LANDSCAPE CONNECTIVITY FOR ELEPHANT MOVEMENT

IN KRUGER NATIONAL PARK, SOUTH AFRICA:

INTEGRATING GEOSPATIAL AND ECOLOGICAL MODELING

by

WENJING XU

(Under the Direction of Marguerite Madden)

ABSTRACT

African elephant (*Loxodonta africana)* population growth in Kruger National Park (KNP) and the subsequent environmental impacts, such as decreased biodiversity, has raised conservation concerns demanding thorough understandings about elephant behavior interplay with landscape dynamics. This thesis aims to examine how African elephant movement is affected by landscape changes in KNP from a combined geographic and ecological perspective. A landscape “Availability-Suitability-Connectivity” framework was employed to systematically evaluate landscape dynamics related to elephant movement by integrating GPS tracking data, satellite imagery and habitat suitability modeling as inputs. Following this framework, the study developed an individual-based model to simulate elephant movements and resulting landscape networks under various landscape conditions. Taken together, this study highlighted appealing features of coupling geospatial technologies and ecological modeling methods to assess relationships between animal movement and landscape connectivity, to evaluate potential impacts of landscape changes, and to inform effective conservation practices.

INDEX WORDS: Individual-based Model, Landscape connectivity, Kruger National Park, African elephant, Animal movement

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DEDICATION

To people and animals born under wondering stars.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

INTRODUCTION

Founded in 1926, Kruger National Park (KNP) is one of the largest wildlife sanctuaries in the world, covering nearly 20,000 km^2 along the eastern boundary of South Africa. It offers critical habitats for African elephants (*Loxodonta africana*), a species that although regarded as endangered worldwide, has undergone a seemingly paradoxical population growth within KNP in recent decades. This over population has raised concerns about habitat overuse by elephants and subsequent decrease in biodiversity within the park boundary. To achieve a scientifically-based elephant conservation and management plan, KNP has shifted conservation emphasis from solely population control to maintaining a healthy and heterogeneous landscape, including managing defragmentation, artificial waterholes, and fence control. Therefore, there is a demand for substantial research on elephant habitat use and landscape structure in order to consistently optimize conservation strategies.

Consisting of 16 macro ecozones, the landscape of KNP is highly diverse and resources for elephants are patchily distributed across the park. Elephants are known to change their movement strategies to optimally use resourceswith distributions related to their preferences of different landscape structures and reflecting their dynamic habitat use (Whyte 2002; Owen-Smith et al. 2006; Chamaillé-Jammes et al. 2013). This relation can be described by species-specific functional connectivity, or the degree to which the arrangement of landscape elements facilitates or impedes movements of species (Taylor et al. 1993).

Understanding connectivity is one of the prime concerns when making conservation decisions for focal species (Freemark et al. 2002; Vogt et al. 2009; Saura and Rubio 2010). Landscape-level graph theory is a powerful concept underlying methods to quantify landscape connectivity, which is defined as a network of ecological flows (links), or animal movement as is in this study, among landscape patches (nodes) (Bunn et al. 2000). However, the landscape is treated as a dichotomous surface such as habitat/non-habitat when defining nodes in most of the graph theory-based models. Additionally, links are usually represented using general knowledge, which lacks support from observational data for specific study areas, and, unfortunately, is not always obtainable.

LITERATURE REVIEW

Kruger National Park and the Study Area

The KNP is located in the northeast portion of South Africa with an area of 19,485 km^2, lying between 22°20’ to 25°32’S and 30°53’ to 32°02’E (Figure 1.1). It was proclaimed as a national park in 1926. KNP is a part of the “lowveld” savanna (Figure1.1 A) with elevations varying from 200 m to 840 m and it is one of the largest wildlife sanctuaries in the world (Codron et al. 2006). As a protected enclosed area, the difference of climate and geology results in a variety of landscapes across KNP (Gertenbach 1983). The primary vegetation regions include Northern Sandveld, Mopaneveld, Savanna Grasslands, Mixed Broadleaf Woodland, Thorn Thickets, Lebombo, South-western Foothills, and Riverine Bush. The landscape is highly diverse and resources for different species are patchily distributed across the landscape (Crooks and Sanjayan 2006). There are in total 16 ecozones in the whole park, mainly classified by dominant vegetation types. The focal study region (see details in Methods) primarily covers two ecozones: Sabie/Crocodile Thorn Thickets, and Mixed Bushwillow Woodlands. The rivers that go through KNP cross into Mazoambique, where the Lowveld extends to coastal floodplains and estuaries. Following Dennis (2000), the whole area is divided into four regions (Figure 1.1A). The climate of KNP is tropical to subtropical, and the average annual precipitation varies from 401 mm to 600 mm. Drought is endemic in this region in the dry season, which typically lasts from March to middle October, followed by the wet season till February (Tyson 1986).

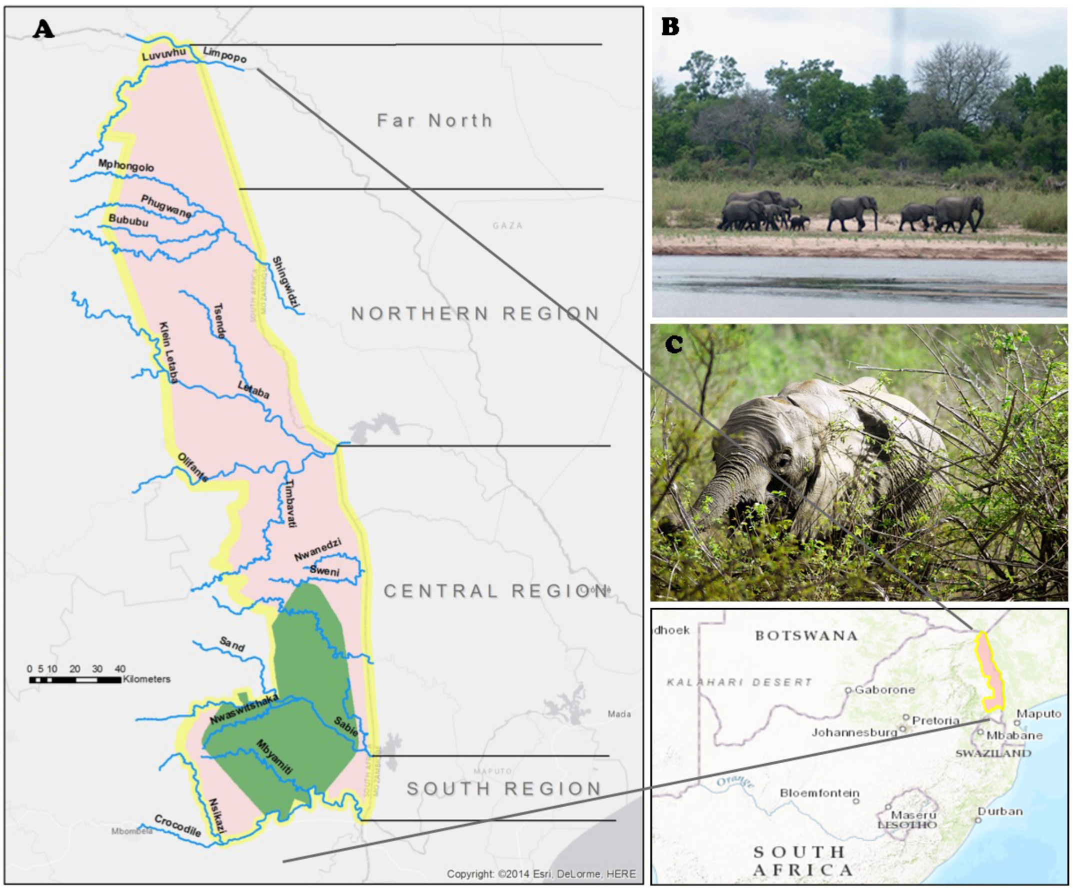

Figure 1.1 Kruger National Park (KNP, pink shade) and location of the study area (green shade) (A); KNP views and elephant (B, C).

The districts that border KNP have a high incidence of human-elephant conflicts (Dunham et al. 2010). These conflicts take forms from crop raiding and infrastructural damage to poaching and injury or death of people and elephants (Hoare 2000). For example, crop raiding has been reported particularly common along borders of KNP at the Mozambique side, and it is strongly correlated with the number of elephants that are killed (Dunham et al. 2010). Problem elephants were often animals that had dispersed from conservation areas to nearby areas that are highly populated. This can attribute to the expanding gap between the increasing human demands on space and resources raised by rural development and the deficiencies on wildlife conservation policies (Tapela and Omara-Ojungu 1999). There are at least two million people living within 50 km of the western border of KNP, with a diversity of cultures and major groups including the Tsonga, the Vhacenda, the Pedi and the Swazi. Though extensive research have been done on human-elephant conflicts in Africa (Osborn and Parker 2002; Sam et al. 2005; Lee and Graham 2006; Sitati and Walpole 2006), this issue has been regarded as one of the most difficult conservation problems and it consistently puts pressure on park managers to optimize management (Hoare 2001).

Elephants Conservation in KNP

Due to the serious mismatch between conservation science and practice concerning elephants, there has been a prevailing growth in the elephant population in KNP (Lindsay 1993; Blake and Hedges 2004; Kerley et al. 2008), which would lead to vegetation degradations and then biodiversity decreases (Valeix et al. 2011). Though elephants are endangered worldwide, the overpopulation of elephants in the park has paradoxically raised concerns for the potential impacts of elephant overabundance on the biodiversity in the park. This paradox is due to how quickly elephants can be eliminated by human persecution and how fast elephant populations can increase once protected (Loarie et al. 2009). Research has shown that the high numbers of elephants, destruction of trees and over grazing can change woodlands to grasslands, resulting in biodiversity loss (Cumming et al. 1997). Maintaining species and landscape heterogeneity has long been a primary management goal in KNP.

In order to avoid the anticipated destruction of the vegetation in the park (Van Wyk and Fairall 1969), the Board of South African National Parks initiated a program of elephant culling as a means of elephant population control. A total population of 7000 was decided as the ideal elephant population size in KNP, which led to 6000 to 8500 individuals being culled or removed from 1967 to 1996 (Aarde et al. 1999). It is claimed that without this intervention, the numbers will double in as little as ten years (Whyte et al. 1998). However, culling is always considered to be controversial among ecologists, and it raises ethical, social, and economic issues over the boundary of KNP. Being challenged by animal rights groups as lacking of scientific ground, this policy was brought to a moratorium. In the meanwhile, elephant population are under no major threat from outside. According to a report from KNP, elephant's population increased by 1088 in 5 years after culling was cease, and 22 elephants were poached during that period (Whyte et al. 1999). Today, the consistent growing elephant population has reached 11500 in the park.

In the recent decade, managing the heterogeneous landscape has been regarded as essential for scientific elephant management and more effective than solely controlling numbers of elephants (Owen-Smith et al. 2006; Van Aarde et al. 2006). Current landscape management in KNP primarily focuses on defragmentation, managing artificial waterholes, and constructing/destructing fences (Van Aarde et al. 2006). Artificial waterholes in KNP were first developed to increase the number of animals with low density because of poaching, diseases, fencing and low permanent water availability (Van Wyk 2011). These artificial waterholes can influence habitat use by herbivores even when natural water is available (Smit et al. 2007). After negative effects from over-developed and unnatural waterholes were realized, a new policy in KNP was proposed, stating all artificial waterholes should be part of natural ecosystem principles and open waterholes should be fully controlled (Pienaar et al. 1997). Other human interventions, such as fences, reduce seasonal difference in elephant movement patterns inter-seasonally and inter-landscape (Loarie et al. 2009). Elephants are regarded as "Keystone" fence breakers in KNP, and bulls are more likely to be the fence offenders. In KNP, it has been long suspected that the Marula tree fruiting season is the seasonal peak of elephant escape (Grant et al. 2008). One non-lethal mitigation method is to protect fences by spraying with chili pepper or indirect protection by aversion therapy (Ferguson et al. 2012).

In 1989, Whyte claimed the effective elephant management in KNP should be built upon a better understanding of elephant movement, which is supported by "Elephant Science Roundtable" held in January 2006 (Whyte 2002; Owen-Smith et al. 2006). The use of triangulation (remote tracking) techniques in elephant studies dates back to the late 1970s, conducted at Sabi Sand Reserve neighboring KNP, and it was proved to be able to offer abundant location information covering a larger area (Fairall 1979). Following the advances in triangulation, remote sensing and geographic information science (GISci) have more recently been incorporated into landscape diversity monitoring and management in conservation lands such as National Parks. These technologies can be used as powerful leverage to record dynamic landscape conditions and are useful tools for conservation planning. South African National Parks has launched Geographic Information System service to support conservation management and research conducted in parks.

