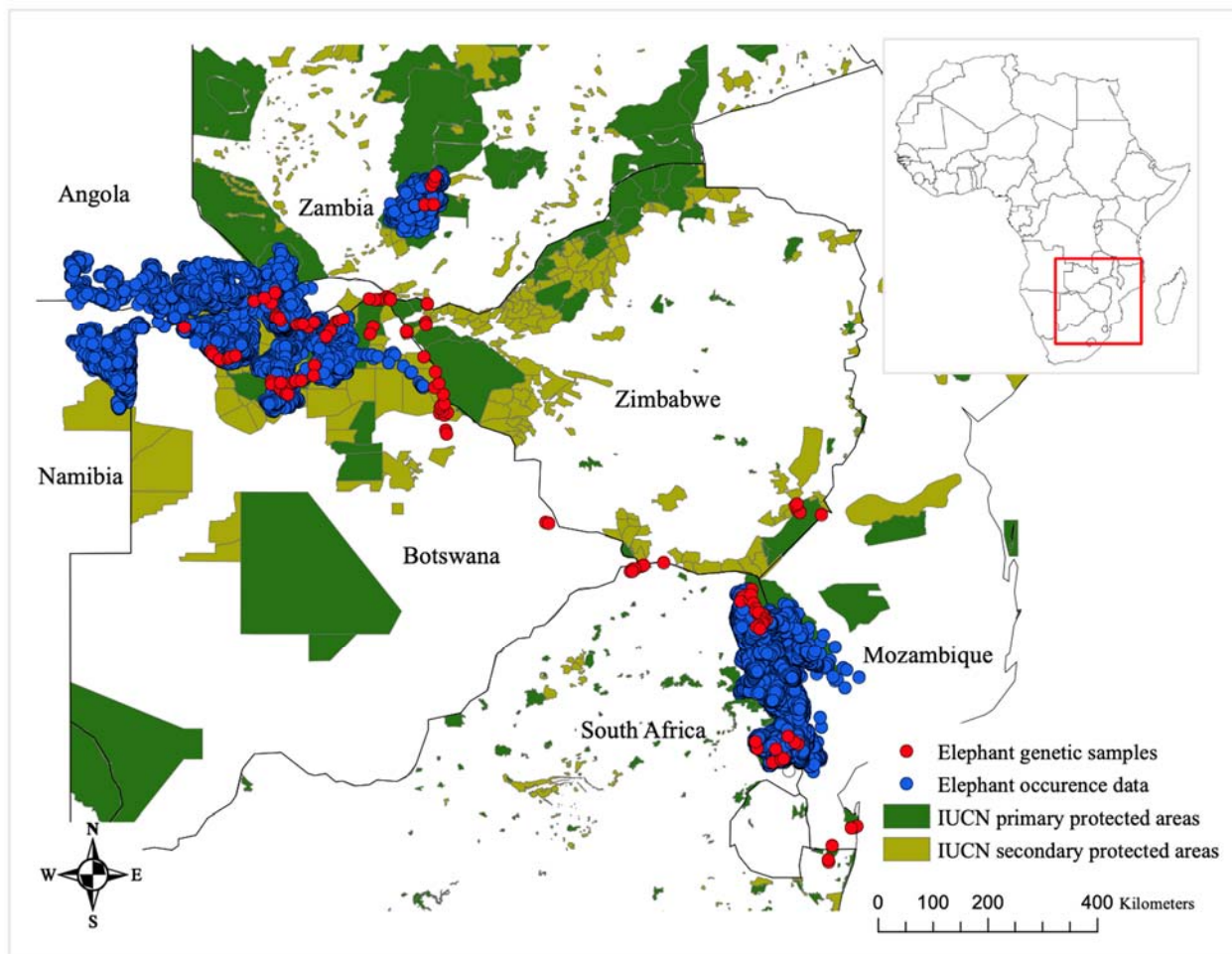
	<i>Linear Transformation</i>			<i>Slight nonlinear transformation</i>			<i>Pronounced nonlinear transformation</i>		
	AIC	R2m	R2c	AIC	R2m	R2c	AIC	R2m	R2c
<i><math>D_{PS} \sim Geo ED</math></i>	-30950.4	0.001	0.099	-30950.4	0.001	0.099	-30950.4	0.001	0.099
<i><math>D_{PS} \sim LCP + Geo ED</math></i>	-30954.4	0.002	0.102	-30953.4	0.002	0.101	-30954.1	0.002	0.102
<i><math>D_{PS} \sim CT + Geo ED</math></i>	-30968.3	0.004	0.103	-30987.4	0.007	0.107	<b>-31006.6</b>	<b>0.010</b>	<b>0.111</b>
<i><math>GD\_Aldiff \sim Geo ED</math></i>	26920.6	0.001	0.099	26920.6	0.001	0.099	26920.6	0.001	0.099
<i><math>GD\_Aldiff \sim LCP + Geo ED</math></i>	26916.6	0.002	0.102	26917.6	0.002	0.101	26916.9	0.002	0.102
<i><math>GD\_Aldiff \sim CT + Geo ED</math></i>	26902.7	0.004	0.103	26883.7	0.007	0.107	26864.4	0.010	0.111
<i><math>GD\_euc \sim Geo ED</math></i>	113.5	0.001	0.095	113.5	0.001	0.095	113.5	0.001	0.095
<i><math>GD\_euc \sim LCP + Geo ED</math></i>	109.5	0.002	0.097	110.6	0.002	0.097	110.0	0.002	0.097
<i><math>GD\_euc \sim CT + Geo ED</math></i>	99.9	0.003	0.098	81.3	0.007	0.107	60.4	0.009	0.106
<i><math>GD\_TotGD \sim Geo ED</math></i>	-46927.4	0.001	0.092	-46927.4	0.001	0.092	-46927.4	0.001	0.092
<i><math>GD\_TotGD \sim LCP + Geo ED</math></i>	-46931.3	0.002	0.094	-46930.2	0.002	0.094	-46930.8	0.002	0.094
<i><math>GD\_TotGD \sim CT + Geo ED</math></i>	-46938.7	0.003	0.094	-46956.8	0.006	0.098	-46978.3	0.009	0.103

