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Publication Date
2014

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By
Miriam Tsalyuk

A dissertation submitted in partial satisfaction of the
requirements for the degree of

Doctor of Philosophy

in

Environmental Science Policy and Management

in the

Graduate Division

of the

University of California, Berkeley

Committee in charge:

Professor Wayne M. Getz, Co-chair
Professor Maggi Kelly, Co-chair
Professor Justin S. Brashares
Professor Mary E. Power

Fall 2014

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Abstract

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by

Miriam Tsalyuk

Doctor of Philosophy in Environmental Science, Policy, and Management

University of California, Berkeley

Professor Wayne M. Getz and Professor Maggi Kelly, Co-chairs

Rangelands cover about half of Earth's land surface, encompass considerable biodiversity, and provide pivotal ecosystem services. However, rangelands across the globe face degradation due to changes in climate, land use, and management. Moreover, since herbivory is fundamental to rangeland ecosystem dynamics, shifts in the distribution of herbivores lead to overgrazing and desertification. To better understand, predict, and prevent changes on rangelands it is important to monitor these landscapes in a timely and efficient manner. Remote sensing can be a viable tool for measuring such change. However, the high spatial and temporal variability of rangeland vegetation, high reflectance from soil background and senesced vegetation during prolonged parts of the year, present challenges to the application of remote sensing in these ecosystems. The goal of my dissertation is to address these challenges and advance the application of remote sensing and geographic information system (GIS) to quantify vegetation and herbivores on rangelands across the world. My dissertation aims to address the connections among three main components of rangelands: the landscape, herbivores and human factors. I first develop a method to characterize the rangeland landscape by measuring and mapping detailed vegetation variables in Etosha National Park, Namibia. Etosha is a 22,270 km^2 semiarid savanna, which encompasses great diversity of flora and fauna. I then examine how landscape variables affect the movement patterns of a large mammalian herbivore that is a keystone species in Etosha, the African elephant (*Loxodanta africana*). Finally, I develop tools to monitor how herbivory affects the productivity of rangelands conservation easement in California.

In the first chapter, I outline the importance of rangelands and the threats these ecosystems face. I review the main challenges of measuring change processes on rangelands and describe some of the remote sensing based approaches that have been used to address these challenges. In the second chapter, I show that time series analysis of Moderate Resolution Imaging Spectroradiometer (MODIS) vegetation indices can produce excellent results in predicting detailed field measurement of vegetation in Etosha. Using three innovative approaches I improve the prediction of both woody and herbaceous vegetation on the landscape, providing good measurements of vegetation cover, density, and biomass over large spatial extents. First, I develop field methodology that combines visual estimation of vegetation cover and vegetation

type together with accurate field measurements. Second, by integrating time series of remote sensing data over six years and consolidating this information with partial least square regression, I achieve accurate models of vegetation measurements. Third, by using four different MODIS-based vegetation indices: Normalized Difference Vegetation Index (NDVI), Enhanced vegetation index (EVI), Leaf Area Index (LAI), and Fraction of Photosynthetically Active Radiation (FPAR), I measure different vegetation forms – grasses, shrubs, and trees, and thereby provide valuable information for monitoring and conserving Etosha's savanna vegetation. An exciting result from this chapter is the ability to transfer the application of these models in space, to other parts of the reserve, and in time, to other seasons and years. This emphasizes the validity of the models I have developed for predicting vegetation measurements and the ability to use these models in other locations.

In the third chapter, I use the detailed vegetation maps I have created for Etosha National Park to understand resource selection of African elephants. I show how landscape variables affect both the speed and the direction of elephants' movements. Elephants prefer to move into areas with higher grass and shrub biomass, but lower tree biomass. Moreover, elephants prefer to be closer to water sources and, interestingly, to roads. Elephants' resource selection is influenced by the sex and the age of the individual. Importantly, temporal variation significantly influences the movement in response to the landscape: elephants choose different resources at different times of the day, which illustrates the behavior underpinnings of their resource selection. Moreover, they respond differently to resources at different times of the year, which highlights the ecological importance of these resources to the elephants. This chapter provides valuable information on how to manage resources in a manner that will promote the conservation of these magnificent keynote animals.

In the fourth chapter, I use MODIS satellite data to monitor the effects of grazing on rangeland conservation easements in California, using as a study case the Simon Newman Ranch, a conservation property own by The Nature Conservancy. I use time series information of three vegetation indices to measure Residual Dry Matter (RDM), which is the dry grass matter left on the ground in the fall, at the end of the grazing season. RDM is a measure of grazing pressure; moderate levels of RDM are correlated with the health of rangeland ecosystem, soil stability, water retention and biodiversity of native plants and wildlife. Therefore RDM levels are used by The Nature Conservancy and other land managers as a conservation easement compliance measure. I develop a rapid, easy to use, efficient and robust methodology to predict RDM in the fall using spring maximum and annual sum of vegetation index values. My results show that MODIS-based Leaf Area Index (LAI) is the best measure of dry grass biomass. Most importantly, I demonstrate that MODIS data can be efficiently used by range managers and conservationists to estimate RDM easement compliance.

In summary, in this dissertation I develop the use of quantitative spatial tools to measure both vegetation and herbivores on rangelands and to characterize landscapes on large spatial scales. I conduct interdisciplinary research connecting landscape ecology, remote sensing science and wildlife ecology. I demonstrate how freely available MODIS satellite imagery and open source software can be used by conservation managers to understand vegetation patterns and wildlife distribution in relatively easy, cost efficient, rapid and robust ways. The tools I develop in this dissertation identify and quantify change in rangelands. My results inform targeted management and conservation practices, and contribute to improve monitoring and to the understanding of these imperiled ecosystems.

In Loving Memory of my Grandmother, Polina Rozin
who taught me to marvel at the wonders of nature

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List of common abbreviations

ANOVA - Analysis of Variance
EVI – Enhanced Vegetation Index
FPAR - Fraction of Photosynthetically Active Radiation
GIS – Geographic Information Systems
GPS - Global Positioning Systems
LAI – Leaf Area Index
MODIS – Moderate Resolution Imaging Spectroradiometer
NDVI – Normalized Difference Vegetation Index
PLSR – Partial Least Square Regression
RMSEP – Root Mean Square Error of Prediction
RDM – Residual Dry Biomass
SSF – Step Selection Function
VI – Vegetation Index

Acknowledgements

My PhD years were a rich intellectual and personal learning experience. I am deeply grateful to many people who have accompanied, taught, supported, and inspired me throughout this adventure.

First and foremost, I am grateful to my two wonderful advisors: Professor Wayne Getz and Professor Maggi Kelly, without whom I would not be here today. Wayne – thank you for welcoming me to Berkeley and for opening so many possibilities for me. Coming to UC Berkeley is to have the world at your feet: world-leading researchers, luminaries in multiple fields, people working in every part of the plant, and rich access to resources, facilities, and literature. No one could have opened me the doors to this grand world as well as you did. Thanks to you I had the wonderful opportunity to work in the beautiful Etosha National Park, Namibia, and was connected to work with wonderful colleagues from Namibia, South Africa, Israel, Germany, and the US. Your sharp and broad-minded thinking has always challenged and inspired me. The wealth of your new and big ideas keeps amazing me. Above all, I am grateful for your kindness and your generosity. I am also grateful to Jenny Getz for opening your heart and your home to us, Wayne's grad students, and for being such a great role model for a fantastic family.

Professor Maggi Kelly was deeply involved with all parts of my graduate education. She served on any type of committee possible on the Berkeley campus: she was my qualification exams committee member, my teacher, my dissertation committee member, and eventually – my dissertation adviser. Maggi - Your inspiration and support in every step of the way were invaluable. You have excited me about remote sensing and enabled the interdisciplinary and applied nature of my work. After each and every meeting we had I came out not only full with new ideas, clear direction, and a definite plan, but also infused with renewed energy and excitement for my research. Your mentorship in every part of the process was priceless. You stood by me in the hardest moments and helped me keep going. I couldn't have done this without you.