On the one hand, data collection and analysis techniques have developed with unprecedented speed; on the other hand, conservation problems associated with elephants still exist. Therefore, there are always demands for better use of advancing technologies for elephant conservation for KNP.

Landscape connectivity and graph theory

The distribution and movement of elephants is greatly influenced by the distribution of resources, since elephants may change their movement strategies in order to optimally use resources (Chamaillé-Jammes et al. 2013). Facilitating elephants' local movements and regional dispersal could relieve elephant intensive range use for certain regions (Van Aarde et al. 2006). Therefore, substantial research is required to help understand the relationship between elephant habitat use and landscape patterns (Van Aarde et al. 2006; Loarie et al. 2009). One way to quantitatively describe this relation is to measure species-specific functional connectivity. Landscape functional connectivity, or the degree to which the arrangement of landscape elements facilitates or impedes movement and other ecological flows of species (Taylor et al. 1993), is a prime concern when making conservation decisions for a focal species (Freemark et al. 2002; Vogt et al. 2009; Saura and Rubio 2010). Understanding connectivity is of special importance when resources are fragmentally distributed (Lookingbill, 2010).

Landscape-level graph theory was introduced into ecological applications across landscapes by Urban and Keitt (2001), and is defined as a network of ecological flow (links), or animal movement as is in this study, among landscape patches (nodes). In the recent decade, graph theory has become a powerful leverage describing and quantifying functional connectivity (Bunn et al. 2000; Urban et al. 2009; Dale and Fortin 2010). It is able to combine landscape patterns and focal species biology to demonstrate process-based connections (Hanski 1998; Urban and Keitt 2001). With reduced data requirements, it can provide a heuristic framework for landscape-level conservation management such as sensitive area detection and impact assessment (Bunn et al. 2000; Urban et al. 2009; Galpern et al. 2011). Resources for elephants in the savanna of KNP (i.e., surface water and forage vegetation) are patchily distributed.

Additionally, landscape structure is critical for effective elephant movement (Chamaillé-Jammes et al. 2007). Both of them make the savanna landscape at KNP an ideal landscape to assess graph-based functional connectivity.

In landscape ecology, a classic graph describing functional connectivity is a model of a binary landscape system of habitat and inhospitable matrix (non-habitat), compromising a set of nodes (habitat patches) and links (potential connections between patches) (Urban and Keitt 2001). In most cases, links represent the geographic distance between nodes and only exist when this distance is below a universally applied ecological threshold, such as the dispersal ability of a certain species (Galpern et al. 2011). Some others define links using model-based simulations, where connections are identified by modeled dispersal events (Lookingbill et al. 2010). However, there are two problems associated with these graph-based models that may severely constrain their use for conservation management aiming at maximizing the persistence for focal species (Baguette et al. 2013). First, the prediction of links usually has not been tested by observations. Although sometimes empirical measurements are used as parameters in graphs (Awade and Metzger 2008; Andersson and Bodin 2009), actual connectivity, measured by observational movement data such as Global Positioning System (GPS) tracking records, is usually not incorporated (Galpern et al. 2011). Second, in reality, habitat quality varies continuously but also subtly. Especially for large mammals, the landscape is not strictly dichotomous between habitat and non-habitat (Boyce and McDonald 1999). Hence, when defining nodes, the binarism of landscape as habitat/non-habitat would be inappropriate (Urban and Keitt 2001).

Individual-Based Model

Ecological modeling is frequently used to prioritize areas for conservation actions. Multiple methods and software tools have been applied to spatial conservation planning (Moilanen et al. 2009; Guillera-Arroita et al. 2015). Developed as early as 1960s, Individual-Based Modeling (IBM) has grown tremendously in the field of ecology in the past two decades. It is an effective method to determine the interrelationships between individual traits and spatial explicit landscape properties (Albeke et al. 2010; Grimm and Railsback 2013). For example, how do individuals respond to previous and current status? (Dunning Jr et al. 1995). The essence of IBM is to derive the properties of a system from the properties of the individual constituting these systems (Łomnicki 1992). IBM treats animals as unique individuals with different characteristics (Grimm 1999), and are able to integrate individual responses with landscape heterogeneity by specifying locations of individuals and their spatial relationship with landscape features. Once integrated with spatial information, IBM allows simulations of spatial relations between animals and landscape features, e.g., animal movement across landscapes (Albeke et al. 2010; Bartoń et al. 2012). It is especially desirable given the myriad landscape patterns that can result from different management practices, and the limited availability of observational animal locomotion data. This method has been proved effective to evaluate the sensitivity of connectivity to variations in movement parameters (Zollner and Lima 1999; Pe'er and Kramer-Schadt 2008; Palmer et al. 2011).

Early attempts to model elephant-landscape interaction generally ignored spatial heterogeneity, which are in line with arguments that they are inadequate to describe the dynamic environment (Jeltsch et al. 2000). In addition, when considering elephant-environment interactions, the complexity of reality is usually either over-simplified or too specific and loses flexibility to adapt to different ecosystems. This study will produce an IBM for elephant movement considering a series of landscape features while maintaining the flexibility for changing landscape structures. Therefore, landscape connectivity can be calculated under different landscape scenarios to reveal how the change of landscape structures will affect elephant movement and habitat use.

Individual-based models (IBM) offers a solution for deficiencies on ecological process data and has been increasing applied to animal studies because of the growing interests on relation between this individual-level process and its population-level impacts (Tischendorf 1997; Turchin 1998; Grimm and Railsback 2005; Nathan 2008; Black and McKane 2012). For example, Baxter and Wayne (2005) developed a grid-based model of elephant-savanna dynamics based on KNP, with focus on tree-grass interactions affected by elephant consumption, fire, and rainfall. Further, IBM considers the stochastic nature of ecological process, as is shown in animal movement, and also can be easily integrated with spatial-specific data (DeAngelis and Mooij 2005; Grimm and Railsback 2005; Tang and Bennett 2010; Albeke et al. 2015). Thus, it has been extensively applied to spatial-related animal behavior simulations, for example, movement and home range dynamics (Turner et al. 1994; Nibbelink and Carpenter 1998; Dumont and Hill 2004; Morales et al. 2005; Bennett and Tang 2006; Wang and Grimm 2007; Albeke et al. 2015). Additionally, IBM is flexible enough to be incorporated with well-established ecological models such as graph theory-based landscape network (Morzillo et al. 2011; Albeke et al. 2015). However, we do not aware any IBM designed specifically for elephant movement with relation to landscape connectivity.

OBJECTIVES

This thesis research aims to understand how African elephant (*Loxodonta africana*) movement is affected by landscape conditions changed by natural or managing processes in

Kruger National Park (KNP), South Africa. Systematically, external factors that drive animal movement and thus affect landscape connectivity include resources availability and habitat suitability (Roshier et al. 2008; Graham et al. 2009; Tang and Bennett 2010). The difficulties to collect observational movement data across the landscape, along with the stochastic nature of ecological processes, raised a demand for applications of ecological Individual-Based Models (IBMs). Specific research questions and hypothesis for the two manuscript style chapters were as below.

Chapter 2: Resources availability, habitat suitability and landscape connectivity for elephant movement

The goal of Chapter 2 is to characterize landscape functional connectivity targeting elephant movement in KNP using observational GPS tracking data and satellite imagery. In this chapter, an "Availability-Suitability-Connectivity" framework was applied to analyze interactions between landscape conditions and elephant movement by integrating geospatial technologies and ecological modeling methods. In this chapter I address these questions:

1) How to make use of observational movement data to inform real connectivity?

I hypothesize that the GPS tracking recordings can reveal movement efficiency and directly reflect connectivity of elephant movement. Therefore, I test the use of a temporal criterion to define links in landscape network and to measure connectivity. I expect a higher connectivity among resources patches that elephants can travel to in a shorter time.

2) How to incorporate landscape heterogeneity into landscape network construction and connectivity evaluation?

I predict landscape patches as nodes in landscape networks are by themselves heterogeneous and therefore show different attractive levels for elephant movement. Thus, I conducted habitat suitability modeling to examine node attributes. When evaluating connectivity, I considered both patch availability and suitability in order to more systematically gain evaluations for the landscape conditions.

3) How can connectivity evaluation inform conservation management?

I predict a visualization and quantification of the landscape Availability-Suitability-Connectivity patterns will allow us to differentiate the importance of different landscape features and therefore guide landscape conservation management.

Chapter 3: Individual-based model to simulate elephant movement and landscape connectivity

Following the Availability-Suitability-Connectivity framework in Chapter 2, Chapter 3 aims to overcome the lack of observational data and to develop an individual-based model elephant movement and landscape networks simulations. Different scenarios are modeled and analyzed under changing landscape conditions and potential conservation implementations of the model are demonstrated. Research questions that I examined are:

1) How do landscape conditions affect elephant movement?

I expect multiple landscape features have strong effects on elephant movement, including relocation distances and relative turning angles. For example, considering the management practices carried out in KNP, I hypothesize locations of waterholes has a strong effect on elephants. Nevertheless, interactions between landscape elements and movement are complex and difficult to model. Therefore, I use habitat suitability as a single covariate to test elephant movement response.

2) How can we model elephant movement while keeping the stochastic nature of this behavior?

I hypothesize that the relation between landscape suitability and elephant movement cannot explain all the variations of elephant movement. Actually, it reflects the stochastic nature of movement (Tang and Bennett 2010). Therefore, I use individual-based modeling to incorporate this stochasticity and also be able to simulate movement and resulting landscape connectivity under changes of resources availability and habitat suitability.

3) Does temporal scale affect measures of landscape connectivity for animal movement?

I hypothesize landscape connectivity is also scale-dependent. Considering the Availability-Suitability-Connectivity framework is built upon elephant movement efficiency among landscape patches and the connectivity in this study is supposed to be higher under a larger temporal scale. To test this, I examined connectivity changes against a series of temporal units to define link existences.

4) How can the model inform conservation management for elephants in KNP?

I expect the model can differentiate patches importance in the park and reveal connectivity change under manipulation or change of resources availability or habitat suitability. Habitat suitability would be changed when, say, artificial waterholes are removed. Using the IBM, I simulate a series of landscape conditions and examine how connectivity and patch importance change accordingly. I expect a better connectivity when either availability or suitability is higher. I also expect a lower connectivity with removal of artificial waterholes.

This thesis is organized in this way: The first chapter reviewed the current landscape conditions and elephant conservation status in KNP. Literature reviews were also conducted for graph-based landscape connectivity analysis, as well as ecological individual-based model. Chapter 1 was followed by two manuscript style chapters with objectives demonstrated above. Taken together, these two chapters used geospatial technologies (satellite imagery and GPS tracking technologies) and ecological modeling methods (habitat suitability modeling, landscape network modeling, individual-based modeling) to systematically evaluate landscapes for wildlife movement. Additionally, I examined how landscape dynamics introduced by natural processes or management practices affect elephant movement and, in turn, landscape connectivity to achieve more effective conservation planning and landscape management.

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CHAPTER 2

COUPLING AFRICAN ELEPHANT MOVEMENT AND HABITAT MODELING FOR LANDSCAPE AVAILABILITY-SUITABILITY-CONNECTIVITY ASSESSMENT IN KRUGER NATIONAL PARK, SOUTH AFRICA

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ABSTRACT

Context Making appropriate conservation decisions 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.

Objectives We explore how to incorporate African elephants' (*Loxodonta africana*) movement data into an "Availability-Suitability-Connectivity (ASC)" landscape assessment framework which integrates habitat suitability modeling and graph-based network analysis, and how to then implement connectivity information to inform conservation management addressing locally intensive habitat utilization by elephants.

Methods In our ASC analysis, node availability was identified by satellite imagery classification while node suitability was estimated by MaxEnt model. Links represented movement efficiency and were determined by effective movement between nodes in 3 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.

Results 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 study area. Our zonation map demonstrates zones for landscape management surrounding the central area that can facilitate elephant range expansion.

Conclusions Our integrative framework quantified the ASC interactions between animal movement and landscape features. The results highlighted the potential for coupling geographic

and ecological methods to effectively identify and focus conservation efforts, therefore to achieve a more operative conservation planning and management.

Keywords Landscape connectivity, graph theory, elephant movement, Kruger National Park, habitat suitability

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 (Taylor et al., 1993), is a prime concern when making conservation decisions for a focal species (Freemark et al., 2002; Vogt et al., 2009; Saura and Rubio, 2010; Hanski, 1998). It is of special importance when resources are patchily distributed (Lookingbill, 2010) and it can provide an experimental framework for landscape-level conservation management, such as sensitive area detection and impact assessment (Bunn et al., 2000; Urban et al., 2009; Galpern et al., 2011). Two types of models are commonly used to calculate connectivity: discrete models such as graph-based habitat networks analysis (Urban et al., 2009; Alagador et al., 2012) and continuous models based on resistance surface such as ecological circuits (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 (Bunn et al., 2000; 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 which originated from mathematics and computer science (Bunn et al., 2000; 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 (Tischendorf, 1997; Wiens, 2001).

