Coupling African elephant movement and habitat modeling for landscape availability-suitability-connectivity assessment in Kruger National Park

Article *in* Pachyderm · June 2017

Wenjing Xu
University of California, Berkeley

Richard A Fayrer-Hosken
San Diego Zoo

Marguerite Madden
University of Georgia

Lan Mu
University of Northern Iowa

Coupling African elephant movement and habitat modeling for landscape availability-suitability-connectivity assessment in Kruger National Park

Wenjing Xu[1], Richard Fayrer-Hosken[2], Marguerite Madden[3], Chenay Simms[4], Lan Mu[3] and Andrea Presotto[5]*

[1]Department of Environmental Science, Policy, and Management, University of California-Berkeley, 130 Hilgard Way, 94720 Berkeley, CA, USA
[2]San Diego Zoo, San Diego Zoo Institute for Conservation Research, 15600 San Pasqual Valley Road, Escondido CA 92027, USA
[3]Department of Geography, University of Georgia, 210 Field Street 30602, Athens, GA
[4]SANParks Scientific Services, Kruger National Park
[5]Department of Geography and Geosciences, Salisbury University, 1101 Camden Ave. 21801, Salisbury, MD, USA
*corresponding author: richardfh@me.com

Abstract

Making an appropriate conservation decision often requires understanding the functional connectivity of the landscape for focal species. Graph theory and continuous surface methods have become powerful tools to quantify landscape connectivity for animal movement. However, a key limitation of these methods is the use of thresholding to define either habitat patches or links between patches.

We explore how to incorporate African elephants' (*Loxodonta africana*) movement data into an "Availability-Suitability-Connectivity (ASC)" framework which integrates habitat suitability modeling and graph-based network analysis, and how to implement connectivity results to inform conservation management that addresses locally intensive habitat utilization by elephants. In our ASC analysis, node availability was identified by satellite imagery classification and node suitability was estimated by MaxEnt model. Links were determined by effective movement between nodes in three days. Differences of Integrative Index of Connectivity (dIIC) and its fractions were calculated to prioritize patch importance, which were then used for mapping an example landscape management zones to reduce elephant local ecological impact. In total, 544 nodes and 1345 links were identified in the landscape graph. Although suitable nodes were spread across the landscape, elephants intensively used habitat at the central area. Our zone map demonstrates areas for landscape management that can facilitate elephant range expansion. The integrative framework quantified the ASC interactions between animal movement and landscape features. The results highlight the potential for coupling geographic and ecological methods to effectively identify and focus conservation efforts.

Résumé

Prendre une décision de conservation appropriée demande souvent une compréhension de la connectivité fonctionnelle du paysage pour l'espèce en question. La théorie graphique et les méthodes de surface continue sont devenues des outils puissants capables de quantifier la connectivité du paysage pour le mouvement des animaux. Cependant, une limitation de ces méthodes est l'utilisation de l'indexation pour définir les petites zones d'habitat ou les liens entre ces zones. Nous explorons comment l'on peut inclure les données sur le mouvement des éléphants africains (*Loxodonta africana*) dans un cadre de "Disponibilité-Pertinence-Connectivité (DPC)" qui intègre la modélisation qui mesure si l'habitat est convenable avec une analyse du réseau graphique et comment l'on peut mettre en œuvre les résultats de connectivité pour influencer les gestionnaires de la conservation qui s'occupent de l'utilisation intensive de l'habitat par les éléphants. Dans notre analyse DPC, la disponibilité nodale a été identifiée par la classification d'imagerie satellitaire et la pertinence nodale a été estimée par le model MaxEnt. Des liens ont été déterminés par le mouvement effectif entre les nœuds en 3 jours. Les différences des Indices Intégratifs de Connectivité et ses fractions ont été calculées pour prioriser l'importance des zones ce qui a été par la suite utilisé pour cartographier un exemple des zones de gestion du paysage afin de réduire l'impact local et écologique des éléphants. En tout, 544 nœuds et 1345 liens ont été identifiés sur le graphique du paysage. Même si des noeuds étaient répartis à travers le paysage, les éléphants utilisaient surtout l'habitat dans la zone centrale. Notre carte des zones montre des endroits pour la gestion du paysage qui pourraient faciliter l'agrandissement de l'habitat des éléphants. Le cadre intégratif a quantifié les interactions DPC entre le mouvement des animaux et les caractéristiques du paysage. Les résultats mettent en lumière le potentiel de combiner les méthodes géographique et écologique afin d'identifier et focaliser de façon efficace les efforts de conservation.