I am grateful to my other dissertation committee members. Professor Justin Brashares, the heart of wildlife ecology at Berkeley, always shared exciting new ideas, valuable advice, and helpful comments on my work all along. Professor Mary Power taught me to think like an ecologist and has inspired my work. As graduate students in Berkeley we are lucky to learn from many other incredible professors. I am specifically grateful to Professor Louise Fortmann, who taught me to look at the social perspective of environmental problems and who tirelessly supports women researchers. Professor Maureen Lahiff taught me everything I know about statistics and was kind and patient enough to continue helping me along the way. Professor John Radke has made GIS incredibly fun and relevant for just about - anything.

It had the good fortune to belong to the fabulous community of the Environmental Science Policy and Management (ESPM) department's graduate students. I am honored to be part of such talented, driven, and kind group of people, who are truly committed to protect this Planet. Special thanks to my lab mates both in the Getz and in the Kelly lab, for sharing countless advices, ideas, support, and many lunches and glasses of beer. Special thanks to Wendy Turner, Andy Lyons, Holly Ganz, Karen Weinbaum, Pauline Kamath, Steve Bellan, Carrie Cizauskas, Royi Zidon and Sliman Ben Miled, for valuable help with ideas and analysis. I am grateful to the Kelly lab for welcoming me into your group and for their valuable support and feedback. I thank all the many friends and colleagues I met in conferences, meetings, and summer schools along the way. You kept reminding me that we are all part of a wonderful conservation ecology community and that together we can make a difference.

I thank the Namibian Ministry of Environment and Tourism (MET) for permission to conduct field work and for providing facility resources for work in Etosha National Park. I am grateful to the staff at the Etosha Ecological Institute (EEI) for providing valuable data and for scientific and technical assistance, particularly Werner Killian, Shayne Kòtting, Wilferd Versfeld, Marthin Kasaona, Birgit Kòtting, Ndapanda Kanime, and Erastus Ithana. Many thanks to Etosha's wardens and rangers and to the staff of Namibia Wildlife Resorts (NWR) in Etosha, for joining me for field work, enduring long days of sun and rain together, and for protecting my life. I have learned so much from them about the ways of the animals in Etosha. I am grateful to my field assistants, Emilia Haimbili and Maria Johannes, for incredibly hard work collecting field data and for teaching me about life in Namibia. The National Herbarium of Namibia performed excellent work identifying plant species samples. The bright UC Berkeley students: Audrey Taylor, Janelle Dorcy, Ashley Poggio, Angie Pettenato and Jake Toy, helped in digitizing immense amounts of data and managing my databases. It was great to work with you guys.

The Geospatial Innovation Facility at UC Berkeley provided state of the art facilities and geospatial support. Specifically, I thank Kevin Koy for teaching me so much about remote sensing and GIS and for always keeping a smile and good spirit. Mark O`Connor and Brian Galey have assisted with GIS analysis, data management, and technical challenges.

I am thankful to the San Francisco office of The Nature Conservancy, and to my collaborator, Scott Butterfield, for enabling me to do applied conservation research. I thank Professor Björn Reineking, from the University of Bayreuth, Germany, for collaboration on the elephant movement research, valuable ideas and help with analysis. Animove 2013 summer school at the Max Planck Institute for Ornithology, Radolfzell, Germany, was a superb learning experience that has significantly advanced my ability to analyze spatial and movement data. I am particularly grateful to Martin Wegmann, Kamran Safi and Nathalie Pettorelli for excellent teaching and organization of this school.

Many thanks to my dissertation writing group: Siew Chin Chua, Aghaghia Rahimzadeh, Karen Andrade, and Esther Kim. I am grateful for multiple revisions of drafts, endless support, and holding each other accountable through challenging times. Sabrina Soracco, from the Berkeley graduate division has provided our group with valuable guidance and taught us so many things we even didn't know we don't know.

My research was made possible thanks to generous funding by the Oran Pollak grant and graduate student research support from The Nature Conservancy; Science and Engineering Fellowship from the Center for Emerging and Neglected diseases (CEND); the Andrew and Mary Thomson Rocca dissertation research fellowship; Bob Lane Endowed Graduate Fellowship; summer grants from the ESPM department; NIH Grant GM083863 and a USFWS Grant to Wayne Getz.

During my years in Berkeley there have been heated debates on the future of public education in California. My personal story tells there should be no debate. I was raised in a poor family. The only way I could surpass my humble upbringing was thanks to the excellent public education I was lucky to receive for free, all along the way: from my wonderful K-12 school up to a PhD from the finest public university in the world. A successful society is a society that can reap the talents of all its members, for the benefit of all. The only way to ensure that all of us can share our unique contributions is to allow free public education of the highest quality possible, to anyone, at any age, from any socioeconomic class.

I have been fortunate to learn from remarkable spiritual teachers who have taught me the wisdom of the heart and kept me strong, peaceful, and focused on true meaning. Dena Robbins-Deckel has been a true life-teacher for me, and helped me to find my inner resources through thick and thin. The teachers at the Tibetan Nyingma Institute in Berkeley, and especially Sylvia Gretchen and Olivia Hurd, have shared unconditional love and invaluable wisdom with me. They and the many wonderful yoga teachers in Berkeley were the calm at the eye of the storm that my life has become at times.

I am grateful to all my amazing friends around the San Francisco Bay Area, who have been my family here, encouraged, helped, and shared so many special moments together over the years. Special thanks to my dear friend Hanna Seltzer: you are the embodiment of kindness and compassion. You have redefined what true friendship really means to me. The wonderful Seltzer family: Guy, Yonatan and Naomi, have given me a warm home away from home. To my dear ones: Siew Chin Chua and her husband Shin Woei Leow, Lisa Motenko, Dan Landau, Taly Arbel and Jessica Moll, thank you for fun times and great memories. My friends back in Israel were my most enthusiastic cheer leaders and hosted me on my trips back there: Roni Ceder, Inbal Dangoor, Shani Glikman, Shunit Mazeh, Hila Avtalyon, Noga Pressman-Tal, Tamar Kashti, and Noga Yerushalmi. I love you all so much!!!

Finally, I am incredibly grateful to my family who has supported and believed in me throughout the years. I thank my parents, Raya and Yefim Tsalyuk and my dearest brother, Raphael Tsalyuk, for endless love and support, to my beautiful sister-in-law Osnat Lachman-Tsalyuk, my grandmother Isabella Tsalyuk, my aunt and uncle, Tanya and Simon Tsalyuk, and to my cousins, Bradley and Jonathan Tsalyuk. My grandmother, Polina Rozin, may her memory be blessed, has raised me and was my first ecology teacher. She was a biologist and a geographer and she taught me to look at nature with deep curiosity, careful examination, and an admiring heart. Every plant has flourished under her hands and she taught us what it means to care deeply and work persistently to see the changes we want to see in the world. This dissertation is dedicated to her.

Chapter 1: Introduction. Using landscape ecology for rangeland conservation

Rangelands cover 51% of the Earth’s land surface, encompass considerable biodiversity, and provide pivotal ecosystem services (Heady and Child 1994). However, rangelands across the globe face degradation due to changes in climate, land use, and due to altering fire and grazing management. Moreover, since herbivory is fundamental to rangeland ecosystem dynamics, shifts in the distribution of herbivores lead to overgrazing and, in some case, desertification (Kassas 1995). To better understand, predict, and prevent rangeland change, it is important to be able to monitor such change in a timely and efficient manner. However, the vast areas rangelands cover and their high spatial and temporal variability make their monitoring challenging. The goal of my dissertation is to advance the application of remote sensing and geographic information system (GIS) tools for quantifying rangeland vegetation and for understanding the relationship between herbivores and the landscape in these ecosystems.