Applying thresholds in the process of defining habitat patches or links between them could be inappropriate for connectivity analysis and result in the loss of information (Urban and Keitt 2001; 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 (Koen et al., 2010). 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 (Seoane et al., 2005; Spear et al., 2010). Since resistance is based on relationships between landscape variables and underlying biological functions such as relative abundance (Gonzales and Gergel, 2007), researchers commonly equate resistance to the inverse of habitat preferences (e.g. Chetkiewicz et al., 2006; Gonzales and Gergel, 2007; LaRue and Nielsen, 2008). However, movement through the landscape is not necessarily equal to habitat suitability, and animal movement is often condition-dependent (Ronce et al., 2001). Incorporating actual or simulated movement data is one improvement to the performance of surface-based connectivity models (Epperson et al., 2010), 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 limitations and merits and a combination of them is valuable for landscape connectivity examination (Cushman et al., 2013). 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 (Urban and Keitt 2001; 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 employ 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 (Chamaillé-Jammes et al., 2007), which may in turn impact landscape conditions (Whyte 2002; 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; Chamaillé-Jammes et al., 2007; Van Aarde et al., 2007). Understanding of the interplay between elephant movement and landscape conditions is valuable for identifying locations to focus management efforts (Owen-Smith et al., 2006; Roever et al., 2013). 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 2.1). 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 (Gertenbach, 1983). 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 of differing requirements which 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. 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 (Figure 2.1). This focal region primarily covers two ecozones: Sabie/Crocodile Thorn Thickets, and Mixed Bushwillow Woodlands

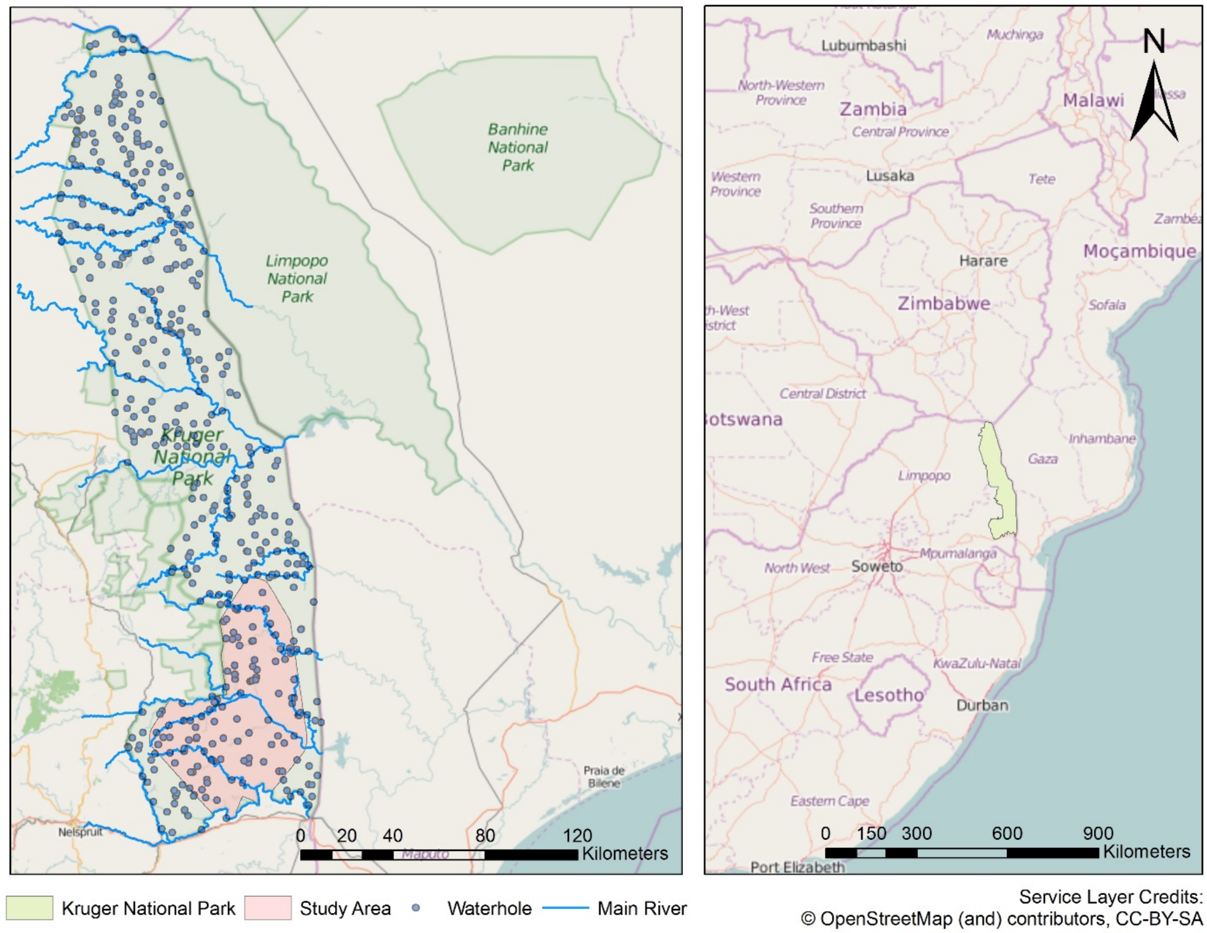

Figure 2.1 KNP (green shade) and location of the study area (pink shade) and its relative locations in South Africa.

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 landcover classification; 2) determine patch suitability by MaxEnt habitat suitability modeling; and 3) determine links connecting nodes by elephant movement (Figure 2.2).

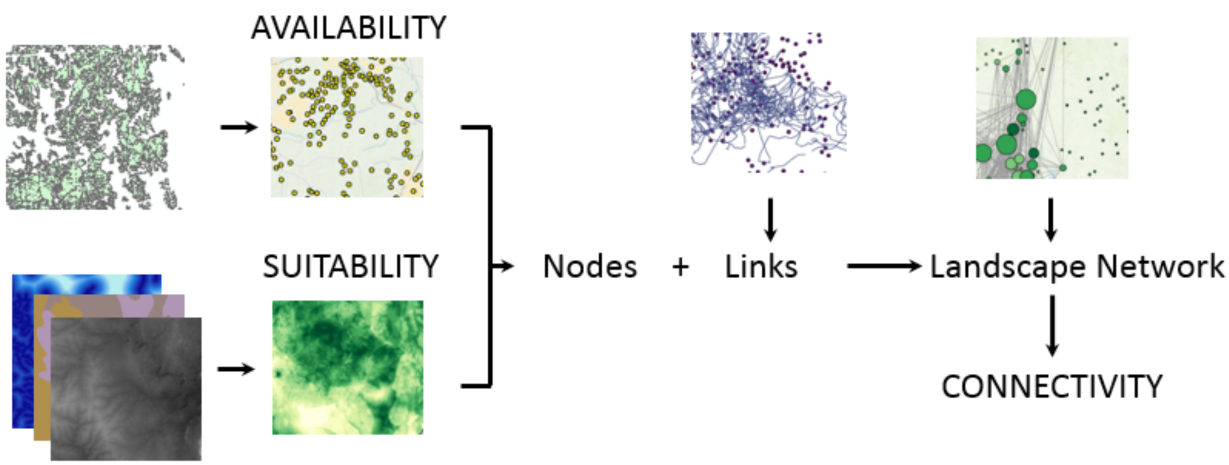

Figure 2.2 The "Availability-Suitability-Connectivity (ASC)" workflow for landscape evaluation.

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; Shannon 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 (Barnes, et al., 1994; Swanepoel, 1993). Thus locations of woodland patches 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 5 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 (Phillips and Dudík, 2008). The output raster map denotes species occurrence probability and is proportionate to habitat suitability for the species (Elith et al., 2011; Decout et al., 2012). Node suitability was calculated as the average pixel suitability within a patch.

Table 2.1 Environmental variables in MaxEnt.

Environmental Variables	Type	Contribution to the 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%

In order to reduce the effect of spatial and temporal correlation, we extracted the GPS location at 8 pm 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 8 pm 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 2.1. All the predictor raster layers had a pixel resolution of 30 x 30 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; Elith et al., 2011).

Determination of Links

Connectivity can be regarded as a global property approximating the number of effective movements occurring among patches (Baguette, 2007). In most cases links between patches are determined by patch distance relative to the upper limit of animals' movement ability (Kindlemann and Burel, 2008). For African elephants, who have large home ranges varying from 15 to 3,700km^2 and high mobility (Douglas-Hamilton 1972; Leuthold1977), 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 30km 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 3 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 3 days.

The final constructed landscape network consisted of nodes representing woodland patch availability with suitability as an attribute and links representing at most 3-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 (Bodin and Saura, 2010) 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:

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

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 *dIIC* 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):

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

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:

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

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 the contrast, areas containing nodes currently heavily used would generate less importance for connectivity management. We 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, 2014). 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 2.3A). 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 denotes the locations of woodland patches (Figure 2.3B). 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 2.1 in order of contribution to the model. Figure 2.3C 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 2.3D).

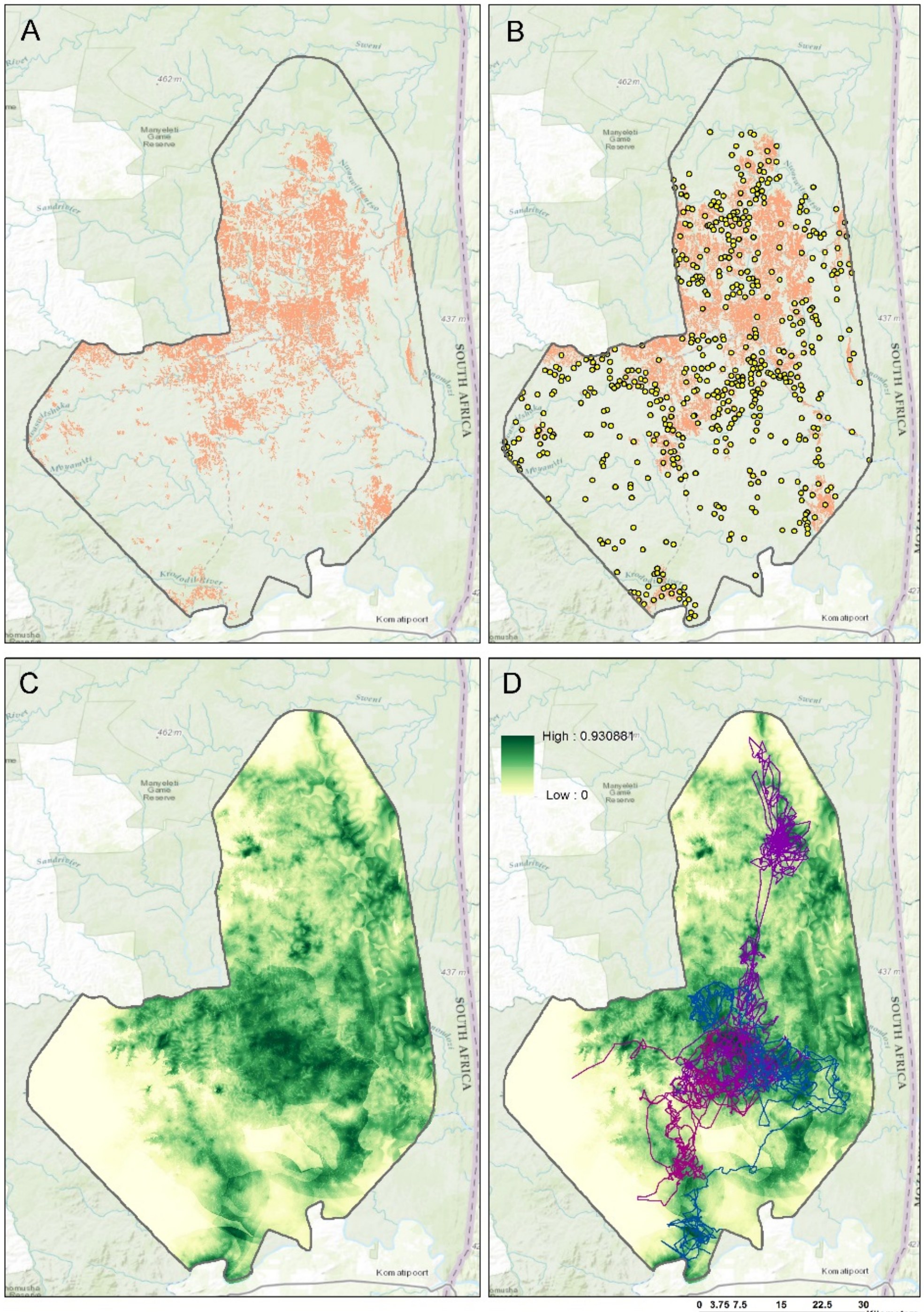

Figure 2.3 The distribution of patches (A); nodes as representations of patches (B); MaxEnt-generated habitat use probability map in shades of green denoting habitat suitability (C) and the map with movement paths overlaid (D).