Introduction

Landscape functional connectivity, or the degree to which the spatial arrangement of landscape elements facilitates or obstructs movement and other ecological flows of species, is a prime concern when making conservation decisions for a focal species (Saura and Rubio, 2010). It is of special importance when resources are patchily distributed (Lookingbill, 2010) and can provide an experimental framework for landscape-level conservation management, such as sensitive area detection and impact assessment (Urban et al., 2009). Two types of models are commonly used to calculate connectivity: discrete models such as graph-based habitat networks analysis and continuous models based on resistance surface such as ecological circuits (Urban et al., 2009,; McRae et al., 2008).

A landscape graph is a representation of functional connectivity in which the landscape is classified as either habitat nodes or non-habitat matrix and in which connectivity is depicted by links between nodes (Galpern et al., 2011). It is able to combine landscape patterns and species biology to examine process-based connections with very little data. It also takes advantage of efficient computational algorithms that originated from mathematics and computer science (Urban and Keitt 2001; Moilanen, 2011). As powerful as they are, these models are commonly limited by binary classifications of habitat patches (nodes) and universal thresholds (critical dispersal distance) in identifying links (Galpern et al., 2011; Moilanen, 2011). However, habitat quality continuously varies across landscape. In fact, classification of the landscape to habitat and non-habitat is a fundamental limitation in analysis of heterogeneous landscape (Chetkiewicz et al., 2006). Additionally, organisms are expected to alter their movements according to dynamic habitat attributes (Lookingbill et al., 2010). Applying thresholds in the process of defining habitat patches or links between them could be inappropriate for connectivity analysis and may result in the loss of information (Moilanen, 2011).

On the other hand, continuous resistance surface-based models depict landscape using resistance values to reflect the hypothesized ease of movement of individuals (McRae et al., 2008). It is the most commonly used type of explicit connectivity modeling and it is sufficiently flexible to incorporate heterogeneous landscape information (Zeller et al., 2012). Nevertheless, the biggest challenge of calculating resistance surfaces is assigning resistance values to different landscape features (Spear et al., 2010). Since resistance is based on relationships between landscape variables and underlying biological functions such as relative abundance, researchers commonly equate resistance to the inverse of habitat preferences (LaRue and Nielsen, 2008). However, movement through the landscape is not necessarily equal to habitat suitability, and animal movement is often condition-dependent (Lookingbill et al., 2010). Incorporating actual or simulated movement data is one improvement to the performance of surface-based connectivity models, so long as they are not deteriorated by the computational demands of analyzing movement paths compounded with raster-based landscape surface (Zeller et al., 2012).

Both types of connectivity models have their merits and limitations, and a combination of them is valuable for landscape connectivity examination. Decout et al. (2012) combined graph-theoretical and surface-based connectivity analysis to achieve an "Availability-Suitability-Connectivity (ASC)" landscape assessment. In this framework, habitat availability and suitability influence how animals move through the landscape, and in turn determines how we quantify and analyze connectivity for animal movement. When integrating habitat attributes with corresponding functional processes, movement data in our case, landscape connectivity measures can efficiently analyze ecological networks, landscape, and habitats (Saura and Rubio 2010; Decout et al., 2012). The framework maintains variances among habitat patches, offers straightforward connectivity visualization, and conducts efficient connectivity computation. Nevertheless, the thresholding applied when quantifying links in the landscape network is still a key issue (Decout et al., 2012).

We demonstrate how to incorporate movement data instead of using a threshold for ASC examination. We employed this method to examine connectivity for African elephant (*Loxodonta africana*) movement in Kruger National Park (KNP), South Africa. Landscape conditions are critical for the movement efficiency of elephants, which may in turn impact landscape conditions (Codron et al., 2006). Manipulation of limiting resources for elephant distribution in landscape has been proposed with the objective to increase connectivity, promote dispersal, and thus reduce local impacts on vegetation (Owen-Smith 1996). Understanding of the interplay between elephant movement and landscape conditions is valuable for identifying locations to focus management efforts (Owen-Smith et al., 2006). Here, we integrated individual GPS recordings for a systematic assessment of habitat availability, suitability, and connectivity. We quantified connectivity and demonstrated how the ASC results can inform conservation zone planning. This study highlights the potential of coupling geographic and ecological data and methods to guide effective conservation practices.

Methods

Study Site and Data Description

Kruger National Park is located in the northeast portion of South Africa, with a total area of 19,485 km^2 (Figure 1; see next page: 100). It was proclaimed as a National Park in 1926 and is one of the largest wildlife sanctuaries in the world. KNP is a part of the "lowveld" savanna with distinct wet and dry seasons and is located at an altitude varying from 200 m to 840 m (Codron et al., 2006). As a protected enclosed area, the differences in climate and geology result in a variety of landscapes across the park. The climate type in KNP varies from tropical to subtropical, with a range of average annual precipitation from 401 mm to 600 mm. This highly diverse landscape provides diverse resources for many species which differing requirements and are patchily distributed within 16 ecozones classified by dominant vegetation types (Crooks and Sanjayan, 2006).