Biodiversity and ecosystem value of rangelands

Rangelands have enormous economic, ecological and conservation value. Rangelands are defined as ecosystems where rainfall is too scarce or irregular for crop cultivation, and therefore these habitats are managed primarily for grazing, by wildlife and/or livestock (Holechek et al. 1995). Types of rangelands include savanna, grassland, shrubland, woodland, chaparral, steppe, prairie, tundra and desert (Heady and Child 1994). Since grazing is a central ecological process on rangelands, these areas account for most of the world’s animal products, including dairy, meat, leather and wool. Rangelands provide 16% of the world’s food production (Holechek et al. 1995). In Southern Africa, for example, savannas cover 54% of the land area and provide important source of food and other commodities (Vogel and Strohbach 2009). Furthermore, rangelands have a crucial role in provisioning clean water supply, water infiltration and water purification. Maintaining soil structure, stability, and diversity are additional services provided by these ecosystems (Xie et al. 2000, Havstad et al. 2007). With accelerating global climate change carbon sequestration has become an increasingly important ecosystem service provided by rangelands. Rangelands are a considerable carbon pool, accounting for 20% of the world’s soil carbon, in addition to the carbon sequestered by above ground biomass. Economic benefit from carbon offsets market is a further incentive to protect rangelands (Follett and Reed 2010, Booker et al. 2013). Finally, rangelands provide vast open spaces for tourism and recreation.

In addition to their ecosystem service value, rangelands encompass considerable biodiversity and serve an important role in conservation (West 1993, Fuhlendorf and Engle 2001). Unique coevolution of plants and herbivores made rangelands among the most diverse ecosystems in the world (Alkemade et al. 2013). Rangelands move between two ecological states, each of which promotes different species composition: a fire regulated state that is dominated by grasses, and a grazing regulated state that is dominated by woody vegetation. As a results of these coexisting communities, a large diversity of plant and herbivore species are supported by rangeland ecosystems (Perrings and Walker 1997). In the U.S., for example, more than 3,000 species depend on rangelands for at least part of their range (Yoakum and Davis 1996): 84% of mammals, 74% of birds, 58% of amphibians, and 38% of fishes in the country can be found in these ecosystems (Krausman 1996). Moreover, rangelands play an important role in conservation since the vast spaces they cover are important for habitat connectivity, migration corridors for wildlife, and provide territory for wide roaming species (Bolger et al. 2008, Brennan and Kuvlesky Jr 2005).

Threats to rangeland ecosystems

Despite their great biological, social and economic importance, rangelands across the world face considerable threats due to changes in land use, climate, fire and grazing regimes. Land conversion to urban development or croplands is driving the rapid loss of rangelands worldwide. More than 80% of all savannas, grasslands, and shrubland globally have already been converted by human use (Ellis et al. 2010). In the U.S., for example, more than 12 million acres of privately owned rangeland were converted to other land uses in a 15 year period from 1982 to 1997 (Brown et al. 2005). Increase in meat consumption and livestock production cause further significant decrease in biodiversity of rangelands (Alkemade et al. 2013). Increasing temperatures and changes in rainfall regimes exacerbate erratic patterns of precipitation and lead to prolonged droughts. Fire is an additional key process on rangelands; repetitive cycles of fire suppress growth of woody species and allow competitive advantage for fast growing grasses. Suppression of fire regimes changes this dynamic and leads to loss of native grass species (Perrings and Walker 1997). Changes to herbivore distribution imposed by construction of fences and roads, provision of artificial water sources, and changes to livestock stocking rates, modify natural grazing regimes and cause overgrazing. The combination of grazing and erratic climate leads to short term changes in the phenology and biomass of vegetation, especially of the herbaceous layer (Kisen et al. 2007). On the other hand, persistent reduction in vegetation cover reduces productivity, leads to soil erosion and results in long term degradation. Further changes in vegetation composition cause bush encroachment and reduced floral biodiversity. Severe and continuous overgrazing combined with reduced rainfall and prolonged droughts may lead to desertification, a phenomenon that is spreading dangerously around the world (Ludwig and Tongway 1995). For example, 31% of African savannas are affected by degradation processes (Vogel and Strohbach 2009). These degradation processes result in a decline in the ecosystem services rangelands provide and are a considerable threat to biodiversity.

Rangeland model

The rapid global decline of rangelands demands new approaches for their management and conservation. For my dissertation research, I developed a conceptual model for assessing the factors that influence rangeland dynamics. My model focuses on the interplay between four key elements of rangeland ecosystems and explains their dynamic. This rangeland model focuses on the interplay between four key components in rangelands: *landscape*, *climate*, *humans* and *herbivores* (Fig. 1). The rangeland *landscape* is characterized by its land use and land cover (LULC) class. It is further described by the location of anthropogenic features such as buildings, roads and fences, and by its natural environment traits such as topography, soil type, distribution of water, and vegetation quantity and quality. The vegetation is classified by its cover types (e.g. forest, grassland, shrubland), species composition or functional groups. Vegetation is further described by measures of cover, density, and biomass (Taylor et al. 1996). In turn, landscape characteristics are strongly influenced by the *climate*. For example, water availability depends on precipitation, and soil formation is influenced by patterns of wind and precipitation (Jenny 1941). Likewise, vegetation type and phenology tightly follow climatic patterns (Zhang et al.

2003, Du Plessis 1999). Climate also influences human activity by determining settlement location and possible land uses.

Large mammalian *herbivores*, animals adapted to feed specifically on plant material, are key components of the rangeland dynamic. Mammals specifically coevolved with rangeland ecosystems are ungulates (*Ungulata*) and near-ungulates (superorder *Paenungulata*). True ungulates are hoofed mammals that walk on tiptoe (Estes 1991). Herbivory (grazing and browsing) is pivotal for rangeland ecosystem function and regeneration (Brown and McDonald 1995). Herbivory promotes vegetation regeneration, specifically of grasses; grass species that are adapted to grazing respond to removal of the plant top with compensatory growth and enhanced photosynthesis (McNaughton 1979). Herbivores also play central roles in nutrient recycling, they fertilize the soil through defecation and play a key role in seed dispersal and seed germination (Traveset 1998, Cochrane and Reef 2003, Howe 1986). For example, *Acacia spp.* is a dominant genus of trees and bushes in savannas across the world. Acacia seeds collected from mammalian herbivores feces are better protected from damage by Bruchid seed beetles and have significantly higher germination rates (Lamprey et al. 1974) . On the other hand, herbivores, wild and domestic, can contribute to degradation processes through overgrazing. Persistent grazing around focal areas, such as perennial water sources, mineral licks or bedding areas, may lead to the creation of a *piosphere*, an area with reduced vegetation cover and high soil erosion caused by concentrated herbivore use (Washington-Allen et al. 2004). Trampling and damaging plants directly by bark striping and breaking tree are additional threats imposed by large herbivores to savanna vegetation. For instance, African elephants bark strip, and break and uproot trees with such intensity that they alter habitat for other species and may even completely transform the vegetation type from a woodland to grassland in a relatively short time (Valeix et al. 2011). Such processes affect vegetation quantity and community composition, soil stability, soil chemical composition, and water infiltration.