**SI Table 4.** MaxEnt models that included background data (n = 10,000) from the entire geographic extent of our study area had the highest area under the receiver-operator curve (AUC), while the range-based background dataset resulted in slightly higher AUC than use-based background dataset.

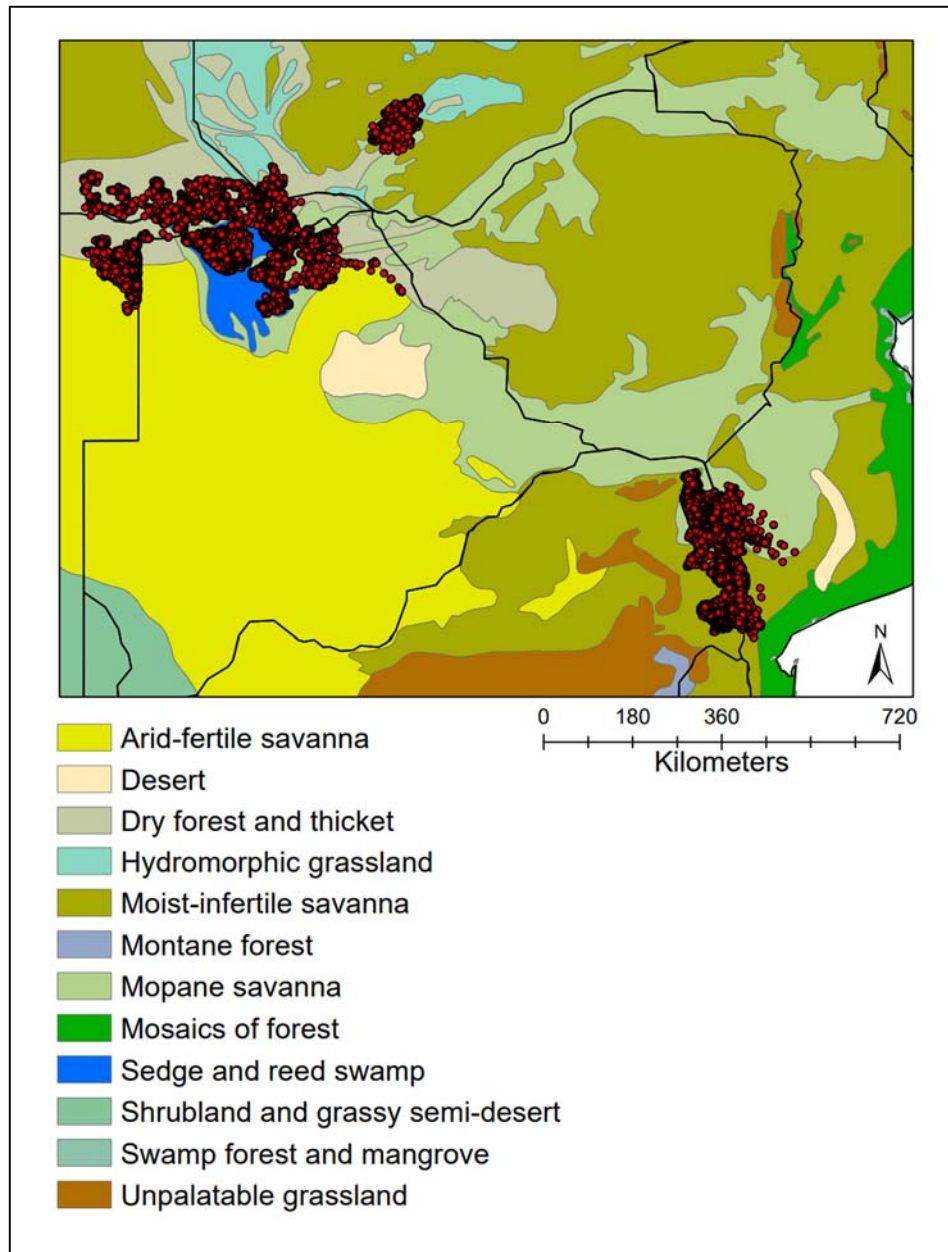
Background data	Maxent regularization parameter	Regularized training gain	AUC
<i>Range-based background data</i> *	$\beta = 1$	0.039	<b>0.786</b>
	$\beta = 2$	0.034	0.781
	$\beta = 3$	0.030	0.775
	$\beta = 4$	0.027	0.764
<i>Use-based background data</i>	$\beta = 1$	0.039	0.758
	$\beta = 2$	0.035	0.755
	$\beta = 3$	0.032	0.751
	$\beta = 4$	0.030	0.745