Hourly geographic coordinates from October 1998 to February 1999 were collected from three female elephants using GPS collars by Lotek fish and wildlife monitoring system. Three of four were in completely separate herds and two co-matriarchs were in the same herd representing their collective movements. No bulls were collared. Data were saved cumulatively in the random access memory of the GPS units, including individual ID, geographic coordinates, position accuracy, time, and ambient temperature (Fayrer-Hosken et al., 1997). The GPS collars generated 6,527 geographic coordinates in total. The home range of the females was defined as our area of interest using a minimum convex hull to incorporate all GPS records. The resulting study area is 6073 km^2. This focal region primarily covers two ecozones: Sabie/Crocodile Thorn Thickets, and Mixed Bushwillow Woodlands.

Vector data of KNP, including landscape types, vegetation, rivers, water holes (including bore holes and concrete dams), tourist sites, and roads were provided by the South Africa National Parks Scientific Services (SANSPark). Landsat 7 Enhanced Thematic Mapper Plus (ETM+) imagery of December 1999 was used to extract woodland from the rest of the landscape. The year 1999 was dryer than average (Presotto, 2015), thus it is a relatively conservative estimate of woodland extent.

Constructing the Landscape Graph

We adapted ASC assessment to comprehensively describe landscape conditions. The workflow to construct landscape networks can be described as: 1) identify resource patches as nodes based on land-cover classification; 2) determine patch suitability by MaxEnt habitat suitability modeling; and 3) determine links connecting nodes by elephant movement.

Node Availability

Woodland, defined as open canopy forest, provides both diet and daily activity sites (e.g. resting) for elephants in open savanna such as KNP (Codron et al., 2006; Harris et al., 2008). Though elephants eat both grass and tree leaves and the literature are divided on the relative diet proportions, there seems to be more support for larger trees being preferred. Thus location of woodland patches