In our landscape network, which demonstrates the A-S-C pattern (Figure 2.4A), 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 (Figure2.4B). The node ‘i’ denoted in Figure 2.4B 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 2.4C provide an example of an isolated component (ii) in the south of the study area.

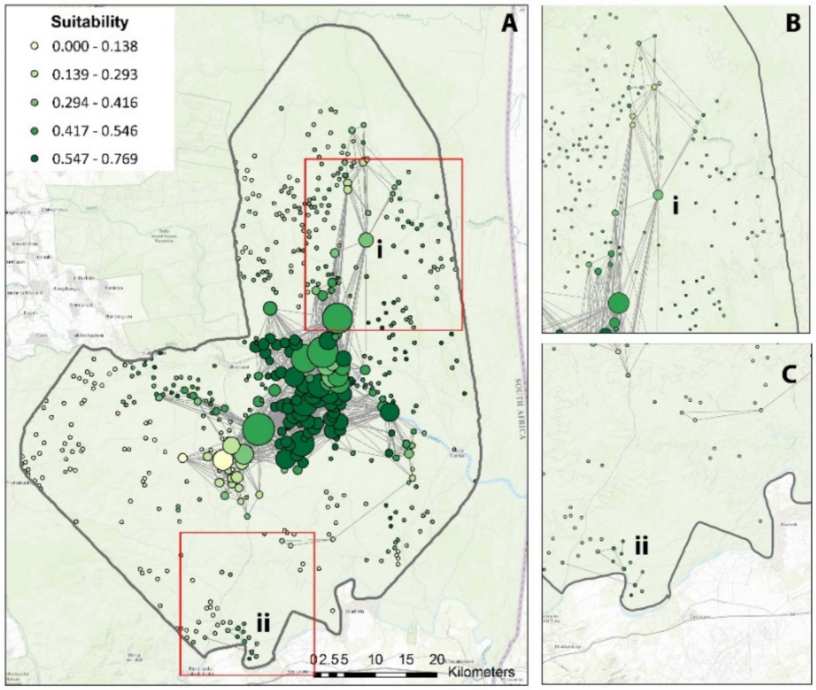

Figure 2.4 Landscape network constructed based on the "Availability-Suitability-Connectivity" workflow. Node size is proportionate to the Degree values, which range from 0 to 65. Node i is an example functioning as a "bridge" to connect two components; Node ii shows a component isolated from the major component in the center of the study area.

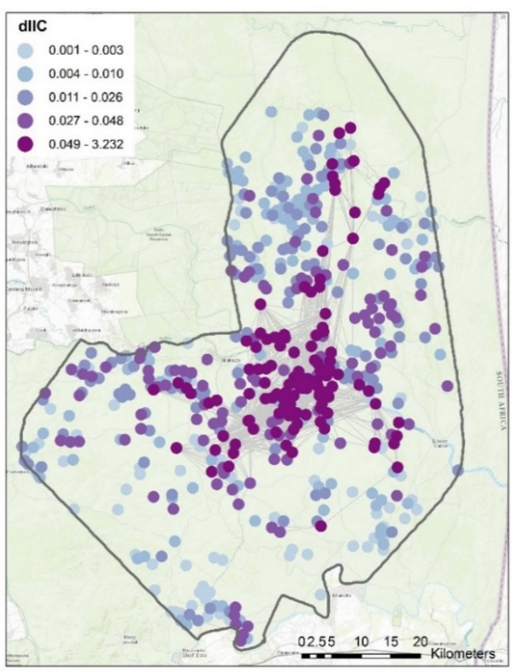

Figure 2.5 *dIIC* measures for patch importance classified by quantiles.

The landscape level IIC is equal to 711.7, which was later used to calculate node importance *dIIC* at patch-level (Figure 2.5B). 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 2.6 shows 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 2.6B 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 areas that intensively used by 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.

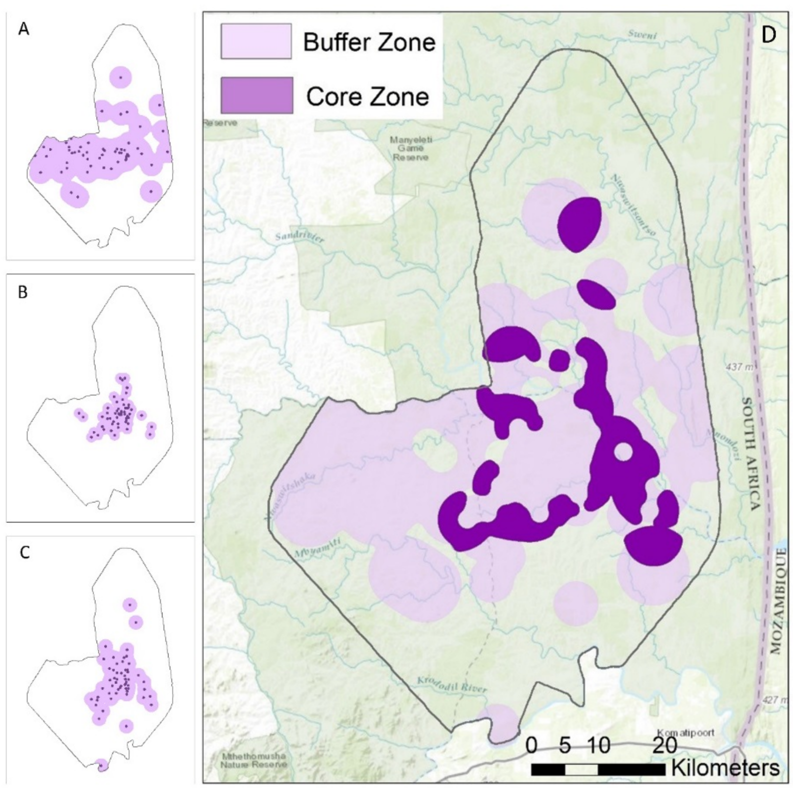

Figure 2.6 Nodes with top 10% $dIIC_{intra}$, $dIIC_{flux}$, and $dIIC_{connector}$ values (A, B, C) and example of utilizing *dIIC* fractions for conservation zonation (D).

The conservation zonation mapping based on the three *dIIC* fractions evaluates landscape management priority across the study area (Figure 2.6). 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 2.6D indicates areas that would be used by elephants more frequently after expanding their inter-patch movement.

DISCUSSION AND CONCLUSION

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 (Galpern et al., 2011). 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 2.3). 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 2.6B). Elephants, especially female groups, act cautiously in exploring new areas (Douglas-Hamilton, et al., 2005; Druce et al., 2008). However, as they spend more time traveling through a given new area, this cautious behavior decreases (Druce et al., 2008). 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 2.6). 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 conservation in South Africa (Van Aarde and Jackson, 2007; Gallagher, 2012). 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 (Hanks, 2003; Van Aarde et al., 2007). 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 2.6D). 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 (see Figures 2.3A and 2.4A) 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 (Bunn et al., 2000; 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; Bergerot et al., 2013).

To conclude, 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. 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.

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CHAPTER 3

LANDSCAPE CONNECTIVITY FOR INDIVIDUAL AFRICAN ELEPHANT MOVEMENT IN RESPONSE TO LANDSCAPE CHANGES

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ABSTRACT

One of the major conservation issues in Kruger National Park (KNP) in South Africa is the locally intensive habitat use by African elephants (*Loxodonta Africana*) and its subsequent impacts on landscape conditions. It has been proposed to manipulate limiting resources for elephant distribution in order to promote landscape connectivity and alleviate their local impact. It is thus highly important to understand the interplay between elephant movement and landscape conditions to facilitate landscape management efforts. However, actual elephant movement data is usually limited in spatial extent, sample size, or temporal resolution. This study aims to model emergent landscape connectivity network corresponding to simulated elephant movement and to examine how landscape management of resources availability (waterhole and woodland) or suitability would affect landscape connectivity. We used elephant GPS collar records to parameterize movement simulation in the model. Remote sensing imagery classification results and MaxEnt models were applied to characterize woodland availability and suitability. By calculating graph-based landscape connectivity indices, we were able to examine how landscape connectivity for elephant movement responds to varying woodland patch availability and suitability conditions. A comparison between network connectivity generated by GPS records and simulated movement confirmed the robustness of the simulation. Results showed a strong positive correlation between woodland availability and landscape connectivity, whereas an increase in overall patch suitability would cause a moderate decrease in connectivity. Artificial waterhole removal did not result in significant connectivity change. We therefore suggest management focus efforts more on maintaining or increasing woodland patch quantity rather than on only improving existent patch quality for local habitat utilization management. Generally, our model provides a viable method to overcome movement data deficiency; it also

offers a systematic evaluation for landscape conditions and predicts the effects of natural processes or landscape management practices.

INTRODUCTION

Landscape conditions - such as resource availability, forage quality, and habitat suitability - dynamically interact with animal movement and subsequent habitat use across the landscape (Stokke and Toit, 2000; Smit et al. 2007; Young et al 2009), eventually affecting other elements of the landscape (Wang and Grimm 2007, Buchmann et al., 2012). Relations between animal movement and landscape conditions can be quantified by metrics of landscape connectivity; this has become a prime consideration when making conservation decisions (Adriaensen et al. 2003; McRae et al. 2008; Saura and Rubio, 2010).

One of the major conservation problems in Kruger National Park (KNP), South Africa, is local African elephant (*Loxodonta africana*) over-population and its subsequent impacts on vegetation due to patchily intensive habitat use (Whyte 2002; Kerley et al. 2008; Smit and Ferreira, 2010). One of the current management strategies in KNP is to improve connectivity in order to encourage elephant dispersal, thereby reducing their local influences on vegetation and helping to maintain landscape heterogeneity (Owen-Smith 1996; Owen-Smith et al. 2006; Van Aarde et al., 2007). Specific management practices include waterhole provisioning, fencing, and vegetation patch mosaic burning (Biggs et al. 2003; Chamaillé-Jammes et al. 2007a,b); these efforts deal with either availability or quality of resources. Yet few studies explicitly consider how changes in resource availability and suitability can affect landscape connectivity with respect to elephant movement.

Graph-based landscape networks are one of the most popular landscape connectivity models; they model connectivity by using animal movement data to identify links and incorporating species-specific traits in their calculations (Lookingbill et al. 2010; Decout et al. 2012; Xu et al. 2016). Although there is a high demand for observational or experimental movement data to inform models, it is financially prohibitive and labor intensive to collect observational movement data at optimal time intervals across the entire targeted landscape (Lookingbill et al., 2010; Bergerot et al., 2013). One way to resolve this problem is to use simulated movement data, which can be computer generated at almost no cost. However, implementing movement simulations in traditional model construction is usually difficult, considering that movement is dependent upon a complex array of variables, such as organisms' internal state, behavioral tendencies, and environmental cues (Patterson et al. 2008).

Individual-based models (IBM), however, have the potential to address movement data limitations and to quantify elephant-landscape interactions. IBM has been extensively applied to simulate wildlife response to changing environments such as home range dynamics, foraging behavior, and movement patterns (Turner et al. 1994; Nibbelink and Carpenter 1998; Dumont and Hill 2004; Morales et al. 2005; Bennett and Tang 2006; Wang and Grimm 2007; Morzillo et al., 2013; Albeke et al. 2015). The popularity of IBM can be attributed to its 1) ability to connect individual-level processes and population-level impacts 2) incorporation of the stochastic nature of movement processes; and 3) flexibility to incorporate well-established ecological models, such as graph theory-based landscape network (Tischendorf 1997; Grimm and Railsback 2005; DeAngelis and Mooij 2005; Nathan 2008; Tang and Bennett 2010; Black and McKane 2012). Multiple models have been developed dealing with elephant-landscape interactions, employing elephant habitat use as a driver of vegetation change (Ben-Shahar, 1996; Duffy et. al., 1999; Duffy et. al. 2000; Baxter, 2003; Baxter and Wayne, 2005). However, very few studies have addressed potential cascading effects on landscape conditions, which can be regarded as landscape-elephant-landscape dynamics.