\*The top MaxEnt model that was calculated using the range-based background dataset and a regularization parameter of  $\beta = 1$  for subsequent analyses because it outperformed the use-based dataset.

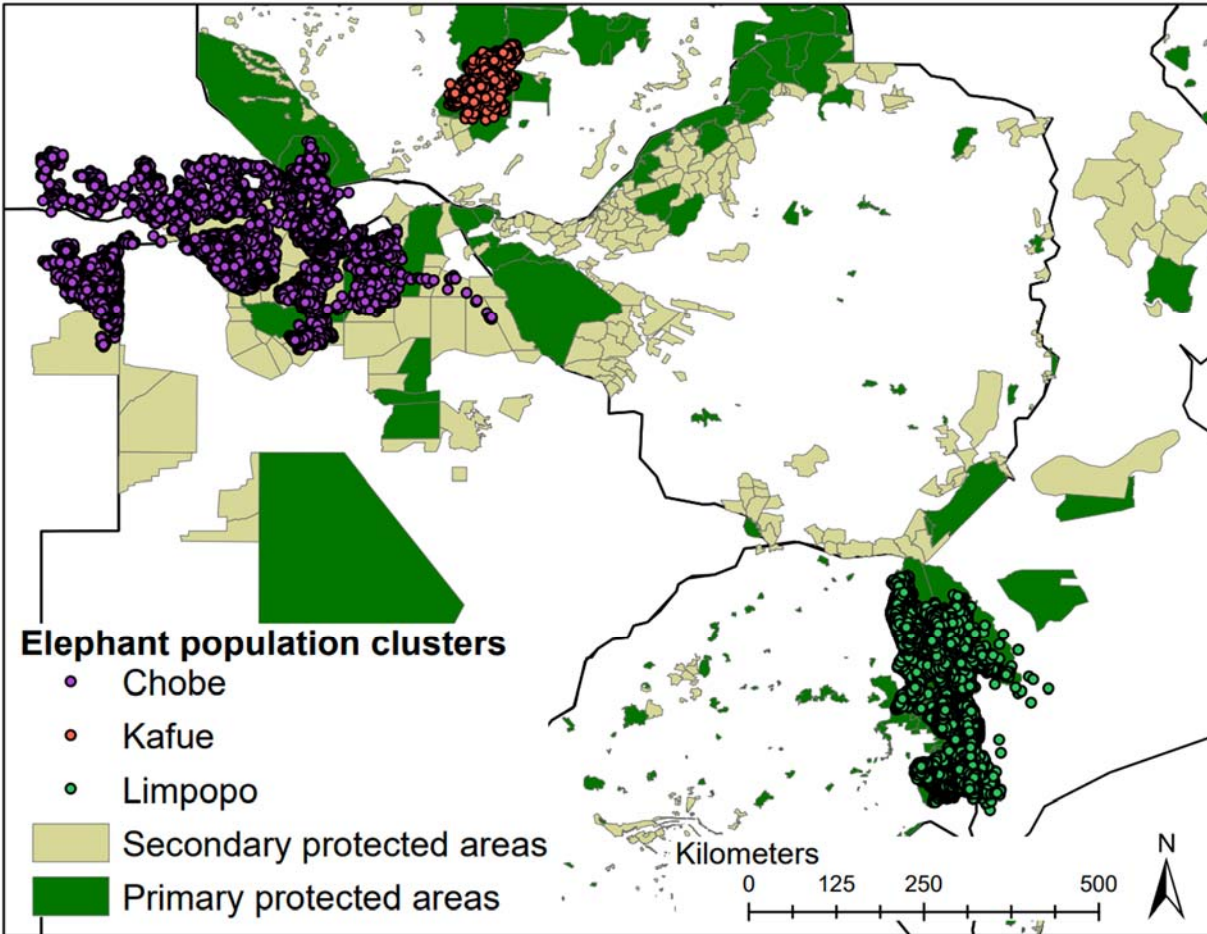
## Supplementary Figures



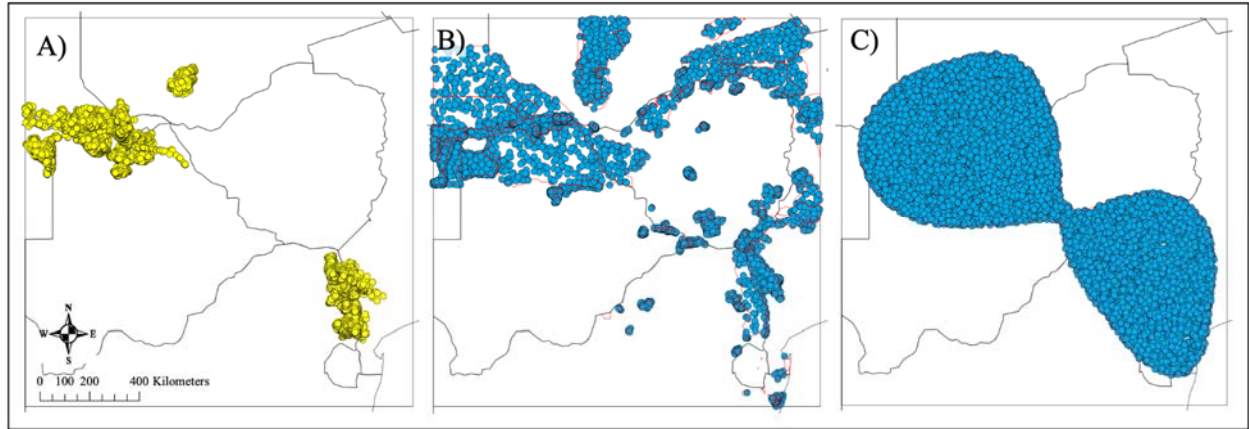
**SI Figure 1.** Map of the study area spanning seven countries across southern Africa, including Angola, Botswana, Mozambique, Namibia, South Africa, Zambia and Zimbabwe. These countries together contain >70% of the number of elephants in Africa and >42% of the total range of elephants in Africa (Thouless et al., 2016). Occurrence data (GPS telemetry points) from 80 elephants are shown in blue, and locations at which genetic samples were collected are shown in red.