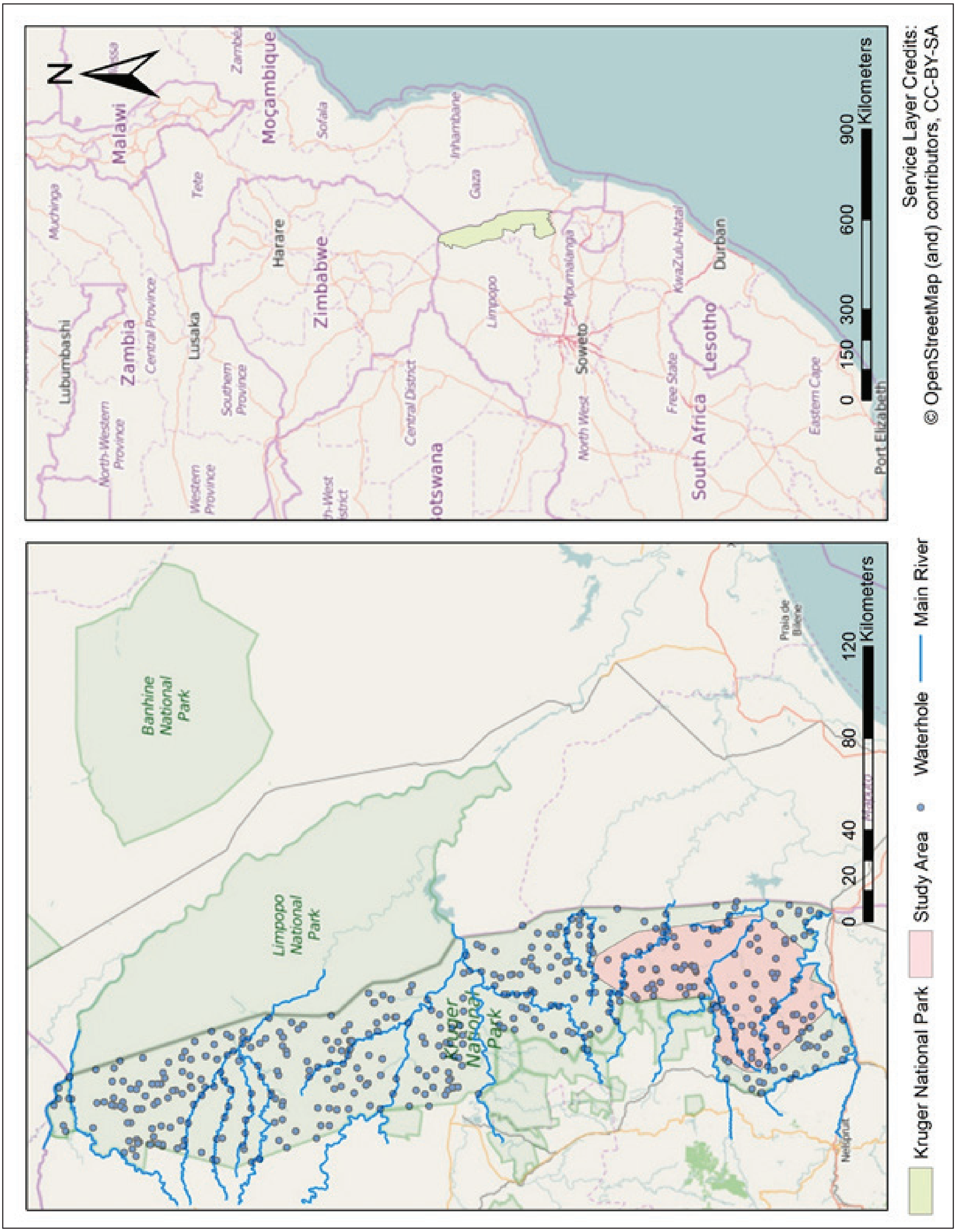

Figure 1. KNP (green shade) and location of the study area (pink shade) and its relative locations in South Africa.

were used to determine nodes. We performed supervised classification of a Landsat 7 satellite image in ArcGIS 10.2 using a maximum likelihood algorithm and classified the landscape into 5 classes: Grassland, Mixed Vegetation, Woodland, Bare soil, and Water. High spatial resolution imagery from Google Earth was used as a reference for the selection of training data for the five classes. The signature (or spectral mean of reflectance values) of the training areas were then used to assign pixel classes to the entire image scene. We then extracted woodland pixels from the rest of the landscape. After aggregating adjacent woodland pixels into patches, the centroids of patches with area larger than 0.1 km^2 were considered as available nodes in the landscape network.

Node Suitability

We used habitat suitability to describe node quality. The MaxEnt approach was implemented to generate a suitability map across the landscape using the freely available MaxEnt software 3.3.3k (Phillips et al., 2006). MaxEnt is a species distribution model based on relations between habitat environmental variables and animal presence/background locations. It is one of the most commonly used species distribution models for habitat analysis in last recent decade. The output raster map denotes species occurrence probability and is proportionate to habitat suitability for the species (Decout et al., 2012). Node suitability was calculated as the average pixel suitability within a patch.

In order to reduce the effect of spatial and temporal correlation, we extracted the GPS location at 20.00 hrs every day from the total elephant record pool. This subset of 532 GPS records was used as input occurrence points into the MaxEnt model. The time 20.00 hrs was selected because it had the most complete data record across the study period. Environmental predictors related to the ecological requirement of elephants in MaxEnt are summarized in Table 1. All the predictor raster layers had a pixel resolution of 30x30 meters. A total of 75% of these points were used as training data for MaxEnt model construction, and the remaining 25% were used as test data for model assessment. We generated 10,000 random background points and averaged 50 replicates in the construction of the MaxEnt model. The final model was selected according to the Receiver Operating Characteristic analysis and omission rate as well as tenth percentile training presence cut-off values (Phillips et al., 2006).

Determination of Links

Connectivity can be regarded as a global property approximating the number of effective movements occurring among patches. In most cases links between patches are determined by patch distance relative to the upper limit of an animal's movement ability. For African elephants, who have large home ranges varying from 15 to 3,700 km^2 and high mobility, all of the patches throughout the landscape of the study area can be considered linked, making distance an inappropriate proxy.

The longest distance across the study area from south to north is 106 km. Since elephants can travel up to 30

Table 1. Environmental variables in MaxEnt and their contributions to the model.

Environmental variables	Type	Contribution to overall model
Elevation	Continuous	36.4%
Landscape type	Categorical	17.5%
Distance to main rivers	Continuous	13.9%
Distance to tourist sites	Continuous	11.2%
Distance to woodland patches	Continuous	5.5%
Distance to roads	Continuous	5.0%
Distance to bore holes	Continuous	4.1%
Distance to seasonal rivers	Continuous	3.4%
Distance to concrete dams	Continuous	3.0%

km in a single day (Presotto, 2015), it is possible for an elephant to cross the entirety of the study area in an efficient manner in about three days. We used movement efficiency, measured as travel time, as a proxy for links between patches. We considered no links to exist if an elephant did not travel between patches in the same amount of time that it could cross the whole study area. We applied this criterion by assigning the time of GPS points as a time stamp to the underlying patches. We then calculated temporal differences for all pairs of patches and created links between corresponding nodes if the difference was less than three days.