Both *landscape* and *climate* affect distribution and abundance of *herbivores*. The distribution and the abundance of species are tightly interrelated (Brown 1984); Individual herbivores respond to landscape and climate by movement towards favorable foraging and cover conditions. Aggregated individual movement patterns result in distribution patterns of whole populations and species. The ability of a population to establish itself in a suitable habitat influences the fitness of its individuals (birth rate, survival), ultimately affecting population sizes and the total abundance of a species. This response of herbivores to the landscape at various scales – from an individual animal to the distribution of a species – extends the effect herbivores exert on rangelands to larger spatial areas. Animals use different resources in different times of the year which affects their seasonal response to the landscape and results in seasonal changes in animal distribution patterns. As a result, the effect of herbivores on the landscape is different in various temporal scales. For example, large seasonal migration of wildebeest through the Serengeti plains results in a short term reduction in grass biomass (McNaughton 1976). On the other hand, permanent confinement of herbivores to fenced areas leads to long term changes in plant community composition and to enduring degradation (Todd and Hoffman 1999, Vogel and Strohbach 2009).

The fourth component of the rangeland model, *humans*, depends on the *landscape*, the *climate*, and on *herbivores*. Human choice of where to settle and what land use to employ are greatly influenced by climate, availability of water, landscape features, and distribution of herbivores (Diamond and Ordunio 1997). At the same time, humans inflict enormous changes on the landscape, changing as much as 83% of the planet’s land surfaces (Sanderson et al. 2002).

Humans also influence the distribution of herbivores either directly by managing livestock stocking rate, hunting, and relocating wildlife, or indirectly, by the effect of land use change and anthropogenic landscape features on herbivores.

My dissertation is situated within the context of the rangeland model and aims to address the connections between three of the four main components in the model: (1) I develop methodologies to characterize the rangeland landscape by measuring and mapping detailed vegetation variables, (2) I examine how landscape variables affect the movement patterns of large mammalian herbivores, in particular the African elephant, and (3) I develop tools to monitor how herbivory affects the productivity of rangelands. The tools I develop in this dissertation enable quantifying and identifying change in rangelands, inform targeted management and conservation practices, and contribute to improve monitoring and understanding of change in these imperiled ecosystems.

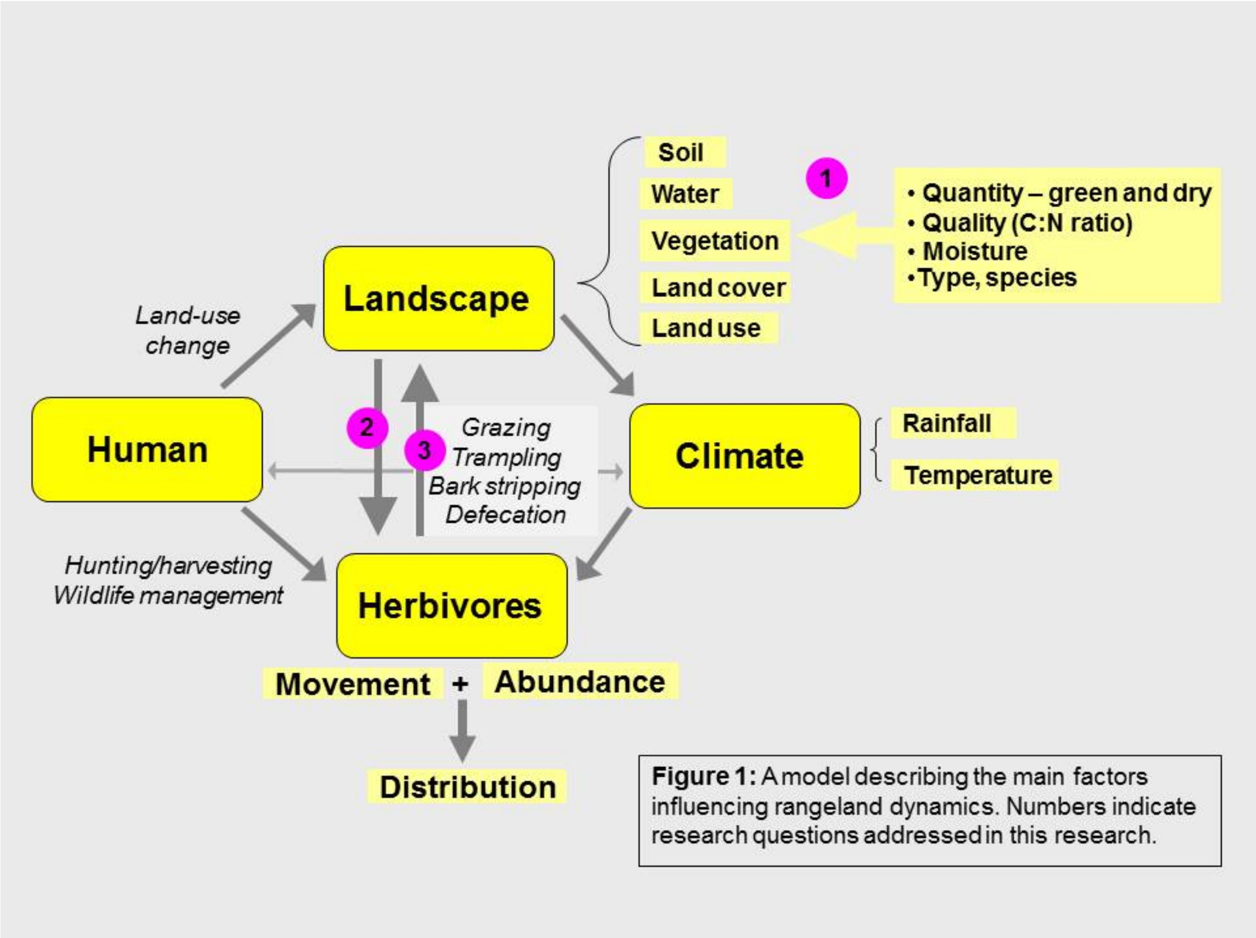


Figure 1: A model describing the main factors influencing rangeland dynamics. Numbers indicate research questions addressed in this research.

Measuring vegetation change on rangelands

The fast pace of changes on rangelands and the severe consequences of these changes accentuate the need to measure change of rangeland vegetation. While field-based monitoring techniques are widespread, they are not always viable since rangelands encompass large spatial extents, or are located in remote and often inaccessible areas. Moreover, it is impractical to employ field monitoring with a frequency that is sufficient to capture both the seasonal and inter-annual variation in vegetation conditions. Lastly, field monitoring is expensive and time demanding, resources that are not always available to community or conservation organizations that manage rangelands.

Remote sensing is a viable alternative for monitoring and managing rangelands (Marsett et al. 2006). Remote sensing is defined as the "art and science of obtaining information about an object without being in a direct physical contact with the object" (Jensen 2007). More specifically, in remote sensing data is collected by detecting the electromagnetic energy reflected from the Earth using sensors on board satellite or airborne platforms. Imagery from these platforms covers an extensive spatial extent and is available in fine spatial resolution. In fact, remote sensing data of several types is available for the whole planet, including remote and inaccessible areas. Moreover, satellite imagery has the fine temporal resolution and the temporal continuity that are needed to capture rapid changes on rangelands (Kerr and Ostrovsky 2003). For example, the Moderate Resolution Imaging Spectroradiometer (MODIS), an instrument on board the Terra/Aqua satellites, provides daily imagery for the whole world. Such fine temporal resolution can detect the fast pace of landscape change, including phenological, seasonal and inter-annual changes. High temporal resolution of imagery can help to distinguish short term seasonal alternations, which happen due to erratic weather or grazing, from long term change in vegetation composition and degradation processes (Kerr and Ostrovsky 2003). Satellite imagery can also provide long term, continuous information that is valuable to assess the cumulative effects of change. Landsat satellites, for example, have been providing information on Earth's cover since 1972, and are often used for change detection and monitoring (Cohen and Goward 2004). Furthermore, freely available imagery from NASA satellites such as Terra and Landsat may significantly reduce the cost of monitoring. Lastly, the increased availability of preprocessed imagery provides information that is rapid and easy to use by land managers with little or no remote sensing training (Butterfield and Malmstrom 2006).