In this study, we constructed an IBM to model emergent graph-based landscape networks corresponding to simulated elephant movement and to examine how landscape management of resources availability or suitability would affect landscape connectivity. Specifically, we combined GPS records and habitat suitability model to parameterize elephant movement simulation. The model overcomes actual movement data limitations and it allows to quantify landscape connectivity by integrating elephant movement with graph-based network analysis under varying landscape conditions.

METHODS

The ASC framework combines habitat suitability modeling and graph-based network analysis (Decout et al. 2012). Xu et al. (2016) demonstrated how to incorporate GPS movement recordings into the framework to develop a realistic landscape connectivity model. Building upon this, here we show how to implement IBM to simulate movement, overcoming GPS data limitations for connectivity analysis. In the following, we describe data and study area. Secondly, we describe input landscape scenarios for IBM of varying patch availability and/or suitability. We then briefly presented the IBM, including elephant movement simulation and generating emergent landscape network connectivity. Model details can be found in Supplementary Material Appendix I, which follows the standard Overview, Design concepts, and Details (ODD) protocol (Grimm et al. 2006; Grimm et al. 2010). Finally, we illustrated methods for results analysis and sensitivity examination.

Data and study area

The model was constructed from environmental data collected in southern KNP. Differences in climate and geology across the park produce a variety of landscapes (Gertenbach 1983) such that resources for different species are patchily distributed (Crooks and Sanjayan 2006). Environmental vector data of the study area, including landscape regions, surface water sites (waterholes), camp sites, and roads were provided by the South Africa National Parks Scientific Services (SANSPark). The waterhole data set contains a “status” column representing enclosure plan: “Closed”, “Open”, and “To Be Closed”. Landsat 7 Enhanced Thematic Mapper Plus (ETM+) classified imagery in Xu et al. 2016 was used to derive information about woodland locations.

Hourly geographic coordinates collected by Lotek GPS collars were used to parameterize movement patterns of elephants and were subsequently incorporated into the IBM. GPS collars were deployed on three female elephants. Though limited in sample size, the high temporal resolution offers detailed movement patterns. The collection was conducted from October 1998 to February 1999, generating 5628 coordinates in total (Fayrer-Hosken et al. 1997).

Landscape scenarios

Landscape is defined by resource availability and suitability, specifically woodlands, which provide both food and daily activity sites (e.g., sleeping and resting) for elephants in open savannas, the main habitat/ecotype in KNP (Codron et al. 2006; Harris et al. 2008). We defined resource availability as the presence of woodland patches with an area larger than 1 km^2. Patch suitability was estimated by a MaxEnt model (Phillips et al. 2004), one of the most commonly used pixel-based species distribution models for habitat analysis (Phillips and Dudík, 2008). It predicts species occurrence probability according to the relation between animal presence data and environmental variables. For modelling purpose, we only used points from three elephants collected at 8 pm each day to diminish spatial and temporal correlation of the presence data, giving us 392 presence points. Nine environmental variables were used in the MaxEnt model with a 300-meter pixel size: elevation, landscape zone type, distance to the main river, distance to seasonal rivers, distance to tourist sites, distance to woodland patches, distance to roads, distance to boreholes, and distance to concrete dams. Of the 392 presence points, 75% were used as training data, and the remainder were used to test the discriminative capacity of the model. We generated 10,000 random background points to construct the presence/background MaxEnt model and 50 replicates were processed for model construction (Phillips et al. 2006; Elith et al. 2011). The resultant predicted probability of elephant occurrence can be considered a proxy for habitat suitability (Elith et al., 2011; Decout et al., 2012).

In the baseline scenario S0, availability and suitability were derived from actual landscape data, which we called baseline landscape. S1-S5 are hypothesized landscape conditions (Table 3.1): in S1 and S2 we adjusted overall patch suitability; in S3 we projected the MaxEnt model fitted by baseline landscape, to a new waterhole provisioning situation according the waterhole file, in which we only retained waterholes with "Open" status as designated by park management; we modified woodland availability either randomly (S4) or by suitability rank (S5). It should be noticed that distance to patch is one of the MaxEnt variables, thus changes in patch availability would also affect suitability.

Movement and network simulation

We developed a model in NetLogo 5.2 to simulate elephant movement and build corresponding landscape connectivity network (Tisue and Wilensky 2004. Source code available upon request to the corresponding author). The model was initialized by two raster files (a

MaxEnt generated suitability map and an ETM+ landscape classification map with pixel values showing woodland patch ID, Figure 3.1). The raster used to define the background landscape of the model contains 230 columns and 350 rows of grid cells, where one cell represents an area of $300m^2$. One model operation lasted for 1800 time ticks, with each tick representing 2 hours such that the the model represented 5 months - the time span of GPS collection. Four model entities were modeled in the IBM: elephants, nodes, links, and pixels (For state variables of each entities, refer Appendix I). Nodes are displayed as the centroid of woodland patches.

Table 3.1 Model simulation for landscape scenarios and sensitivity analysis.

Landscape scenarios	
Scenario	**Model Adjustment**
S0	Baseline. Resource availability and suitability derived from remote sensing imagery and landscape data offered by KNP
S1	-20% Suitability for all patches
S2	+20% Suitability for all patches
S3	Projected suitability with only waterholes that are planned to “remain open”
S4	Randomly delete 20% nodes
S5	Delete nodes with top 20% suitability values
Sensitivity Analysis	
Adjusted Parameters	**Details**
Movement used for constructing network	While the IBM constructed landscape networks using simulated movement, GPS recorded movement was applied to test model robustness, denoted as **S-real**.
Time-span for defining links	We considered links to exist if an elephant could travel from one node to another within 3 days after we tested 1-day through 15-day time units, denoted as D1 – D15.

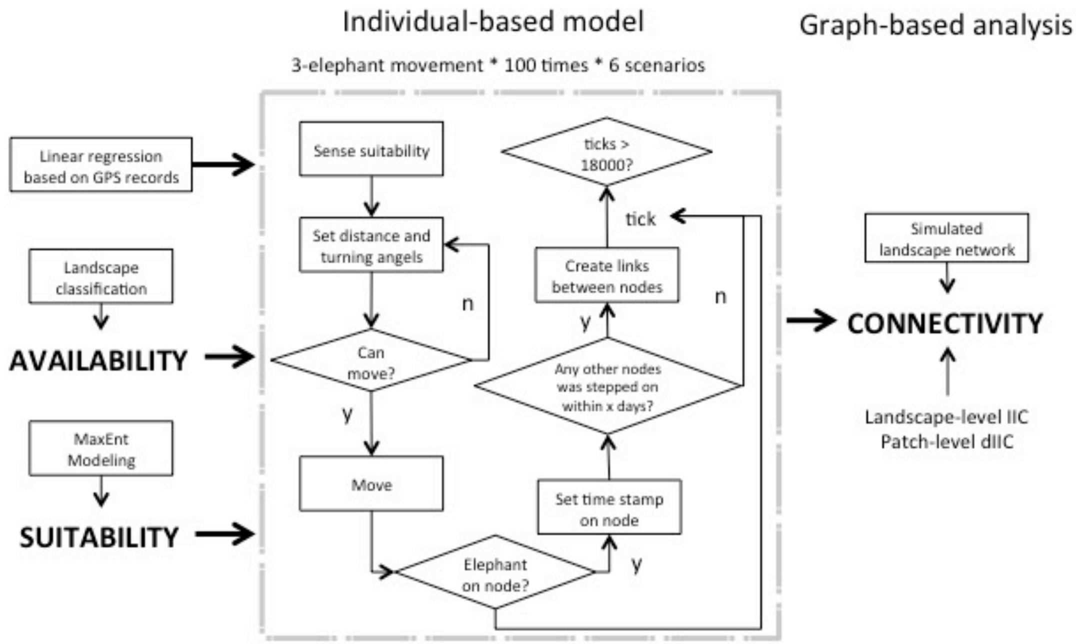

Figure 3.1 Model scheduling following "availability-suitability-connectivity" analysis.

The first part of the model simulates elephant movement according to woodland availability and patch suitability. Each step an elephant takes was achieved by deciding distance and turning angle according to the suitability of the pixel it is located in. A linear regression fitted by GPS records was used to predict the response of the elephant's relocation distance for the subsequent tick in response to the suitability value. The residual of the linear model shows a normal distribution and therefore can be regarded as stochasticity in the movement process (Appendix I). The linear model is fitted by GPS data from the three elephants and is denoted as:

$$Distance \ = \beta_0 + \beta_1 \times Suitability + Stochastisity$$

Equation 3.1

We did not find significant simple linear relationships between turning angles and patch suitability. However, the turning angle distribution is close to a normal distribution as shown in GPS records. We applied this distribution to turning angles at each tick in the model.

The second part of the model is a landscape connectivity network built according to the previously simulated elephant movement. We employed movement efficiency as a proxy for linkage between patches, measured by time spent traveling between patches. Following Xu et al. 2016, we considered no link to exist if an elephant could not travel between two given patches in 3 days. During the operation of the model, elephants left a time stamp on the pixel they were standing in at each tick. Temporal differences for all pairs of patches were calculated for each tick and subsequently links were created if the difference was less than 3 days.

All scenarios contained 300 operations to simulate 300 individual elephants moving across the landscape, generating 300 node-link landscape networks. We aggregated the 300 networks by adding up all of the non-repeating links in order to average individual difference and to quantify overall landscape connectivity.

Sensitivity analysis

We examined the model robustness from two aspects. First, we assessed whether similar landscape connectivity situations can be attained from simulated movement and actual movement. We also constructed a network with only GPS records (S-real in Table 3.1). Since this actual movement data only contained three elephants, we expected simulated networks would contain the same connectivity structures as in S-real but also adding extra connectivity information, while connectivity measures for connectivity generated from one operation (one elephant movement) would be close.

Second, we tested whether using 3-day for defining effective elephant movement in constructing landscape network was a justifiable assumption. In order to examine model sensitivity to time unit and to test the robustness of using 3-day as default setting, we adjusted the time unit for establishing links between patches. We adjusted the unit from 1-day to 15-day

(D1 – D15 in Table 3.1, in which D3 is equal to S0). We expected a longer time unit would result in higher IIC measures since elephant movement can travel across more patches in longer time.

Graph-based connectivity analysis

Graph-based landscape network analysis was conducted in R and Conefore 2.6 (Saura and Torne 2009; R-Core-Team 2014). For landscape scenarios (S0 – S5), we calculated simple indices describing network structure: total number of links, average degree, and graph density. Graph density is a measure of how close the graph is to a complete network where all nodes are connected. It is independent of landscape attributes and can offer a simple and direct demonstration of structural features of various landscape networks.

For sensitivity analysis cases D1-D15 and S-real, we calculated Integrative Indices of Connectivity (IIC) for each operation, which effectively represents connectivity conditions (Pascual-Hortal and Saura 2006, Saura and Pascual-Hortal 2007):

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

Equation 3.2

To examine the robustness of our movement simulation, we also conducted a t-test for S-real and D3 (S0) to compare IIC generated by actual movement and simulated movement.

RESULTS

According to GPS movement records, the northern and central area were the two regions most frequently visited by elephants (Figure 3.2A). Land cover classification revealed 554 woodland patches distributing across the study area. The baseline landscape was heterogeneous in terms of suitability (Figure 3.2B). The eastern area had high suitability, though elephants seldom visited it. The Area Under the Curve (AUC) value of the MaxEnt model was 75.0%.