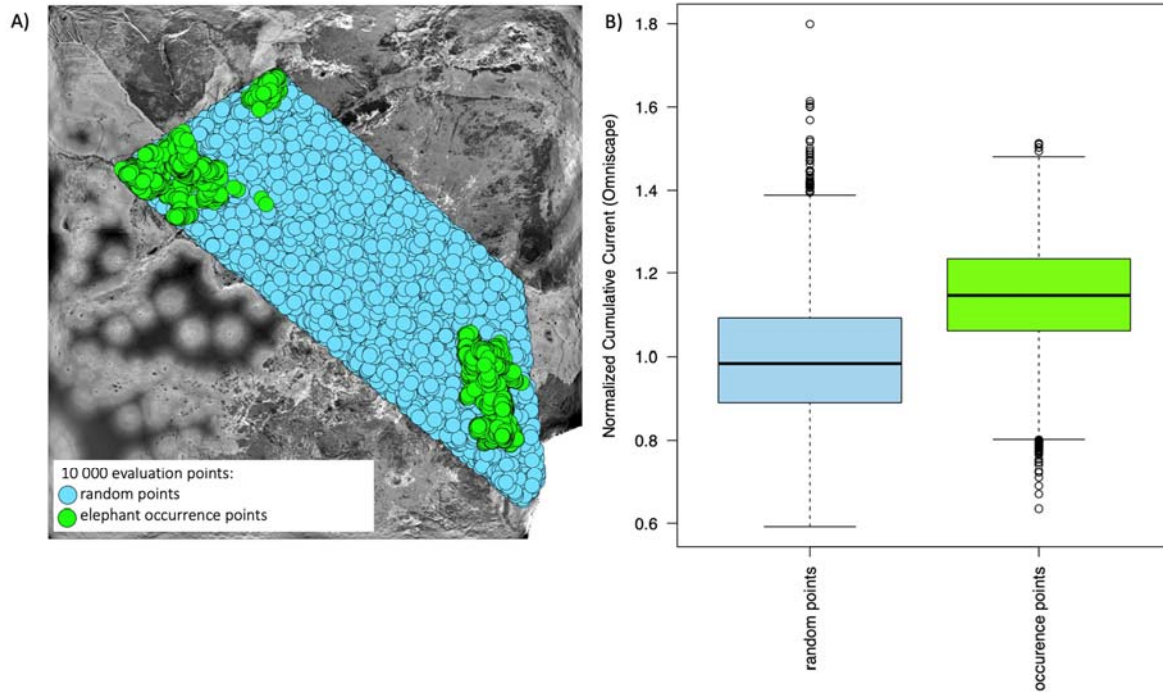
**SI Figure 2.** The study area includes seven Southern African countries (delineated by black lines) namely Angola, Botswana, Mozambique, Namibia, South Africa, Zambia and Zimbabwe. Elephant occurrence data (red dots) spans a range of different vegetation classes (White, 1983) across the study area.



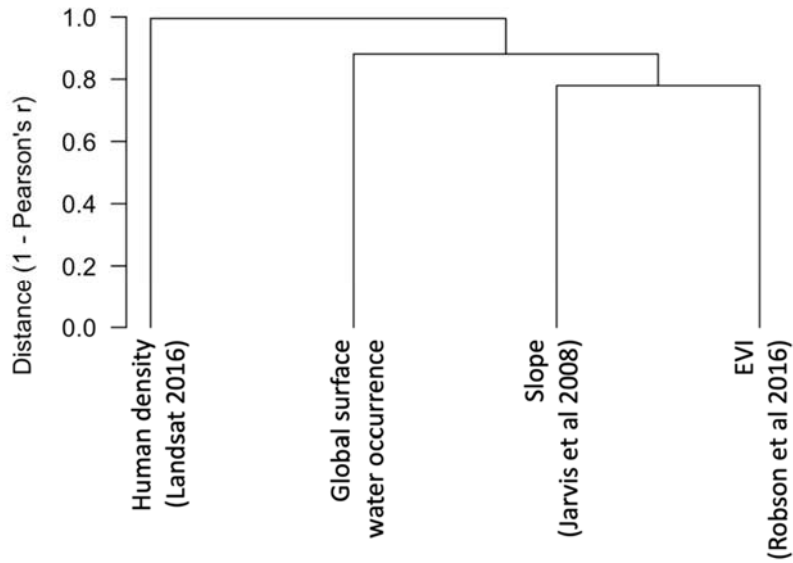
**SI Figure 3.** Spatial location data from 80 elephants, forming part of 3 regional population clusters that include the Chobe, Kafue, and Limpopo elephant population clusters.