The final constructed landscape network consisted of nodes representing woodland patch availability with suitability as an attribute and links representing at most three days of traveling between these nodes.

Graph Analysis

We performed connectivity analysis based on graph theory, including landscape-level and patch-level assessments. For landscape-level analysis, we calculated the numerator of Integral Index of Connectivity IIC (Pascual-Hortal and Saura, 2006). Numerators of IIC for all patches in a landscape are able to take into account purely topological features with ecological attributes of landscape elements and thus this index is able to perform as an efficient indicator for connectivity formed by the node availability and suitability. It is given by:

$$IIC_{num} = \sum_{i=1}^{n}\sum_{j=j}^{n}\frac{(a_i a_j)}{1 + nl_{ij}}$$

Equation 2.1

where a_i is the suitability of nodes and nl_{ij} is the number of links between patch *i* and *j*.

At the patch level, we used Degree, and the difference in the *IIC (dIIC)* in order to quantify importance of structures for landscape connectivity within the graph network. Degree is a measure of the number of adjacent nodes connected to a specific node. The Σ values for each node were calculated by removing each node in turn and measuring the difference in the IIC for the landscape (Pascual-Hortal and Saura 2006):

$$dIIC\,(\%) = 100\,\frac{(IIC - IIC_{\mathrm{remove}})}{IIC}$$

Equation 2.2

This index indicates the relative ranking of each patch/node by measuring their capacity to maintain the overall landscape connectivity. Under the ASC framework, this index regards nodes as connectivity providers in terms of resources availability and habitat suitability.

We also calculated partitioned *dIIC* to evaluate different contributions made by individual patches: $dIIC_{intra\text{-}k}$, $dIIC_{flux\text{-}k}$, and $dIIC_{connector\text{-}k}$ (Saura and Rubio, 2010). The $dIIC_{intra}$ value is the contribution of node *k* considering its intra-patch connectivity, or the overall node attribute (in this case suitability) that is provided by node *k*. The $dIIC_{flux}$ value measures how well node *k* is connected to other nodes in the landscape, which is directly related to the number of links node *k* contains. A high $dIIC_{flux}$ value thus shows areas intensively visited by elephants. Finally, $dIIC_{connector}$ measures how important that node is for maintaining connectivity between the remaining nodes.

Landscape Zonation

In order to demonstrate how ASC can inform landscape management, we conducted zonation to prioritize regions that can promote elephant dispersal under proper landscape management. While we are aware that the movement data from only three females may not be able to show population traits, our purpose was to demonstrate the utility of the ASC framework for management planning.

For each of the three *dIIC* fractions, we extracted nodes with the highest 10% values. We then conducted a kernel density analysis and took the 90% kernel areas to convert the nodes into rasterized surface with raster value of 1, which shows nodes density. With the objective to encourage elephant dispersal from intensively-used habitat to other suitable habitat, we applied an equation to generate a surface which shows levels of importance (L) for landscape management efforts:

$$L = dIIC_{\mathrm{connector}} + dIIc_{\mathrm{intra}} - dIIC_{\mathrm{flux}}$$

Equation 2.3

L therefore ranged from -1 to 2. This calculation highlights regions that are both suitable (with high $dIIC_{intra}$) and able to maintain connectivity among nodes (high $dIIC_{connector}$). In contrast, areas containing nodes currently heavily used would generate less importance for connectivity management. We excluded regions with L smaller than 1 and defined regions with L equal to 2 as Core Zone and those with L equal to 1 as Buffer Zone.

The graph was constructed using Python code and can be obtained from the author upon request. Graph indices were calculated using Conefor Sensinode 2.2 and R (Saura and Torne, 2009; R-Core-Team, 2013). Mapping and statistical analysis of the retrieved patch attributions were carried out in ArcGIS 10.2 by either pre-coded functions or customized Python programming.

Results

We classified the Landsat-7 image and generated 554 patches as available nodes in the study area (Figure 2A; see colour plates: page v). Patch area ranged from 0.1 km^2 to 45 km^2, with an average of 1.02 km^2. Once overlaid with patches, nodes clearly denote the locations of woodland patches (Figure 2B; see colour plates: page v). According to the Area Under the Curve (AUC) model assessment value, the MaxEnt model revealed a habitat suitability model with an average discriminative capacity of 75.0%. The environmental variables included are listed in Table 1 in order of contribution to the model. Figure 2C (See colour plates: page v) shows habitat suitability in the study area, where the variance of suitability values across the study area reflects the heterogeneity of the landscape. The areas with high suitability values are generally concurrent with woodland patches and the river system in KNP. Elephants generally did not visit area with low suitability (Figure 2D; see colour plates: page v).