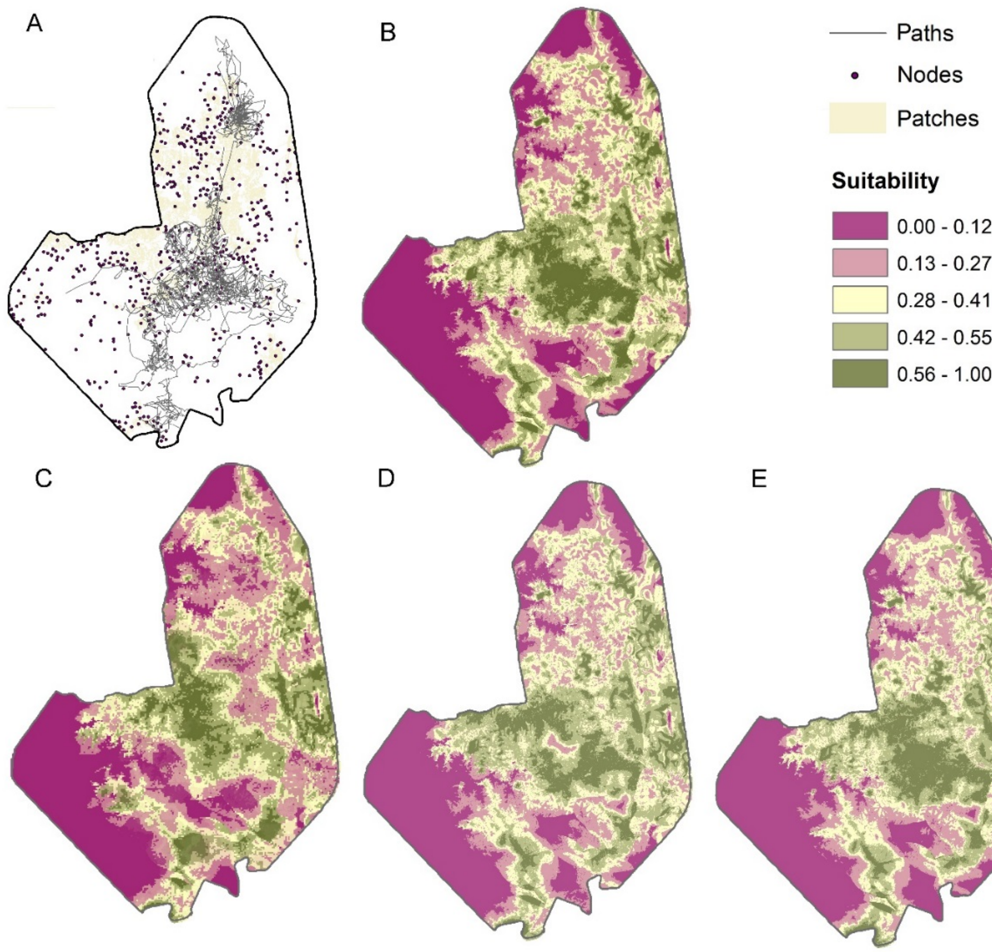

Figure 3.2 Distribution of nodes extracted from actual landscape information with GPS-recorded path overlaid. Landscape suitability maps of S0 (S-real, B), S3 (C), S4 (D) and S5 (E). Suitability maps for S1 and S2 are not presented since direct adjustments for suitability value from S0 did not change spatial patterns of suitability.

Suitability conditions change among scenarios with adjustments to woodland patch conditions (Figure 3.2C-E). S3 yielded the greatest alteration to landscape suitability patterns after removing waterholes: suitability of the central area decreased and the suitable area in the south expanded. A random removal of 20% of all nodes (S4, Figure 3.2D) did not lead to much change in suitability. Removing nodes with the highest 20% suitability values resulted in some suitability decreases at the center, though the general suitability pattern remained similar to S0 (Figure 3.2E).

Table 3.2 Rankings of environmental variable contributions to MaxEnt model in different scenarios and percentage contribution of the top three variables.

	S0*	S3	S4	S5
Elevation	1 (36.4%)	1 (37%)	1 (37.7%)	1 (37.0%)
Landscape zone types	2 (17.5%)	2 (18.7%)	2 (16.2%)	2 (18.2%)
Distance to main rivers	3 (13.9%)	4	3 (12.1%)	4
Distance to tourist sites	4	3 (13.2%)	4	3 (11.6%)
Distance to woodland patches	5	5	5	5
Distance to roads	6	6	7	7
Distance to bore holes	7	9	9	9
Distance to seasonal rivers	8	7	8	8
Distance to concrete dam	9	8	6	6

* S0 has the same suitability base map as S-real. S1 and S2 were directly calculated from S0, thus variable contributions remain the same.

Elevation and landscape zone type were the two most important variables for MaxEnt models in all scenarios, although elevation was consistently twice as important as landscape zone type (Table 3.2). Both types of waterholes only contributed a small proportion; after removing waterholes in S3, distance to bore holes and dams became the least important variables. When patches were removed in S4 and S5, the importance of distance to concrete dams increased while distance to bore holes remained unimportant.

When only using GPS records, the network is more complete in the center whereas there are almost no links in marginal areas, despite high suitability in the south and east (Figure 3.3A). There were 1344 links in total for the 554 nodes; 398 nodes had no links at all and were detached from the landscape network. The graph density for S-real is 0.009 (Table 3.4), indicating the network is far from structurally complete.

Our linear regression of the moving distance at each tick revealed a model with intercept (β_0) equal to 2.6746, and slope (β_1) equal to -0.2671 (Appendix I). Landscape networks created from the simulated movement of S0 through S3 were visually similar. In baseline scenario S0 there were two major clusters (I and II) with high connectivity (Figure 3.3B). Cluster I overlapped with the cluster shown in S-real, though it was more expansive. Adjustments in landscape suitability (S1 and S2) introduced few changes to the overall landscape connectivity structure (Figure 3.3C and D). Though the removal of waterholes (S3) shifted the spatial arrangement of landscape suitability, connectivity structure remained similar to S0 (Figure 3.3E). However, randomly removing woodland patches in S4 caused a significant connectivity decrease in terms of the absolute degree values (Figure 3.3F). Nevertheless, the clustering at I and II were still visible. After removing nodes with highest suitability in S5, cluster II disappeared from the network while cluster I remained well connected (Figure 3.3G).

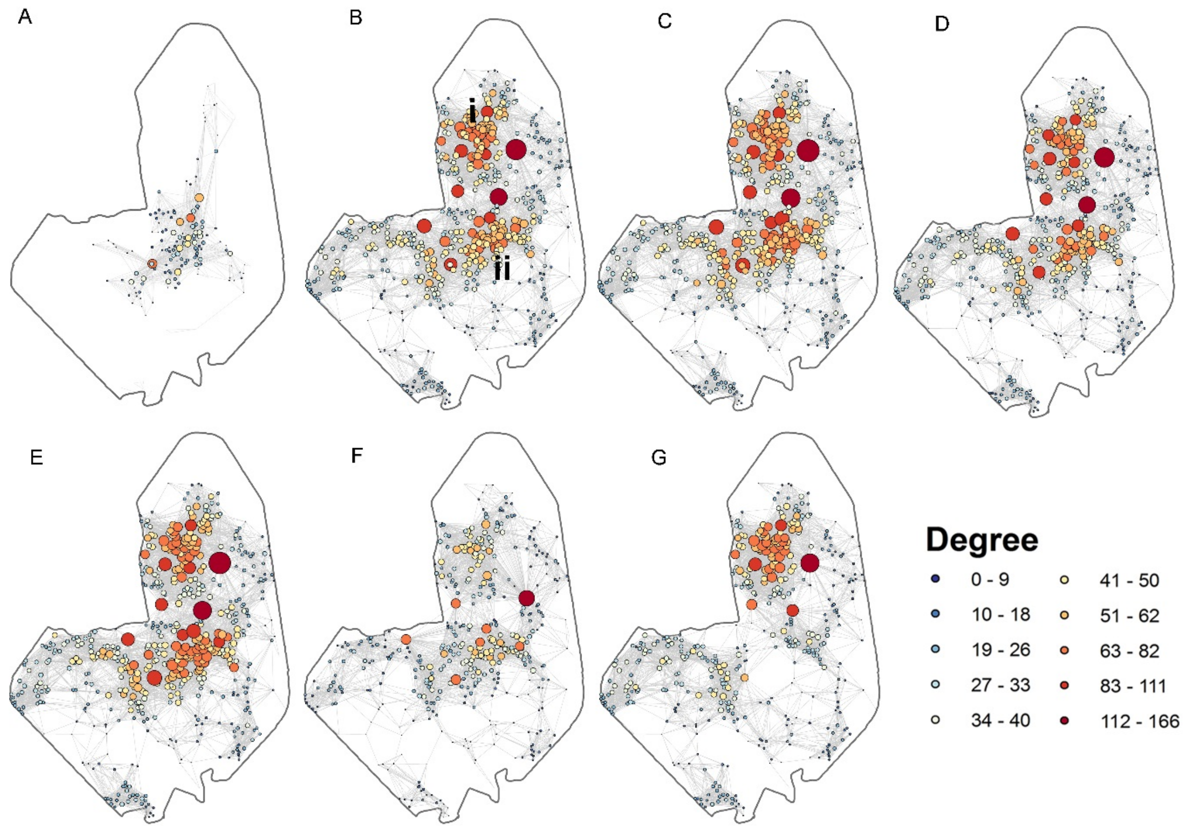

Figure 3.3 Landscape networks for GPS-recorded elephant movement (A) and for networks summarizing all 300 individuals in S0 (B), S1 (C), S2 (D), S3 (E), S4 (F), and S5 (G). Node size is proportional to Degree values.

Landscape-level graph indices describing connectivity structure are summarized in Table 3.4. A comparison among S0, S1, and S2 revealed that patch suitability has a negative correlation with connectivity level: a decrease in patch suitability (S1) caused an increase in average degree and graph density (i.e. increased connectivity), whereas an increase (S2) led to decreases in both indices. Conversely, woodland availability is positively related to connectivity. A 20% decrease in woodland availability in S4 was associated with a graph density reduction of 32.3%. In comparison, removing nodes with the top 20% suitability values (S5) produced a relatively moderate decrease in connectivity (- 17.4%). Though the impact of waterhole removal on landscape network structure is not visually easy to detect, graph density increased by 4.8% in S3.

Table 3.4 Graph description of landscape networks in different scenarios

Scenario	Total number of links	Average degree	Graph density
S-real	1,344	2.43	0.009
S0	9,512	17.17	0.062
S1	10,177	18.37	0.066 (+ 3.2%)
S2	9,021	16.28	0.059 (- 4.8%)
S3	10,011	18.07	0.065 (+ 4.8%)
S4	5,028	11.35	0.042 (- 32.3%)
S5	5,137	11.57	0.051 (- 17.4%)

D1-D15 proved that a longer time unit for landscape network construction produced higher landscape connectivity levels in terms of IIC. IIC increased quickly from 1D to 3D, but the rate slowed down after 3D when IIC tended to be saturated (Figure 3.4). The IIC of the 300 elephants simulated in S0 has a mean of 741.702, while the average IIC generated from each of the 3 females is 711.714. The t-test results revealed a p-value equal to $2.2e^{-16}$ (< 0.05) thus proving that the IBM modeled landscape connectivity network using 3-day time unit was statistically not different from the one created from GPS data of real elephants.

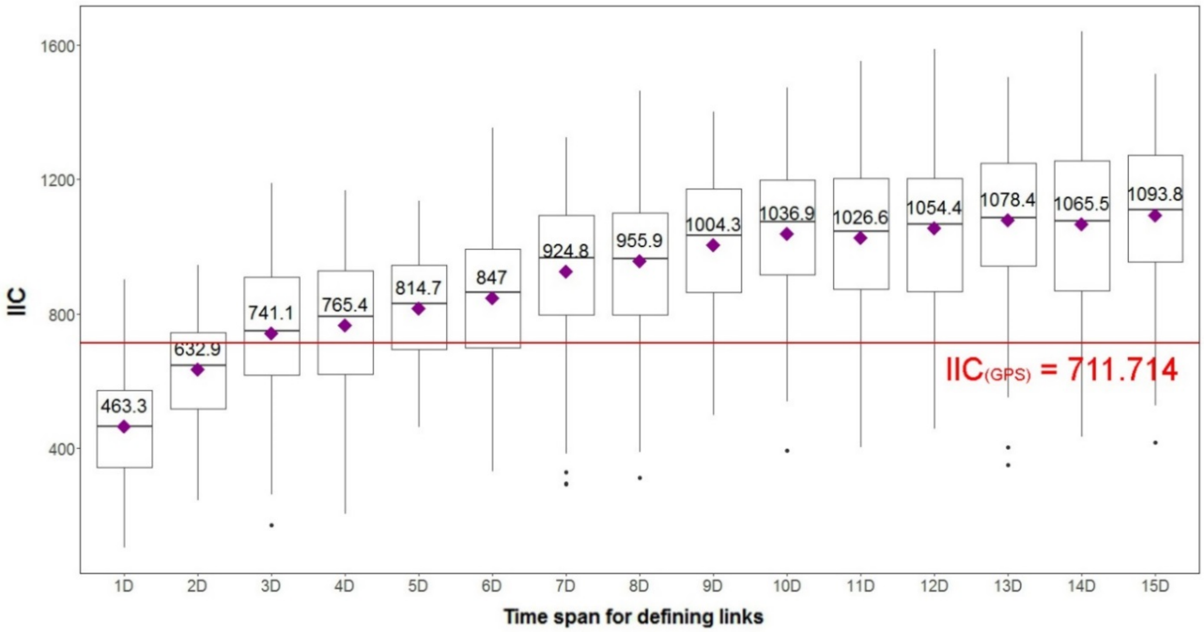

Figure 3.4 (A) Summary of Landsacpe IIC for 300 runs versus time span for defining links. Purple dots stand for mean IIC values for each time span and box denotes the median, 25% quantile, and 75% quantile. Red line denotes average IIC generated by the 3 GPS-collared elephants.