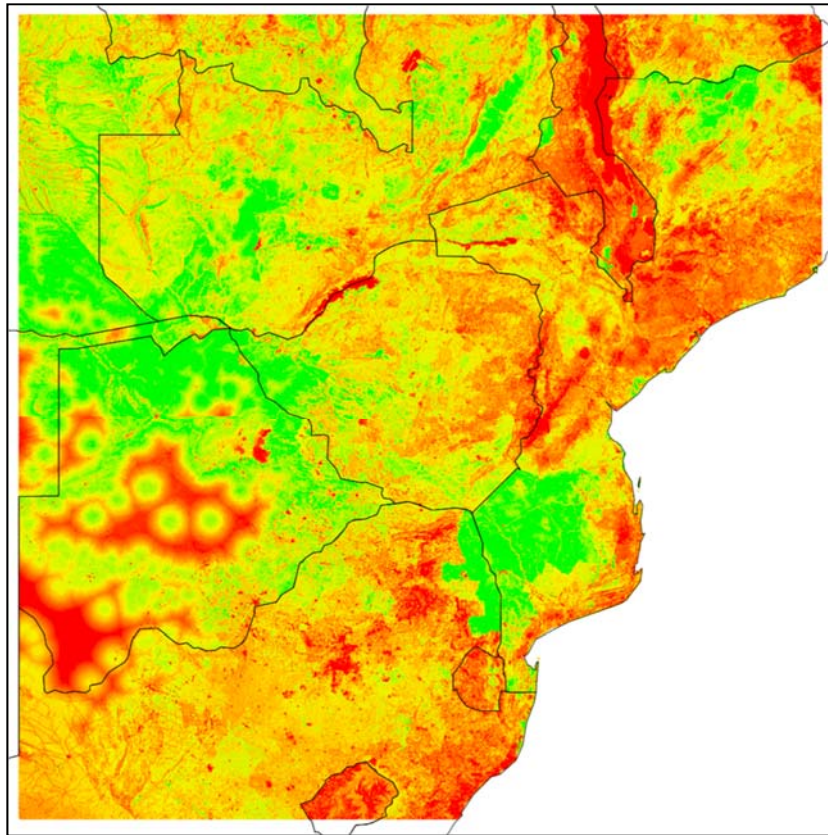
**SI Figure 4.** MaxEnt compares environmental conditions at background location data points to environmental conditions at known presence (occurrence) locations (panel A – yellow points). Background data should reflect the environmental conditions that are relevant to the species for which the model is generated. We tested two different background datasets: background data generated for areas of known elephant range (range-based) as demarcated by the IUCN Red List of Threatened Species (panel B – red lines indicate known range from Blanc, (2008)); and background data from areas included in an 80% convex hull of presence points (panel C – red lines indicate 80% convex