Application of remote sensing for rangeland monitoring

In the past couple of decades there has been an increase in the use of remote sensing data for rangeland monitoring and management (Hunt et al. 2003). For example, remote sensing data have been used to predict forage production and to measure forage quality for livestock (Bastin et al. 2012). Likewise, remote sensing was applied to quantify the effect of restoration on forage provisioning (Malmstrom et al. 2009) and to monitor the effect of stocking rates on vegetation conditions (Hunt and Miyake 2006). Recently, MODIS imagery was used to measure rangeland carbon sequestration potential (Li et al. 2012). In natural habitats, satellite imagery has been used to measure herbaceous biomass, predict savanna tree cover, tree density, and species composition (Eisfelder et al. 2012). Remote sensing with high spatial and radiometric resolution is also being applied to rangeland science. For example, Light Detection and Ranging (LiDAR) technology was used to measure savanna biomass and structure in Kruger National Park in South

Africa (Asner et al. 2009). Hyperspectral imagery has been used to measure rangeland vegetation nutrient content and community composition (Ramoelo et al. 2013).

Challenges in applying remote sensing in rangelands

In spite of the growing use of remote sensing for rangeland management and conservation, some prominent challenges exist in applying remote sensing in these ecosystems. The use of remote sensing for vegetation measurement often relies on reflectance in the red and Near Infrared (NIR) wavelengths, which measure absorption by chlorophyll and by a plant's spongy mesophyll, respectively. Since each wavelength measures different properties of the plant, a combination of a few wavelengths serves as a proxy for structural or functional traits (Jensen 2007). A vegetation index in remote sensing typically is a mathematical combination that uses two or more wavelengths in order to measure specific vegetation traits. Common vegetation indices used for the measurement of vegetation greenness and productivity, such as Simple Ratio and the Normalized Difference Vegetation Index (NDVI), are based on the ratio of red and NIR wavelengths.

The application of these common indices, however, is often challenging on rangelands. Rangelands have sparse and irregular vegetation cover that causes strong signal from soil background (Huete 1988). As a result, a mix of bare soil and vegetation may be covered by the same imagery pixel, which makes the vegetation signal harder to distinguish. Small patches of vegetation may not be identified due to a dominant soil background. Additionally, land cover is often not discrete but rather characterized by variety of growth forms including grass, shrubs, and trees. This high heterogeneity in cover of different growth forms, mixture of these forms, and high plant species diversity, lead to sub-pixel changes in vegetation composition (Gessner et al. 2013).

An additional challenge to remote sensing of rangelands is that due to limited and highly seasonal rainfall, the vegetation is senesced for much of the year. Dry vegetation has high reflectance in both the red and the Near Infrared wavelengths, which makes it challenging to differentiate vegetation reflectance from the soil background. Furthermore, since dry vegetation has low ratio of infrared to red reflectance, it is hard to quantify biomass with methods often applied in other ecosystems. For example, NDVI has no correlation or even negative correlation with vegetation biomass if the proportion of dead plant cover exceeds 20% (Xu et al. 2014). Another challenge in applying remote sensing for rangelands is the marked changes within and between seasons. These changes lead to different estimates of remote sensing-based vegetation measurements, depending on the time the measurement was performed. These challenges necessitate the use of fine spatial and temporal resolution remote sensing data that are often lacking. Even when such fine resolution data are available, the imagery is often not sufficient to cover a vast area and its cost might be prohibitive.

Some solutions have been proposed to address the challenges of using remote sensing on rangelands. Vegetation indices that incorporate shortwave infrared (around 2000 nm) and red band spectra correct for soil background and can better differentiate soil from dry vegetation. One example is the Soil Adjusted Total Vegetation Index (SATVI) that improves the measurement of grass canopy (Marsett et al. 2006). Few vegetation indices were specifically developed to address the challenge of measuring dry vegetation biomass. For example, the Normalized Difference Tillage Index (NDTI), the Shortwave Infrared Difference Residue Index

(SINDRI), and the Cellulose Absorption Index (CAI), have been used to measure crop residue cover and biomass (Watts et al. 2011, Paul and de Paul 2012). While much of the work in this area aims to measure dry crop residue, it can be applicable for rangeland vegetation as well.

One approach to address the spatial variability of rangelands is to quantify sub-pixel fractional cover of vegetation. Fractional cover is the "areal proportion of the landscape occupied by green or non-green vegetation" (White et al. 2000). In this approach, a relationship is established between the spectral signal of vegetation cover in imagery with high spatial resolution and imagery with relatively coarse resolution. Using this correlation the information from high resolution imagery can be extrapolated to a larger spatial extent. Furthermore, calculating the fractional cover of an imagery that is collected in high frequency, such as MODIS, combine high spatial and high temporal resolutions (Hagen et al. 2012). For example, Gessner et al. used high resolution imagery from QuickBird (0.6m resolution) and IKONOS (1m) to classify cover types in the Kalahari Woodland savanna of Namibia. These data were then extrapolated to Landsat (30m) and MODIS (250m) resolutions, using regression trees to produces information for a larger area (Gessner et al. 2013). A somewhat similar approach to calculate the relative proportion of each cover type within a pixel is spectral unmixing, where the reflectance of a pixel is correlated to a weighted linear combination of the reflectance that corresponds to each vegetation component (Thomas et al. 1996). This method has been used to quantify cover of trees, grass and soil in savanna ecosystems (Theseira et al. 2002).

The aforementioned approaches are often based on hyperspectral or fine spatial resolution imagery. In collecting remotely sensed data, a tradeoff exists among spatial resolution, spatial extent and temporal resolution; high resolution comes at the expense of smaller spatial extent (small area covered) and lowers temporal resolution. These data are often acquired at one time snapshot and hence do not have a temporal resolution appropriate for measuring change over time. Moreover, imagery with both high spatial and high spectral resolution are not available for most areas. Finally, the cost of collecting these data is often prohibitive for conservation organizations, managers, and researchers alike. My goal therefore, is to advance our ability to measure rangeland vegetation using satellite imagery that covers extensive areas, comes at adequate temporal resolution, and is freely available. MODIS data are good candidate for achieving this goal because MODIS provides information for the whole world at daily intervals (Solano et al. 2010). I examine the utility of time series data to account for the spatial variability of rangeland vegetation. This approach uses the phenological cycle of the plant; different plant species have different green-up times, greening duration, and time of senescence. By incorporating imagery from different times I hope to account for multiple vegetation components within the imagery and thus predict vegetation measurement with higher detail and accuracy.

Understanding herbivore distribution on rangelands

As explained above, herbivory, either by livestock or wildlife, has a central role in the ecosystem dynamics of rangelands. Rangeland landscapes affect the distribution of herbivores and in turn, herbivores significantly affect the landscape where they occur. Therefore, my next step after developing methods to characterize rangeland vegetation is to understand how herbivores respond to the spatial and temporal dynamics of vegetation.

Identifying what determines the location of species on Earth is a central theme in Ecology. Distribution of species has been explored in various scales (Johnson 1980); the species *niche* is the combination of the environmental conditions where the species can reside. This includes abiotic conditions such as climate and topography that define the *fundamental niche* of the species, and biotic factors, such as the distribution of comparators, predators, and symbiotic species, that define the *realized niche* of a species (Hutchinson 1957, Hutchinson 1959, Soberon and Nakamura 2009). On a finer scale, the *distribution* of a species or particular populations predicts where the species can be found on the landscape. Most distribution models create a statistical probability relationship between environmental variables and recorded locations of a species. This relationship is then extrapolated to predict the distribution of the species in other locations, based on the environmental conditions there (Guisan and Zimmermann 2000). At the individual scale, "the relative frequency distribution for the points of location of an individual animal over a period of time" describes the utilization distribution (Vanwinkle 1975). The set of the locations on the landscape that an animal uses routinely to meet its needs is the individual's *home ranges* (Laver and Kelly 2008, Fieberg and Börger 2012). The preference for specific landscape attributes determines the home range and varies between individuals and groups. Finally, the *foraging behavior* of an individual describes, on a fine scale, how the animal's location is related to the distribution of feeding patches on the landscape, and the to the location of preferred food items and other resources (water sources, dens/nests, mineral licks, etc.) (Jeltsch et al. 2013). The movement of an individual links fine scale individual location data with home range and utilization distributions, which when scaled up to the population level provide data on the overall distribution of a population at a regional or geographic level (Jeltsch et al. 2013). Movement ecology has therefore been a rising field of research in the past decade (Nathan et al. 2008). However, how movement patterns of individuals respond to the underlying landscape, especially variable landscapes, is still not well understood (Getz and Saltz 2008).