In our landscape network, which demonstrates the "ASC" pattern (Figure 3A; see colour plates: page v), there are 1345 links connecting the 554 nodes with the Degree value of nodes ranging from 0 to 65. According to the map, most of the nodes with high Degree values also have relatively high suitability values. The average suitability of nodes with the top 10% Degree values is 0.55 while the average suitability of all nodes is 0.34. Though some nodes with low suitability may also be well connected, nodes that are physically far from each other are not necessarily isolated (Figure 3B; see colour plates: page v). The node 'i' denoted in Figure 3B is an example of a node that functions like a "bridge", connecting two groups of nodes that are far from each other. Based on movement records from the three elephants, there are 398 isolated nodes. Most of these are located around the central area and are not included in the movement range of the elephants. If all of the unconnected single nodes are omitted, the remaining nodes can be lumped into four graph components (all nodes are connected within the same component but are not connected to nodes from other components). The largest component contained 148 nodes, while the smallest contains only 2. Figure 3C (See colour plates: page v) provide an example of an isolated component (ii) in the south of the study area.

The landscape level IIC is equal to 711.7, which was later used to calculate node importance *dIIC* at patch-level (Figure 4B; see colour plates: page vi). Nodes with high *dIIC* values are concentrated at the center, similarly to nodes with high Degree values. On the contrary, partitioning *dIIC* into three fractions allows for a more detailed evaluation of the differential contributions to landscape connectivity by various nodes. Figure 5A, B, C (See colour plates: page vi) show the nodes with the top 10% values for each of the three fractions of *dIIC*. Nodes with $dIIC_{intra}$ are distributed more evenly compared with the other two dIIC fractions. Figure 5B (See colour plates: page vi) shows that nodes with high $dIIC_{connector}$, those that are well connected to other patches, gather at the center of the study area, indicating the core area of the home range of the three females. However, the nodes most important for maintaining connections among other nodes extended to the north and south part of the area rather than clustered in the center.

The conservation zonation mapping based on the three *dIIC* fractions evaluates landscape management priority across the study area (Figure 5; see colour plates: page vi). Core zone mostly locates along the edge of the high $dIIC_{flux}$ area, indicating areas important to maintain connectivity between the central study areas and the marginal areas. Habitat maintenance for these areas can encourage elephant inter-patch movement thus to relieve pressures on the intensively used areas (high $dIIC_{flux}$ area). The buffer zone in Figure 5D (See colour plates: page vi) indicates areas that would be used by elephants more frequently after expanding their inter-patch movement.

Discussion

This study demonstrates a methodology that combines ground-based observations, remotely sensed as well as modeled habitat suitability information, and an operational graph-based analysis to assist conservation planning. Though wildlife-tracking techniques have developed rapidly in recent years, few studies have directly used such ground-based observations for connectivity analysis or modeling. This ASC framework based on movement data used in our study integrates the better parts from both continuous and binominal connectivity models. It 1) contains landscape heterogeneity information in connectivity analysis; 2) applies well-established graph-based connectivity indices for quantifying connectivity; and 3) utilizes actual animal movement data instead of a subjective thresholding process.

The ACS framework makes it possible to geospatially visualize and quantify the relationship between different landscape attributes, namely resource availability, patch suitability, and landscape connectivity. First, resource availability is measured by remote sensing imagery analysis; it is later used to define nodes in landscape graph. Second, patch suitability evaluated by the MaxEnt model varies across the study area, revealing a heterogeneous landscape (Figure 2; see colour plates: page v). Finally, both the availability and suitability information contribute in quantifying connectivity by involving in calculating *dIIC* and its fractions.

It is commonly assumed in surface-based connectivity analysis that an inverse suitability surface can function as resistance to movement (McRae, 2006). However, our study incorporating movement data shows that for these specific elephants highly suitable areas are not always well-connected and thus don't always facilitate movement. While suitable patches with high $dIIC_{intra}$ are spread broadly across the landscape, elephants limit their daily range to the central area (Figure 5B; see colour plates: page vi). Elephants, especially female groups, act cautiously in exploring new areas. However, as they spend more time traveling through a given new area, this produces a reduction of cautious behavior. Therefore, it is important to consider specific animal behaviors when evaluating species-specific landscape connectivity and to use accurate movement data to provide more realistic connectivity information.