hull). For each of these datasets we generated 10 000 random points (shown in blue in panels B and C) to compare to occurrence data.



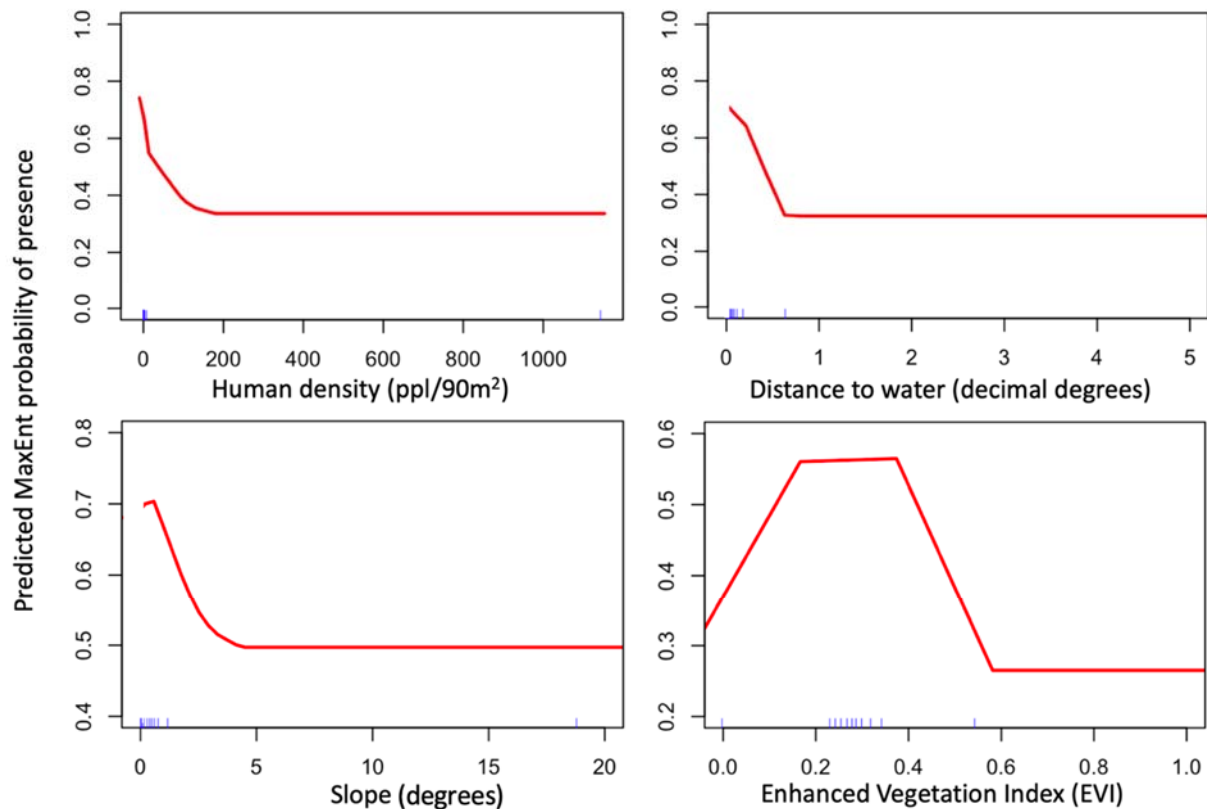
**SI Figure 5.** Omniscape LC map evaluation, which compared Normalized Cumulative Current values at random points (panel A - blue) to values at elephant occurrence points (panel A - green). A two-sample z-test (Kitchens, 2002) showed that the mean Normalized Cumulative Current at elephant occurrence points was significantly higher than the mean at random points ( $z = -78.952$ ,  $p\text{-value} < 0.0001$ , panel B), indicating that the Omniscape landscape connections map has more current, or net random walks at elephant occurrences.