DISCUSSION

Our study integrates remote sensing, habitat suitability modeling, and a simple Individual-Based Model to investigate the impacts of woodland availability and habitat suitability changes caused by management practices or natural dynamics on landscape connectivity. The combined graph-based network and IBM effectively quantify and visualize simulated elephant movement and emergent landscape dynamics. Our model overcomes observational data limitations: when only using GPS data, modeled landscape networks are incomplete and connectivity information for regions not covered by GPS recordings is missing (Figure 3.3A). The three collared elephants did not fully explore the available and suitable landscape in a period of 5 months. However, by using IBM simulation we generated alternative routes to cover the entire area and thus add connectivity information (Figure 3.3). A comparison of the graph density of S0 (0.062) and S-real (0.009) also demonstrates the additional connectivity information introduced by IBM simulation. Moreover, we demonstrated that our IBM-simulated movement and usage of a 3-day time unit for landscape network construction are robust – simulated movement revealed similar landscape connectivity measures to actual individual elephant movement (Figure 3.4).

Connectivity responses to availability and suitability

Landscape connectivity for elephant movement is more sensitive to woodland availability than patch suitability. Changes in connectivity caused by alterations to suitability are less than 5% in terms of graph density measures, whereas alterations to woodland availability produce graph density differences up to 32.3%. The smaller impact of changes in suitability is partly due to an elephant's ability to adjust its movement (e.g. speed and distance) to reach the remaining available woodland patches (Loarie et al. 2009; De Knegt et al. 2011; Chamaillé-Jammes et al. 2013). Nevertheless, the loss of patches both negatively impacts suitability (Figure 3.2D) and impedes elephants' ability to effectively travel between patches in a timely manner.

In addition, while there is a positive relationship between connectivity and woodland availability, connectivity and patch suitability are negatively related. Connectivity level goes down when there are fewer woodland patches. On the contrary, comparisons between S0 and S1, S0 and S2, S4 and S5 reveal that connectivity increases (or decreases less as in S5) when habitat suitability is reduced. Since animals tend to choose habitat with high productivity, they expand their range when their home range does not hold resources of sufficient quality (Wang and Grimm 2007). In other words, lower habitat quality would result in more active animal movement and thus higher connectivity. The negative slope in our linear regression fitted by GPS data also indicates that elephants increase their relocation distance in response to a drop in suitability at their current locations.

The negative relationship between suitability and connectivity shown in our study seemingly contradicts the commonly accepted opinion that suitability and connectivity are positively correlated (Hunter et al. 2003; Poor et al. 2012; Santos et al. 2013). In these studies, a sufficiently high connectivity makes it possible for organisms to cross; this is usually measured by occurrence of movement events (e.g. Decout et al. 2012). However, this contradiction is mainly caused by ecological attributes of studied animal. In this study, the high mobility of elephants and their large size, there is almost nothing that can impede their movement within KNP except for man-made fences. We therefore measured connectivity by moving efficiency of elephant, i.e. time spent moving.

Landscape management for elephant conservation in KNP

One of the conservation concerns raised by managers in KNP was the overabundance of elephants in certain regions. The effectiveness of artificial waterhole provision for managing African elephant populations has long been debated (Chamaillé-Jammes et al. 2007 a; Chamaillé-Jammes et al. 2007b; Smit et al. 2007a; Smit et al. 2007b; Chamaillé-Jammes et al. 2013). According to our ASC analysis for S3, although removal of waterholes changed the overall suitability structure more than any other scenario (Figure 3.2), the change in final connectivity measures were moderate (Table 3.4). One interpretation is that waterhole provisioning may change the suitability structure but not the magnitude of suitability of the region as a whole, considering their small contribution to MaxEnt model performance (Table 3.2). The suitability models and the subsequent connectivity results were therefore insensitive to changes due to waterhole provisioning. Besides, elephants adjust movement strategies to water availability accordingly and therefore they can adapt to a broad range of waterhole availability (Loarie et al. 2009; Chamaillé-Jammes et al. 2013). In addition, female elephants were found to be less associated with areas close to artificial waterholes in KNP (Smit et al. 2007a). However, our dataset was built from entirely female movement data, it may be less responsive to changes in waterholes than a full population.

Researchers who support waterhole management as a population control tool believed that artificial water supply is a major cause of local population density and therefore manipulating waterholes can spread elephant populations across the landscape (Chamaillé-Jammes et al. 2007 a; Chamaillé-Jammes et al. 2007b; Chamaillé-Jammes et al. 2013). However, Smit et.al. (2007a) argued that the efficiency of waterhole provision is area- and population-specific and will depend on management objectives. Elephants, as a species with high dispersal ability, are not surface-water-limited populations, and the easy availability of natural water in KNP may mitigate effects of artificial water management (Smit et al. 2007a; Smit et al. 2007b). Considering our IBM simulation results, we agree that water provision may not be effective as an elephant population management tool in KNP. The waterhole removal based on the closure plan will not have significant impact on connectivity for elephant movement in the park. However, the provision of artificial waterholes does create negative impacts on other animal and plant species, such as desertification and alien infestation (Thrash 1998; Van Wyk 2011). Thus, the policy to gradually close artificial waterholes in KNP can be beneficial for the overall ecosystem.

The simulation results also indicate that woodland patch quantity should be the priority for connectivity maintenance. Connectivity goes down the most when nodes are randomly removed (S4). Therefore, more efforts should be made to maintain or improve the existence of woodlands, even if their quality is poor, rather than protecting only patches with high quality vegetation. Previous studies have shown that the loss of critical nodes with high suitability values, which serve as "bridges" connecting clusters, will cause a significant drop in the ability of animals to reach other high quality patches and therefore decrease in connectivity (Lookingbill et al. 2010). However, highly mobile large animals such as elephants are able to disperse to other nearby habitat patches which may only contain moderate suitability but allow further dispersal (Keitt et al. 1997; Saura and Rubio 2010). As the landscape network shown in Figure 3.3F demonstrates, the loss of the central cluster does not cause critical damage to connectivity in other regions. In fact, the overall graph density decrease is not as serious as S4 (Table 3.4). In this case, the animals actually may explore the landscape more broadly instead of remaining in the central region.

CONCLUSION

Effective elephant conservation and management in KNP requires a thorough understanding of the species' responses to landscape changes. Our model demonstrates that resource availability and habitat suitability have impacts on elephant movement and consequently their habitat utilization. An increase in the number of woodland patches would effectively promote connectivity for elephants. Though the modeled scenarios in this study were mostly hypothetical, they can be used to simulate potential connectivity changes for species management planning. To alleviate locally intensive habitat utilization by elephants in KNP, we suggest management focus efforts more on maintaining or increasing woodland patch quantity rather than focusing on improving existent patch quality. In addition, waterhole removal only affects elephants moderately and may not be a major concern of management. Further movement data for bulls or mixed herds from other regions in KNP will help to improve the IBM by offering additional information to describe population movement in the park. Generally, our study demonstrates the utility of combining remote sensing data, habitat suitability models, and individual-based models to aid a systematic evaluation of landscape conditions.

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CHAPTER 4

CONCLUSIONS

Humans are increasingly altering landscapes, modifying wildlife habitat, and affecting global climate(Parmesan, 2006). For protected areas such as Kruger National Park (KNP) in South Africa, managers and scientists now emphasize the incorporation of ecosystem changes in management plans, which leads to the need to understand the links between different parts of the system(Mabunda, Pienaar, Verhoef, Du Toit, & Biggs, 2003). This thesis demonstrated an example to understand relations between animal movement and the changing landscape conditions.

The first manuscript demonstrated the use of an "Availability-Suitability-Connectivity (A-S-C)" framework for a systematic landscape condition evaluation, coupling satellite imagery analysis, habitat suitability modeling, and graph theory. Following the framework, I developed an individual-based model (IBM) to simulate elephant movement and the emergent graph-based landscape networks in the second manuscript. I applied the model to examine landscape connectivity conditions for elephant movement with varying resources availability and habitat suitability. Overall, the analysis framework offered an integrative perspective to prioritize habitat patches in terms of their importance facilitating elephant movement and form landscape connectivity. The model revealed appealing features to incorporate habitat suitability model and individual-based model in a graph theory framework, which overcomes movement data deficiency, offers a systematic evaluation for landscape conditions, and allows predictions of impacts caused by natural processes or landscape management practices.

KEY FINDINGS

Applying the A-S-C framework in Chapter 2, we prioritized individual habitat patch importance for elephant movement, from which we also identified different ways that patches contribute to overall connectivity. We successfully adopted the observational GPS data into the construction of landscape network by using a time unit to measure efficiency of elephants moving from one patch to another so as to define links. By using the MaxEnt to model determine patch suitability and for node attribution to calculate connectivity indices, we incorporated landscape heterogeneity into the analysis. Based on patch prioritization results, we partitioned the landscape into zones suitable for different conservation plans, though we found that a more detailed zoning requires a more comprehensive movement input. In our zoning example, the Core zone is characterized by high connectivity and compacted arrangement of important nodes and is sensitive to woodland degradation. The Bridge zone is featured by the linear arrangement of highly connected nodes and efforts to maintain current patch availability were suggested.

We filled the gap of our GPS data deficiency by applying the IBM we developed in Chapter 3. The integrative model was able to show that landscape changes indeed have impacts on elephant movement, and therefore, landscape connectivity for movement. However, elevation is the most affective factor and artificial waterholes only contribution a small portion of elephant presences. A simple linear regression was employed to guide movement parameterization in IBM, and the expected large residual variation was used as stochasticity in the model, which allows us to maintain the stochastic nature of movement. Surprisingly, while woodland patch availability is positively related to connectivity level, a moderate decrease in patch suitability may actually help promote dispersals of elephants. As we hypothesized, a larger temporal scale when defining links between patches led to a higher connectivity level of the landscape.

However, our 3-day rule revealed enough space for variations in different scenarios, while still being able to fully describe the connection situation. Based on our simulation results, we suggested more efforts to be put on maintaining woodland patches, but not necessarily on improving patch quality. Waterhole removal is a reasonable strategy that may benefit the general heath of the ecosystem in KNP with only moderate effects on elephant movement.

FUTURE WORK

Further study will focus on model validation using field data and model improvement by incorporating more movement data for bulls or mixed herds of elephants from other regions in KNP will help to improve the IBM, especially to offer additional information to describe population movement in the park. Additionally, I would like to expand this study to other wildlife species in other parts of the world, especially ones with high mobility and actively interact with the changing landscape.

I have been long interested in how to better use quantitative methods to predict species distribution and use of resources at the landscape level. Models based on GIS offer powerful tools to achieve this, yet they mostly depend on species occurrence data(P Anderson et al., 2006) and are therefore problematic when extrapolating information to novel environments. The model I used in this study, MaxEnt, is one of the most popular modeling packages in the recent 10 years (Elith & Leathwick, 2009; Phillips & Dudík, 2008) and is also under debate for its modeling performance(Renner & Warton, 2013). An alternative modeling philosophy is modeling species distribution and habitat using the ecology of organisms based on ecophysiology and organism traits (Kearney et al., 2008). This requires a deeper knowledge about theoretical ecology, wildlife biology, and evolution.

Further, this thesis needs more qualitative inputs from a social perspective, which is one of possible direction to put futures efforts. The nine “Malawi Principles” for setting conservation priorities acknowledged conservation is essentially a matter of social choice(Prins, 1999). Thus, the society benefits in the long run and understandings of how ecosystem functions as a whole should always be considered in conservation related studies. As a geography student, I recognize the social-physical boundary even within the discipline of geography. With this caveat in mind, future efforts will purse questions of conservation from a social perspective and synthesize knowledge from both social and technological sides.

FINAL NOTES

This thesis is a first step using an interdisciplinary perspective to look at a wildlife problem. Throughout the thesis, I aimed to draw on combination geography (geospatial information science, remote sensing science) and ecology (landscape ecology, wildlife ecology ecology). Likewise, a wide variety of research tools were used, including remote sensing imagery analysis, geospatial analysis, statistics, individual-based modeling, habitat suitability modeling, and programming in Python and R. A lesson from this research experience is science, technology, and practice are not, and should never be, limited within disciplinary boundaries.

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Appendix I: Individual-based Model ODD

Overview

This individual-based model description follows the “Overview”, “Design concepts”, and “Details” (ODD) protocol (Grimm et al., 2006). The model was developed in NetLogo 5.2 (Tisue and Wilensky, 2004). Input data were generated using ArcGIS 10.2. All referenced tables and figures, if not shown here, can be found within the manuscript.