The use of remote sensing to characterize the underlying environment of species locations has steadily increased (Kerr and Ostrovsky 2003, Pettorelli et al. 2005, Turner et al. 2003). Remote sensing has been used to measure climate, vegetation, and land cover to predict species distribution. Additionally remote sensing has been used to measure important biophysical parameters that are correlated with biodiversity, such as net primary productivity, phenological cycle and the length of the growing season (Turner et al. 2003). More recently, there have been developments in using remote sensing to directly detect individual organisms. For example, individual trees are identified and measured using LiDAR (Lefsky et al. 2002), while the distribution of Giant Kangaroo rats in central California was predicted using aerial surveys of the bare borrows complexes these animal create (Bean et al. 2012). Despite these advancements, remote sensing is not yet widely used to understand how the landscape affects wildlife behavior at various temporal scales. My research aims to advance the application of remote sensing to understand the relationship between individual movement behavior and the environment. By creating detailed information on the underlying landscape, I aim to understand how elephants respond to their environment at fine spatial and temporal scales.

Common themes in the dissertation

My dissertation addresses the challenges of conserving rangeland ecosystems. I use three key elements in all parts of this research. First, because rangelands encompass large areas and the herbivores that depend on them are far-roaming, I approach my research questions at a landscape level. Landscape ecology deals with the relationship between landscape patterns and ecological processes (Turner 2001). A key concept in landscape ecology, the *scale* of analysis, is an element

I explore extensively. Scale can be defined both in terms of resolution, the smallest unit that can be distinct or accurately measured, and in terms of extent, the area or time covered by the information (Turner 2001). The processes and the rules guiding these processes change depending on the scale. A body of research has demonstrated *spatial scaling* in ecology and shows that "the scale of an investigation may have profound effects on the patterns one finds" (Wiens 1989). Moreover, moving across ecological hierarchies (individuals, population, communities, and ecosystems) changes the observed process or the mathematical function describing the process; a phenomena known as *transmutations* (O'Neill 1979). These findings emphasize the need to adapt the scale of analysis to be relevant to the organism and the ecological process at hand (Bissonette 1997). Throughout this work I examine processes on a large spatial extent and measure the transferability of my results, the ability to apply the models in different locations. Moreover, I explore how the temporal scale and extent of temporal information affect the quality of the models.

A second common theme in the dissertation is the application of spatial quantitative tools to predict and understand the location of organisms. In all parts of the research, I use a combination of satellite imagery, spatial and statistical models to answer ecological questions. The third common theme is the focus on research that is applicable for conservation management. To that end, I worked in collaboration with conservation practitioners in Namibia (Etosha Ecological Institute) and in California (The Nature Conservancy) to better understand the management needs and the conservation challenges they face. I emphasize the use of freely available satellite imagery that is easy to access and use. Moreover, I use open source software for analysis such as R (R Development Core Team 2007) and FWTools, which is a set of open source programs for geographical information systems (Warmerdam 2007). My goal is to develop rapid, cost effective, and relatively simple analytical frameworks that are at the same time robust, repeatable and reliable and can be used by conservation practitioners.

Study sites

My work spans two study sites: Etosha National park, Namibia and Simon Newman Ranch, in central California. While these sites are different in many ways there are a few commonalities: both of the sites are rangelands with semi-arid climate and relatively low rainfall, and each has one main vegetation growing cycle per year. Grazing by either wildlife, in Etosha, or cattle in Simon Newman, has a prominent role in both locations. Fencing and artificial waterholes for herbivores are key management tools. While the degree of management and anthropogenic impacts are different between the sites, human activities have a prominent role in the dynamic of the ecosystem in both places. Both locations have rich biodiversity of fauna and flora and its conservation is a central management goal. However, in both locations conservation goals need to comply with human needs: Etosha is managed for tourism, and has to mitigate human-wildlife conflict on the reserve borders, while Simon Newman also serves to support commercial cattle production.

Etosha National Park

Etosha National Park is a 22,270 km^2 reserve in central-north Namibia. It is a semiarid savanna with a rainfall gradient of 250-400 mm per year. There are three main seasons: the cool dry season (May – August), hot dry season (September –November), and the hot wet season (December – April) (Du Plessis et al. 1998a). Peak rainfall occurs in January – February (Turner and Getz 2010). Annual temperature ranges between a minimum of 17.7°C to a maximum of 34.8°C in November, and a minimum of 6°C to a maximum of 25°C in July (Du Plessis et al. 1998b). The park is primarily flat with some hills to the west. The main vegetation types in the reserve are grassland savanna; Steppe, dominated by *Leucosphaera baenesii* and *Monechma genistifolium*; shrublands, dominated by *Catophractes alexandri* or by Acacia spp., mainly *Acacia nebrownii*; *colophospermum mopane* woodland; and a mix trees woodland dominated by *Ziziphus mucronata*, *Camiphora spp. Combretum*, *Griwia*, *Terminalia prunioides* and *Terminalia sericea* species (Du Plessis 2001, Le Roux et al. 1988). Etosha pan is a prominent feature in the reserve, spanning 4,410km^2. It is a natural saline lake depression that is mostly dry and filled partially with water seasonally. Animals use the pan for drinking and for licking salt and minerals (de Beer et al. 2006)

Etosha was first designated "game reserve No. 2" in 1907 by the German colonialists and was used for hunting. At the time it covered almost 80,000 km^2, which made it the largest reserve in the world (Berry 1997). Etosha received a status of National Park in 1967 with a smaller area of 55,000 km^2. In 1970, the reserve size was reduced again to its current size and was surrounded by a game proof fence to prevent the spread of foot-and-mouth disease between wildlife and domestic animals living outside the park. The park fencing was completed in 1973, enclosing it with 850km of fence, that has been mostly intact since. An additional 130km of elephant–proof fencing was added and electrified in strategic places (Berry 1997). The fencing of the reserve has restricted the migration path of ungulates in Etosha and has dramatically affected their populations. Most notably, the population of blue wildebeest collapsed following fencing of the park (Berry 1982). To compensate for the restriction of natural migration paths, the park authorities provide artificial sources of water throughout the park. There are 93 active water sources in Etosha, including gravel pits, natural depressions, 58 boreholes, nine artesian springs, and four dams (Auer 1997).

Simon Newman ranch

Simon Newman is a 133km^2 ranch located in Stanislaus and Merced counties of California, USA. The Nature Conservancy purchased Simon Newman in 1998 to conserve the great biodiversity on the property, and has been managing it since with the dual purpose of conservation and cattle production (Guenther 2005). The ranch topography is hilly and rocky in the western part and flat in the eastern part. Mean annual precipitation is 280 mm/year. The main vegetation types are annual grasslands, Oak woodland, Chaparral, and riparian vegetation. The area is divided into 51 management units, or pastures, that are separated by fences. It includes a total of 156 km of roads. Water facilities for livestock include 25 springs, 28 windmills, 63 water troughs, and 44 ponds (Guenther 2005). Residual Dry Matter (RDM) is used as a key proxy for sustainable grazing pressure on the ranch, and has been measured on the ground annually since 2000 (Guenther 2012).