**SI Figure 6.** There was no significant correlation between any of the environmental variables included in the MaxEnt model when using “ambient population” distribution as our human density indicator. We tested Pearson’s R cut-off values of 0.7 (which is the least stringent and allows for most collinearity), 0.6, and 0.5 (the most stringent, presented here) and found no significant collinearity for any of the values.



**SI Figure 7.** The predicted habitat suitability model (HSM) using MaxEnt with range-based background data and a regularization betaparameter of 1. Suitable elephant habitat is shown in green while less suitable habitats are shown in shades of yellow and red.



**SI Figure 8.** Response curves from the top MaxEnt habitat suitability model with human density as “ambient population” presence. Distance to water and slope are suitable for elephants at low environmental values (low human densities, close to water, and habitats with low slopes), and all three of these environmental variables decreased in their habitat suitability until they reached threshold environmental values beyond which they were not suitable habitats for elephants. Intermediate values of primary productivity (Enhanced Vegetation Index) contributed the most to predicted habitat suitability.

### References:

- Anderson, R. P. (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. doi: 10.1111/J.1749-6632.2011.06440.X
- Archie, E. A., Moss, C. J., and Alberts, S. C. (2003). Characterization of tetranucleotide microsatellite loci in the African Savannah Elephant (*Loxodonta africana africana*). *Mol Ecol Notes* 3, 244–246. doi: 10.1046/J.1471-8286.2003.00412.X

- Barnes, R. F. W., Barnes, K. L., Alers, M. P. T., and Blom, A. (1991). Man determines the distribution of elephants in the rain forests of northeastern Gabon. *Afr J Ecol* 29, 54–63.
- Blanc, J. (2008). *Loxodonta africana*. The IUCN Red List of Threatened Species 2008: e.T12392A3339343.
- Boyce, M. S., and McDonald, L. L. (1999). Relating populations to habitats using resource selection functions. *Trends Ecol Evol* 14, 268–272.
- Bright, E. A., Rose, A. N., Urban, M. L., and McKee, J. J. (2017). LandScan 2016.
- Chamaillé-Jammes, S., Valeix, M., and Fritz, H. (2007). Managing heterogeneity in elephant distribution: interactions between elephant population density and surface-water availability. *Journal of Applied Ecology* 44, 625–633.
- Chetkiewicz, C. L. B., and Boyce, M. S. (2009). Use of resource selection functions to identify conservation corridors. *Journal of Applied Ecology* 46, 1036–1047. doi: 10.1111/j.1365-2664.2009.01686.x
- Comstock, K. E., Wasser, S. K., and Ostrander, E. A. (2000). Polymorphic microsatellite DNA loci identified in the African elephant (*Loxodonta africana*). *Mol Ecol* 9, 1004–1006. doi: 10.1046/J.1365-294X.2000.00939-8.X
- Dobson, J. E., Bright, E. A., Coleman, P. R., Durfee, R. C., and Worley, B. A. (2000). LandScan: a global population database for estimating populations at risk. *Photogramm Eng Remote Sensing* 66, 849–857.
- Eggert, L. S., Ramakrishnan, U., Mundy, N. I., and Woodruff, D. S. (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, S. J., Hastie, T., Dudík, M., Chee, Y. E., and Yates, C. J. (2011). A statistical explanation of MaxEnt for ecologists. *Divers Distrib* 17, 43–57.
- Fourcade, Y., Engler, J. O., Rödder, D., and 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.
- Guisan, A., Edwards Jr, T. C., and Hastie, T. (2002). Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecol Modell* 157, 89–100.
- Hernandez, P. A., Graham, C. H., Master, L. L., and Albert, D. L. (2006). The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography* 29, 773–785.
- Hoare, R. E., and Du Toit, J. T. (1999). Coexistence between people and elephants in African savannas. *Conservation Biology* 13, 633–639.
- Jarvis, A., Reuter, H. I., 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>).
- Leroy, B., Meynard, C. N., Bellard, C., and Curchamp, F. (2016). virtualspecies, an R package to generate virtual species distributions. *Ecography* 39, 599–607.
- Loarie, S. R., van Aarde, R. J., and Pimm, S. L. (2009). Fences and artificial water affect African savannah elephant movement patterns. *Biol Conserv* 142, 3086–3098.
- Lobo, J. M., Jiménez-Valverde, A., and Real, R. (2008). AUC: a misleading measure of the performance of predictive distribution models. *Global ecology and Biogeography* 17, 145–151.
- Merow, C., Smith, M. J., and Silander Jr, J. A. (2013). A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography* 36, 1058–1069.