At the patch scale, connectivity structures revealed by ASC can help identify critical patches for conservation. For example, nodes with high $dIIC_{connector}$ values produce movement flux to other habitat patches and function as "bridges" to facilitate movement between other patches. When mobility of animals is intermediate relative to the landscape pattern, the loss of a node with high $dIIC_{connector}$ can cause the breakdown of substantial network components into disconnected smaller components, producing a significant drop in overall landscape connectivity (Saura and Rubio, 2010). Though the physical distances among nodes would be the same, they are no longer functionally connected because elephants may not find an efficient path to reach another suitable patch within a reasonable time period.

At the landscape scale, ASC can help delineate conservation zones (Figure 5; see colour plates: page vi). Major concerns caused by elephants in KNP include vegetation degradation and biodiversity decrease in regions heavily used by elephants (Valeix et al., 2011). Promoting elephant movement to more spacious and less occupied habitats has become one goal of elephant conservationists in South Africa. The ongoing creation of Transfrontier Conservation Areas has promoted elephant dispersal at the landscape scale, allowing elephant numbers to fluctuate locally, thereby reducing their impact on vegetation. The zonation map based on the ASC framework defines regions to guide active landscape management at landscape scale, for example waterhole provisioning and vegetation patch burning (see Biggs et al., 2008 for methods overview and appropriateness of options). By applying Equation 2.3, we located the core areas surrounding the central area (Figure 5D; see colour plates: page vi). The overall management goal should be to improve connectivity at the core area but not the central area. Over time, resources in the central area will be degraded by continued heavy elephant exploitation, leading to a natural tendency for elephants to alter their movement patterns to occupy the higher quality Core zone. This zonation method can also be adapted to different conservation goals and other ecological contexts. Planners can focus on different *dIIC* fractions or assign different weights to the three fractions to aid decision-making for their particular problems.

We are aware that the limited amount of GPS in use in this study is a drawback. We were only able to simulate the connectivity condition for regions that were covered by movement records of the three elephants in this study. Though the results showed 398 isolated nodes, this may be more attributable to the lack of elephant movement information (Figures 3A and 2.4A; see colour plates: pages v and vi) than to poor connectivity. Although graph-based network analysis does not require intensive data input, additional data from more individuals covering larger area is always beneficial. Graph-based networks are an additive framework in the sense that, once constructed from observational data, they help to detect areas that lack information. In this way they can guide further data collection or ecological analysis for these locations (Urban and Keitt, 2001). Another way to address animal movement data deficiencies is to use simulated data modeled from observational data via cost-distance modeling or individual-based modeling (Kindlmann and Burel, 2008; Lookingbill et al., 2010; Spear et al., 2010).

Conclusion

We demonstrated the applied value of the "Availability-Suitability-Connectivity" framework using an integrative approach coupling GPS locational data of individuals, satellite imagery analysis, habitat suitability modeling, and graph theory. The use of integrative connectivity indices and its fractions can efficiently quantify the resulting connectivity without losing patch availability and suitability information. This method can be used in diverse landscapes by selecting satellite images from desired regions and the movement of the species interest in the area. We used hourly geographic coordinates, but using a more frequent interval for GPS data may increase the number of connections inside the species home range. We used the open source MaxEnt to understand the most suitable areas for elephants within their home range to determine the links connecting the nodes based on the elephant movement. This method is flexible and can be applied using publically available data and software.

When combined with movement data, our framework offers an ecologically realistic perspective to prioritize habitat patches in terms of their importance for landscape connectivity, and thus aid in identifying critical areas for conservation management. Ultimately, this study is an effort to create a tool which can employ emerging technologies from a myriad of fields along with a continuously growing store of ecological data to efficiently and effectively inform and advance conservation efforts.

Acknowledgements

The authors would like to thank the Kruger National Park SANparks GIS office for offering vector data for this study and JJ van Altena, Douw Grobler, Johan Malan and Jay Kirkpatrick for GPS data collection. We thank Brandon Adams and Dr David Cotten for technical support and Peter Hawman and Brandon Hays for language improvement. Data collection was funded by the U.S. Fish and Wildlife grant.

References

Chetkiewicz, C-LB, CC St. Clair, and MS Boyce. 2006. Corridors for Conservation: Integrating Pattern and Process. *Annual Review of Ecology, Evolution, and Systematics*, 317–42.

Codron, J, JA Lee-Thorp, M Sponheimer, D Codron, RC Grant, and DJ de Ruiter. 2006. Elephant (Loxodonta Africana) Diets in Kruger National Park, South Africa: Spatial and Landscape Differences. *Journal of Mammalogy* 87 (1):27–34.