Research questions and predictions

My research aims to address challenges in remote sensing of rangelands and uses this information to understand the relationship between the landscape and the movement patterns of a large herbivore, the African elephant.

Chapter 2: “Improving the measurement of African savanna vegetation using time series analysis of MODIS vegetation indices”

The goal of Chapter 2 is to characterize the structure of savanna vegetation in Etosha National Park using MODIS time series analysis. I use satellite imagery to predict and map detailed vegetation measurements (density, cover, biomass, greenness) of the three main vegetation forms in Etosha (grassland, steppe, shrubland, and woodland). I then assess the application of these models to other areas. In this chapter I address four main research questions:

(1) What is the best MODIS-based vegetation index to measure vegetation parameters in savanna habitat?
I compare four MODIS-based vegetation indices: Normalized Difference Vegetation Index (NDVI), Enhanced vegetation index (EVI), Leaf Area Index (LAI), and Fraction of Photosynthetically Active Radiation (FPAR) (Knyazikhin et al. 1999). Each vegetation index is based on different wavelengths and uses different algorithm, and measures different structural of functional properties of the plant. Therefore, for each vegetation form (trees, shrubs, or grasses) there might be different vegetation index that predicts it optimally.

(2) What is the optimal temporal scale to predict savanna vegetation using remote sensing?
I predict that integration of satellite information over time will incorporate more of the phenological variability of the vegetation and therefore improve its measurement.

(3) How the vegetation forms and the vegetation cover type affect the quality of model prediction?
I compare the strength and the error of prediction models of the different vegetation types. Vegetation forms that are greener for a longer part of the year (e.g. trees) are more easily quantified by vegetation indices. Therefore, I predict that predictive models for the measurement of these vegetation forms will be more robust. Additionally, prediction models should perform better in homogeneous cover types (e.g. dense woodland or open grassland), since the spatial variability and the patchiness of plants is lower in these areas.

(4) Are satellite-based predictive models of vegetation transferable through space and time?
I examine whether satellite-based models that were calibrated in one area can be used to predict vegetation measurements in another. Specifically, I examine the spatial transferability of the models across climatic gradient: from wetter to drier areas and vice versa. Moreover, I examine the temporal transferability of the models, to test how a model created in the dry season predicts vegetation measurements in the wet season of the following year.

Chapter 3: “African elephant movement in response to spatial and temporal landscape correlates”

In Chapter 3, I explore how landscape variables influence herbivore movements. African elephants (*Loxodonta africana*) are keystone species in Etosha National park that influence the ecosystem greatly by feeding, damaging trees, and altering plant composition for other species. Moreover, elephants cause human-wildlife conflict by raiding agricultural fields in neighboring villages. To understand the key resources that are important for the elephant and to better manage their population in the park, I explore the influence of detailed vegetation characteristics and the location of water, roads, and fences on the movement direction and speed of elephants. In this chapter I examine the following research questions:

(1) What is the relative importance of landscape variables in elephants' movement directions?
I predict that water location will have the strongest effect on elephant locations. Since elephants in Etosha consume grass and browse in similar proportions (Turner et al. 2013), I expect these vegetation forms will have equal effect on movement direction.

(2) How do landscape variables affect the speed of movement?
I hypothesize that elephants will walk slower through habitats that provide better forage or cover. On the contrary, I expect animals will walk faster through less favorable habitat.

(3) How does individual variation affect preference of landscape variables?
I hypothesize that overall the sampled elephants will have similar response to the landscape, but sex and age will affect movement response to the environment since these individual traits affect the nutritional needs of each elephant.

(4) What is the effect of temporal variation on landscape preference?
Because elephants exhibit different behaviors throughout the day and have preferred times for specific activities such as drinking and foraging, time of day should affect the movement response to landscape variables. Furthermore, I predict that the preference of a resource would depend on the seasonal abundance of that resource. For example, preference of greener pastures or surface water will be stronger in the dry season when these resources are more scarce.

(5) How does the temporal scale of analysis affect the relationship between the direction of movement and the landscape?
I examine the effect of landscape variables on elephant movement at different temporal scales by using increasing time intervals between consecutive GPS locations. I expect that increasing time intervals will reveal the resources that are most important for habitat use by elephants.

Chapter 4: "Monitoring the impact of grazing on rangeland conservation easements using MODIS Vegetation Indices"

In Chapter 4, I develop tools to measure the effect of cattle grazing on vegetation quantity. In California, many rangeland conservation areas are managed with the goals of cattle production and biodiversity protection. In order to maintain sustainable grazing pressure on conservation easements, these areas are monitored annually to measure residual dry matter (RDM), the dry grass matter left on the ground at the end of the grazing season. RDM is a measure of grazing pressure and is correlated with rangeland productivity, soil stability, water infiltration and native plant diversity. Current field-based RDM monitoring is time consuming, costly, and the results of the monitoring can be applied only in the next year, after any potential damage to the land has already occurred. I examine the utility of MODIS-based vegetation indices in monitoring RDM easement compliance.

I use twelve years of RDM field measurements in Simon Newman ranch together with time series analysis of MODIS vegetation indices to understand the relationship between field-based and remote sensing data. I compare the correlation between annual summary statistics values of RDM and three vegetation indices: Normalized Difference Vegetation Index (NDVI), Leaf Area Index (LAI) and Fraction of Photosynthetically Active Radiation (FPAR), and examine their ability to monitor RDM. The research questions of this chapter are:

(1) What is the relationship between rainfall and vegetation productivity, as measured by MODIS-based vegetation indices?
I predict that all three vegetation indices will measure both the timing and the extent of vegetation response to rainfall.

(2) What is the relationship between MODIS-based VIs and RDM?
I hypothesize that FPAR and LAI, which incorporate reflectance of mid- and short-infrared wavelengths, would be better predictors than NDVI of dry grass biomass as measured by RDM. I also predict that annual integration of satellite imagery would provide the best prediction of RDM.

(3) How can MODIS VIs be used to improve RDM monitoring and management of conservation easements?
I predict that the relationship between vegetation indices and RDM can be used to predict RDM in the fall. Therefore, MODIS will provide a rapid, effective and robust tool for RDM monitoring. Remote sensing might identify potential problem areas and therefore promote more targeted solutions. Moreover, remote sensing will provide information on forage availability in the spring and therefore inform appropriate stocking rates with healthy foraging pressure.

Taken together, the chapters of this dissertation develop the use of satellite imagery to measure rangeland vegetation and characterize landscapes at large spatial scales. I examine how landscape dynamics affect herbivore movement and how, in turn, herbivores affect rangeland vegetation. I show the effects of spatial and temporal scale of analysis on resulting patterns, and develop the link between landscape ecology, rangeland ecology and wildlife conservation. I demonstrate how freely available remote sensing and GIS tools can be used by conservation managers to monitor changes in vegetation patterns and in wildlife distribution, and how this knowledge can improve ability to manage and conserve rangelands across the world.