Purpose of the model

The model is designed to assess the relationship between woodland patch availability, patch suitability, and landscape connectivity for elephant movement in the Kruger National Park, South Africa. The model contains two parts: 1) Simulating elephant movement which connects woodland patches across the landscape; 2) Generating landscape networks for connectivity analysis.

Entities, State Variables, and Scales

The model has four entities: elephants, links, nodes, and patches. Patches here is a NetLogo-specific concept, which refers to the background cells/squares in the model and it is different from the woodland patch we mentioned in the manuscript. To avoid confusion, we used the word “pixel” to represent the NetLogo patch hereafter. Table I-1 lists details of state variables for the four entities.

The simulated landscape represents the area for GPS collecting. There are 230 columns and 350 rows of grid cells overall. One cell represents an area of $300m^2$. One operation of the model lasts for 1800 time ticks with each tick representing 2 hours. Thus the total temporal extent of the model is 5 months. Both the temporal interval and temporal extent match with the ones of GPS recordings.

Table I-1 Summary of state variables of entities in the IBM.

Entities	Variable	Description	Possible value
Elephant	Distance	Moving distance for this tick	> 0
	Angle	Relative turning angle for this tick	0 – 360
	Destination	The pixel at <Angle> with <Distance>	ID of a pixel
	Location	Map coordinates	x: 0 – 230; y: 0 – 350
Link	End1/2	ID of the end nodes of a link	
Node	ID	ID of the woodland patch that it represents	0 – 554 (differ in scenarios)
Pixel (patch in the original NetLogo definition)	Suitability	Suitability value read from the background MaxEnt suitability maps	0 – 1
	Node-id	If this pixel belongs to a woodland patch, then Node-id is equal to the ID of the node representing this patch	-
	Tick-p	Recording the tick of the most recent moment that an elephant steps on the patch represented by the node	0 – 1800

Process overview and scheduling

At each tick, an elephant will conduct “Sense suitability”, “Set distance and turning angle” and “Move”; Nodes will conduct “Time stamp” and “Create links”. Each of the step mentioned is one submodel (Figure 3.1).

Design Concept

Elephant movement is affected and in turn reflects connectivity conditions of landscape structure. Elephant movement is also directly related with resources availability and suitability. In this model, elephant moving distance is estimated in relation to suitability. Graph theory-based network is then constructed by analyzing whether landscape patches are connected by the simulated movement paths.

Model adaption is achieved by the “set distance and turning angle” submodel. Elephant adjusts its movement for the coming tick according to pixel suitability where it locates at. GPS records show that elephants always relocate in every two hours. Accordingly, elephant in this model consistently move across the landscape.

Stochasticity of the model is fulfilled by the “Set distance and turning angle” submodel. Uncertainties are included in both setting relocation distance and turning angle (Refer submodel section for details).

The goal of this IBM to generate a landscape network based on simulated movement paths. Output for one model operation is a list of links with IDs of two ends, which can be input into R for further graph-based analysis. Elephant moving paths and emergent landscape network are updated in real time in the view window.

Details

Initialization

Landscapes are initialized based on the input raster file (see input for details). For elephant, initialization involves specification of its location, which is a random location within the study area boundary. Elephants are born with a random turning angle, a random Distance, therefore a random destination. For all pixels, Tick-p is set to -9999 at the beginning.

Input data

Input data include two raster files. The two raster files are: 1) A raster layer generated from MaxEnt model. Raster values are assigned to corresponding pixels in IBM as its Suitability. Since maps in NetLogo have to be rectangular, only pixels within the study area have Suitability value, while pixels outside of the area showing Suitability as “NoData”; 2) A raster generated from ETM+ image classification results, denoting the location of woodland patches. Raster values are equal to patch ID and are assigned to the overlay pixels as their Node-id. Only pixels overlaid with existent patches have Node-id value, while other pixels showing Node-id as “NoData”. We operated 6 different landscape scenarios with varying input (Table 3.2). To be specific, S1 and S2 changed patch suitability through decreasing/ increasing the values by 20%. For S3 to S5, either environmental predictor “Distance to waterholes” or “distance to patch” were modified, therefore, node suitability was reprojected in MaxEnt based on the model fitted by the original landscape condition in S0.

Other 16 scenarios belonged to sensitivity analysis. S-real used only GPS data for landscape network construction instead of using simulated movement. Aware that GPS records only provided movement information where these elephants had stepped on during that 5-month data collecting period, we expected S-real can only reflect connectivity conditions for these sampled regions. On the contrary, IBM simulated network would keep the connectivity features for the sampled regions and also would provide additional information for areas where real movement data was lacking. D1-D15 adjusted the time unit for landscape network construction from 1 day to 15 days in order to assess the model sensitivity to network construction rule (Table 3.1, see submodel “Nodes: create link” for details about network construction).

Finally, we generated 22 sets of landscape networks for the 22 scenarios, with 300 networks in each set (except for S-real, which only contained 3 networks).

Submodels

1) Elephants: Sense Suitability

Elephant senses the suitability value of the pixel it currently steps on.

2) Elephants: Set Distance and Turning Angle

Animal movement is a complex phenomenon that is systematically affected by various biotic and abiotic factors and is usually non-linear. We used a linear regression to predict the response of elephant relocation distance for the following tick in response to the suitability value. Residual of the linear model shows normal distribution and therefore can be regarded as stochasticity in movement process. The model is denoted as:

$$Distance\ = \beta_0 + \beta_1 \times Suitability + Stochastisity$$

Equation 4.1

In this model, residuals are treated as stochastisity in movement. From the first GPS point 0, the covariant is the suitability value of corresponding pixel, and response is the distance that the elephant is going to move in the coming tick.

The linear region reveals a model with $\beta_0$equals to 2.6746, and $\beta_1$equals to -0.2671. Figure I-1A shows the histogram of relocation distance in every two hours, Figure I-1B is the validation for the linear model. The stochasticity part reveals a distribution very close to normal. Therefore, a distribution replicating the one of residuals is applied in the submodel. Following the “Sense Suitability” submodel, a distance is calculated using this equation.

We did not find significant simple linear relationships between turning angles and patch suitability. Instead, we directly applied the distribution of turning angle from the GPS recordings (Figure I-1C).

3) Elephants: Move

Elephant relocates to the set destination if it is within the study area. If not, re-do “Set distance and turning angle” until the destination is viable.

4) Pixel: Time stamp

The pixel that elephant stands on will record the time tick.

5) Nodes: Create link

It is not reasonable to define a universal distance threshold represent elephant's daily moving distance since their activity levels vary day by day. Based on our GPS records, the three females move from 7 to more than 30 kilometers. Yet, elephants manage to travel across landscape aiming to reach resources efficiently and their moving is not constrained by Euclidean distance between resource patches (Chamaillé-Jammes et al. 2013). According to this, we use movement efficiency to measure patch connectivity by testing whether the time that two patches are visited by elephants is within a certain time unit or not (Xu et al., 2016). Thus, to determine this time unit is critical. A unit that is too short rarely reveals connections between patches, and a long time span, say, 15-day, will result in most of the patches being connected so that patch importance cannot be differentiated. We consider a 3-day time unit in default setting. However, in scenarios D1 – D15, this time unit was changed to 1 day to 15 days accordingly in order to test sensitivity of connectivity measures to this link construction rule. We expected a longer time unit as temporal network construction rule would result in higher connectivity measures because elephant can travel more areas in longer time. For specific model operation, the pixel that elephant locates at will search the whole map whether there are any pixels with Time stamp smaller than 36 (equal to 3 days). If true, a link would be created connecting the two ends.

We use MaxEnt suitability values as dependent variable of a simple linear regression for relocation distance. Animals tend to adjust their location in space by moving in order to maximize integrative resources use, which is determined by the interaction of various environmental factors (Hebblewhite and Merrill 2009). Using suitability as a covariate, we are able to systematically incorporate effects of various environmental variables without fitting a complex movement prediction model, such as space-space models (Patterson et al. 2008). We are aware that elephant relocation distances may not have a restricted linear relation with habitat suitability and spatial correlation still exists regardless of the fact that we extracted presence points by day. It is impossible to draw the true relationships between covariates and dependent variables in real world situations (Miao et al. 2009), and we do not aim to precisely estimate parameters for our movement model. Instead, we hope to have the general response to direct the "Move" submodel in IBM. Additionally, linear regression offers general trend of how moving distance changes with suitability. It also retains residuals normally distributed as stochasticity nature of animal movement, which is especially important for ecological modeling concerning the stochastic nature of the systematic dynamics and individual-based processes (Black and McKane 2012). Therefore, a linear regression using suitability values as single covariate fits the purpose well.

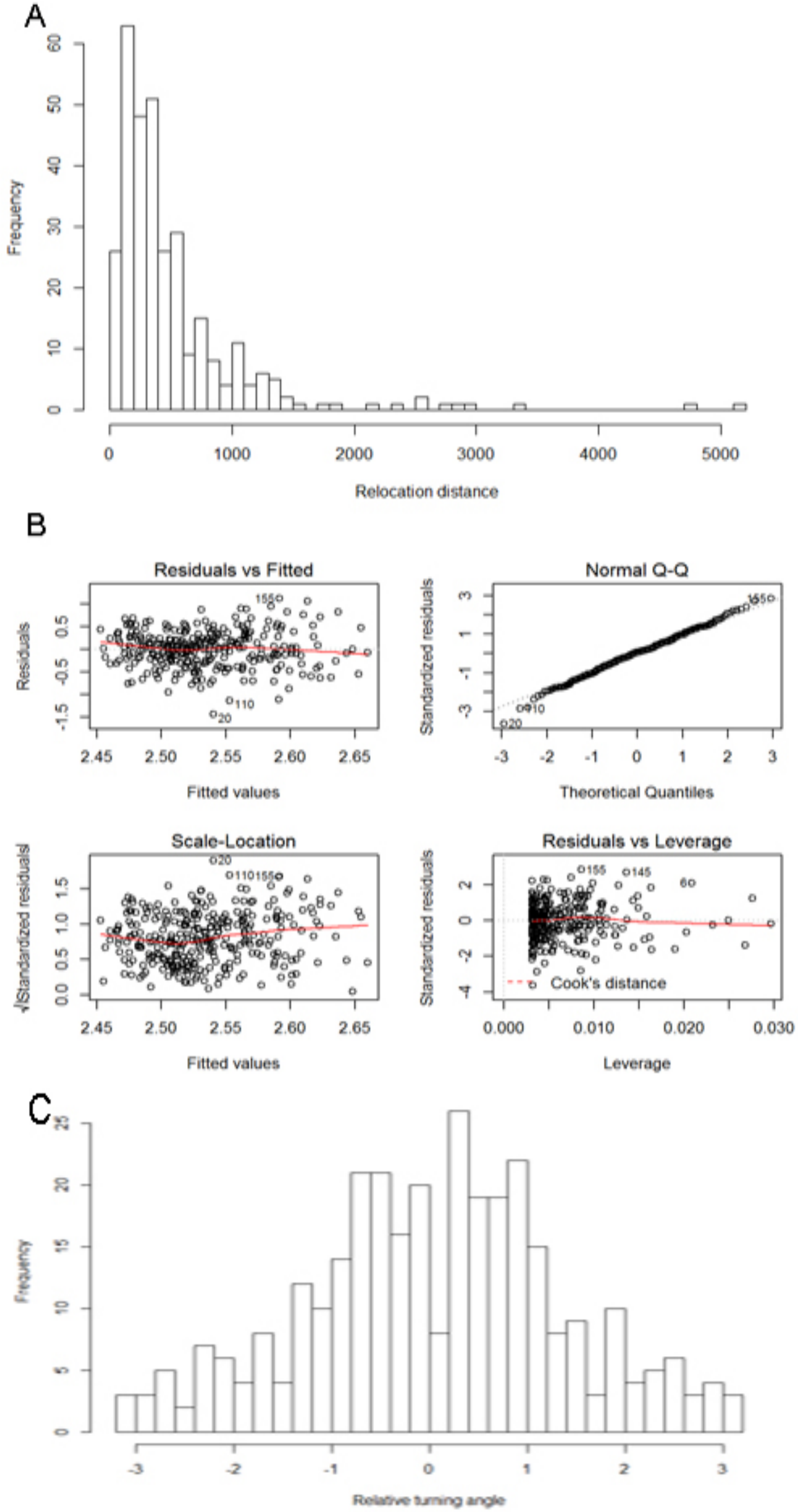

Figure I-1 Statistics summary for GPS recordings: (A) histogram of relocation distance for every two hours; (B) validation for the linear regression; (C) histogram of relative turning angles every two hours.

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