Crooks, KR, and M Sanjayan. 2006. Connectivity Conservation: Maintaining Connections for Nature. In *Connectivity Conservation*. Cambridge University Press. p.1–10.

Decout, S, S Manel, C Miaud, and S Luque. 2012. Integrative Approach for Landscape-Based Graph Connectivity Analysis: A Case Study with the Common Frog (Rana Temporaria) in Human-Dominated Landscapes. *Landscape Ecology* 27 (2):267–79.

Fayrer-Hosken, RA, P Brooks, HJ Bertschinger, JF Kirkpatrick, JW Turner, and IKM Liu. 1997. Management of African Elephant Populations by Immunocontraception. *Wildlife Society Bulletin*, no. 25:18–21.

Galpern, P, M Manseau, and A Fall. 2011. Patch-Based Graphs of Landscape Connectivity: A Guide to Construction, Analysis and Application for Conservation. *Biological Conservation* 144 (1):44–55.

Harris, GM, GJ Russell, RI van Aarde, and SL Pimm. 2008. Rules of Habitat Use by Elephants Loxodonta Africana in Southern Africa: Insights for Regional Management. *Oryx* 42 (1):66–75.

Kindlmann, P, and F Burel. 2008. Connectivity Measures: A Review. *Landscape Ecology* 23 (8):879–90.

LaRue, MA, and CK Nielsen. 2008. Modelling Potential Dispersal Corridors for Cougars in Midwestern North America Using Least-Cost Path Methods. *Ecological Modelling* 212 (3):372–81.

Lookingbill, TR, RH Gardner, JR Ferrari, and CE

Keller. 2010. Combining a Dispersal Model with Network Theory to Assess Habitat Connectivity. *Ecological Applications* 20 (2):427–41.

McRae, BH, BG Dickson, TH Keitt, and VB Shah. 2008. Using Circuit Theory to Model Connectivity in Ecology, Evolution, and Conservation. *Ecology* 89 (10):2712–24.

Moilanen, A. 2011. On the Limitations of Graph-theoretic Connectivity in Spatial Ecology and Conservation. *Journal of Applied Ecology* 48 (6):1543–47.

Owen-Smith, N, GIH Kerley, B Page, R Slotow, and RJ Van Aarde. 2006. A Scientific Perspective on the Management of Elephants in the Kruger National Park and Elsewhere: Elephant Conservation. *South African Journal of Science* 102 (9 & 10):389–94.

Pascual-Hortal, L, and S Saura. 2006. Comparison and Development of New Graph-Based Landscape Connectivity Indices: Towards the Priorization of Habitat Patches and Corridors for Conservation. *Landscape Ecology* 21 (7):959–67.

Phillips, SJ, RP Anderson, and RE Schapire. 2006. Maximum Entropy Modeling of Species Geographic Distributions. *Ecological Modelling* 190 (3):231–59.

Presotto, A. 2015. From Maze to Maps: Geospatial Technologies and the Pattern of Navigation in Wild Animals. University of Georgia.

R Core Team. 2013. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria: ISBN 3-900051-07-0.

Saura, S, and L Rubio. 2010. A Common Currency for the Different Ways in Which Patches and Links Can Contribute to Habitat Availability and Connectivity in the Landscape. *Ecography* 33 (3):523–37.

Saura, S, and J Torne. 2009. Conefor Sensinode 2.2: A Software Package for Quantifying the Importance of Habitat Patches for Landscape Connectivity. *Environmental Modelling & Software* 24 (1):135–39.

Spear, SF, N Balkenhol, M FORTIN, BH McRae, and KIM Scribner. 2010. Use of Resistance Surfaces for Landscape Genetic Studies: Considerations for Parameterization and Analysis. *Molecular Ecology* 19 (17):3576–91.

Urban, D, and T Keitt. 2001. Landscape Connectivity: A Graph-Theoretic Perspective. *Ecology* 82 (5):1205–18.

Urban, DL, ES Minor, EA Treml, and RS Schick. 2009. Graph Models of Habitat Mosaics. *Ecology Letters* 12 (3):260–73.

Valeix, M, H Fritz, R Sabatier, F Murindagomo, D Cumming, and P Duncan. 2011. Elephant-Induced Structural Changes in the Vegetation and Habitat Selection by Large Herbivores in an African Savanna. *Biological Conservation* 144 (2):902–12.

Xu, W, Q Huang, J Stabach, B Hoshino, and P Leimgruber. 2017. Railway Underpass Location Affects Migration Movements and Efficiency in Tibetan Antelope. Unpublished.

Zeller, KA, K McGarigal, and AR Whiteley. 2012. Estimating Landscape Resistance to Movement: A Review. *Landscape Ecology* 27 (6):777–97.