- Pekel, J.-F., Cottam, A., Gorelick, N., and Belward, A. S. (2016). High-resolution mapping of global surface water and its long-term changes. *Nature* 540, 418–422.
- Pettorelli, N., Vik, J. O., Mysterud, A., Gaillard, J.-M., Tucker, C. J., and Stenseth, N. C. (2005). Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends Ecol Evol* 20, 503–510.
- Phillips, S. J., Anderson, R. P., and Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. *Ecol Modell* 190, 231–259.
- Phillips, S. J., and Dudík, M. (2008). Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* 31, 161–175.
- Phillips, S. J., Dudík, M., and Schapire, R. E. (2017). Maxent software for modeling species niches and distributions (Version 3.4. 1). *Biodiversity Informatics*.
- 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.
- Robson, A. S., Trimble, M. J., Purdon, A., Young-Overton, K. D., Pimm, S. L., and van Aarde, R. J. (2017). Savanna elephant numbers are only a quarter of their expected values. *PLoS One* 12, e0175942.
- Roever, C. L., Van Aarde, R. J., and Leggett, K. (2012). Functional responses in the habitat selection of a generalist mega-herbivore, the African savannah elephant. *Ecography* 35, 972–982.
- Roever, C. L., van Aarde, R. J., and Leggett, K. (2013). Functional connectivity within conservation networks: Delineating corridors for African elephants. *Biol Conserv* 157, 128–135.
- Saupe, E. E., Barve, V., Myers, C. E., Soberón, J., Barve, N., Hensz, C. M., 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.
- Shabani, F., Kumar, L., and 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.
- Thouless, C., Dublin, H. T., Blanc, J. J., Skinner, D. P., Daniel, T. E., Taylor, R. D., et al. (2016). African elephant status report 2016. *Occasional Paper Series of the IUCN Species Survival Commission* 60.
- Wall, J., Douglas-Hamilton, I., and Vollrath, F. (2006). Elephants avoid costly mountaineering. *Current Biology* 16, R527–R529.
- Webber, B. L., Yates, C. J., Le Maitre, D. C., Scott, J. K., Kriticos, D. J., 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.
- White, F. (1983). *The vegetation of Africa: a descriptive memoir to accompany the UNESCO/AETFAT/UNSO vegetation map of Africa by F White.*, Natural Re. Unesco, Paris.
- Wisz, M. S., Hijmans, R. J., Li, J., Peterson, A. T., Graham, C. H., Guisan, A., et al. (2008). Effects of sample size on the performance of species distribution models. *Divers Distrib* 14, 763–773.
- Young, K. D., Ferreira, S. M., and Van Aarde, R. J. (2009a). Elephant spatial use in wet and dry savannas of southern Africa. *J Zool* 278, 189–205.

Young, K. D., Ferreira, S. M., and van Aarde, R. J. (2009b). The influence of increasing population size and vegetation productivity on elephant distribution in the Kruger National Park. *Austral Ecol* 34, 329–342.