Chapter 2. Improving the measurement of African savanna vegetation using time series analysis of MODIS vegetation indices

Abstract

African savanna vegetation is subject to extensive degradation as a result of rapid climate and land use change. In order to quantify and understand changes in vegetation structure it is essential to develop methodologies for detailed vegetation measurement across vast spatial scale and fine temporal resolution. However, applying remote sensing techniques to savanna vegetation is challenging because of high spatial and temporal variability of vegetation cover and phenology, and difficulties in differentiating between spectral signals of bare soil and dry vegetation. Here I attempt to resolve these challenges by using time series analysis of four MODIS vegetation indices (VIs) to measure the density, cover, biomass and greenness of the main savanna vegetation forms: grass, shrubs and trees. To ground-truth remotely sensed VIs I performed extensive field sampling in a semiarid African savanna, Etosha National Park, Namibia, during both the dry and the wet season. I then assessed the efficacy of four VIs for predicting ground-measured vegetation. These VIs included Normalized Difference Vegetation Index (NDVI), Enhanced Vegetation Index (EVI), Leaf Area Index (LAI), and Fraction of Photosynthetically Active Radiation (FPAR). My results showed that NDVI yielded strong predictions of tree density (R^2=0.78, error=2.5%), tree canopy cover (R^2=0.79, error=0.35%), and tree biomass (R^2=0.76, error=0.65%) and was the best predictor of shrub biomass and shrub greenness. LAI gave the best models for shrub density and cover, and FPAR was the best predictor of grass biomass. While there is an optimal VI for the prediction of each vegetation measurement, overall, FPAR/LAI based models had a superior prediction power. I compared the optimal time span of VI time series to predict vegetation and found that multiyear models were superior to models based on VI information from a single year or a single date. Finally, I addressed an enduring challenge in the remote sensing of semiarid vegetation by examining the transferability of prediction models through space and time. My results showed that models created in the wet part of Etosha could accurately predict tree and shrub measurements in the dry part of the reserve and vice versa. Moreover, these results demonstrate that models created for vegetation measurements in the dry season of 2011 could be successfully applied to measure vegetation in the wet season of 2012. I conclude that extensive field data combined with multiyear time series of satellite data can produce robust predictive models for multiple vegetation forms in an African savanna. This methodology could advance the monitoring of savanna vegetation change and contribute to improved management and conservation of these valuable ecosystems.

2.1. Introduction

Savanna ecosystems cover about ten million square kilometers around the world, as well as just under half of Africa's land surface (Cahoon et al. 1992, Shackleton and Scholes 2011). These ecosystems provide pivotal ecosystem services including carbon sequestration, water filtration, soil stability, meat and dairy production, and tourism and recreation (Solbrig 1996, Vågen et al. 2005). In addition, African savannas harbor rich biodiversity and provide habitat and connectivity for far-roaming wildlife (West 1993). However, savanna ecosystems face degradation due to changes in land use, climate change and management regimes. Management decisions, such as provisioning of artificial water sources and construction of fences and roads, disrupt the natural distribution of grazers. Concentration of grazers around focal resources leads to overgrazing, bush encroachment, land degradation, and even desertification, a dangerously spreading phenomenon around the world (Kassas 1995). Monitoring these rapidly changing landscapes necessitates a method that maintains a sufficiently high temporal resolution over a large spatial extent. Here, I attempt to advance the monitoring of savannas by assessing the ability of Moderate Resolution Imaging Spectroradiometer (MODIS) derived vegetation indices to predict detailed vegetation measurements. Specifically, I compare the ability of time series of four vegetation indices to predict ground cover and assess the transferability of those predictive models across space and time.

Savannas are extensive, and often remote and inaccessible, complicating protocols for their monitoring. Field methodologies for measuring vegetation change are typically limited in extent, expensive and time consuming. Therefore, the use of low and moderate resolution remote sensing, including MODIS, has been widely applied to characterize savanna vegetation throughout Africa (Eisfelder et al. 2012). Nonetheless, the sparse vegetation in these arid and semi-arid areas and the reflectance of the soil background continue to present a major challenge for the use of remote sensing to measure continuous vegetation parameters (Huete 1988). Moreover, savanna vegetation is highly variable in time and it is senesced during prolonged periods of the year (Eisfelder et al. 2012). Low chlorophyll content of senescent vegetation reduces the red-to-near infrared (NIR) spectral contrast, which reduces the ability to distinguish vegetation from background soil. This presents a challenge in using remote sensing to directly measure dry biomass (Roberts et al. 1993, Huete 1988). One approach in addressing this challenge is to capture phenological vegetation variation using time series of vegetation indices.

Vegetation indices (VIs) combine information contained in a few spectral bands, particularly at the red, near infrared (NIR) and shortwave infrared (SWIR) wavelengths, which are particularly sensitive to vegetation changes, and thus are used to measure vegetation attributes. Notably, the Normalized Difference Vegetation Index (NDVI) has been widely applied to predict vegetation cover, above ground biomass and greenness (Tucker et al. 1983, Tucker 1979, Gamon et al. 1995). While the relationship between NDVI and aboveground green biomass is well established, research indicates the limited capacity of NDVI to predict senesced vegetation (Xu et al. 2014). In addition to NDVI, MODIS provides other pre-processed VIs, including Enhanced vegetation index (EVI), Leaf Area Index (LAI), and Fraction of Photosynthetically Active Radiation (FPAR) (Knyazikhin et al. 1999). I examine the capabilities of these VIs in predicting changes in savanna vegetation across large landscapes.

As with NDVI, EVI incorporates reflectance in the red and the NIR wavelengths. In addition, EVI includes an atmospheric resistance term, using the blue wavelength and a soil adjustment factor. EVI is related to canopy structure and type. There is a strong correlation between EVI and gross primary productivity (GPP) in African ecosystem (Sjostrom et al. 2011, Jin et al. 2013) and there is correlation between EVI, Net Primary Production (NPP) and forage production in rangelands (Li et al. 2012). EVI is known to be sensitive to a wider range of canopy cover than NDVI (Huete et al. 2002). However, MODIS EVI rarely has been applied to predict savanna vegetation biomass.

MODIS-based LAI and FPAR use information on the canopy spectral properties and structural attributes, and hence might be good predictors of dry vegetation biomass (Knyazikhin et al. 1999). Research has demonstrated that both of these VIs have higher correlations with senesced grass height and biomass than does NDVI (Butterfield and Malmstrom 2009). LAI provides information on plant canopy structure by measuring the total green leaf area per unit ground-surface area (Knyazikhin et al. 1999). FPAR is a unitless fraction, measuring the proportion of radiation, out of the total available radiation in the photosynthetically active wavelengths of the spectrum 400 - 700 nm. FPAR could be used to predict vegetation cover and type (Schoettker et al. 2010). For example, FPAR increases with grass litter canopy as well as with green biomass, indicating its ability to measure dry vegetation biomass (Asner et al. 1998).

Biomass of savanna vegetation is highly dependent on rainfall, especially herbaceous biomass, shows considerable seasonal and inter-annual variation (Colditz et al. 2007, Sannier et al. 2002). Time series of the above mentioned VIs captures these phenological variations and therefore are useful in predicting vegetation biomass. Indeed, time integrated (summed over the growth year) and maximum NDVI showed a strong correlation with above ground herbaceous biomass (Tsalyuk et al. In reviewb, Tucker et al. 1981). Annually integrated VI data showed better correlation with field measured herbaceous biomass than single-date VI value (Verbesselt et al. 2006, Du Plessis 1999). The use of additional points on the time series such as the greenup and senescence/dormancy onset and the length of the growing season were used to describe vegetation phenology (Zhang et al. 2003).

In addition to drastic changes within and between years, savanna vegetation is highly variable in space with respect to soil cover and species diversity (Du Plessis 1999). This variation presents a challenge to using established relationship among ground-based vegetation measurements and satellite information in different locations or across years. This impedes the transferability of models developed in one site and applied to others, thereby hindering the application of remote sensing data to savanna monitoring and management applications. Eisfelder et al. identified the transferability of remote sensing-based methods to measure biomass as the major challenge in semi-arid environments (Eisfelder et al. 2012). My study uses extensive field data and multi-year satellite information to assess the transferability of satellite based vegetation measures.

Previous remote sensing studies in Etosha National Park, Namibia, included vegetation classification using Landsat data, based on woody layer cover (Taylor et al. 1996). While a preliminary product, this classification was useful for the reserve management and was the basis of further analysis of vegetation phenology and dynamics in the reserve (Sannier et al. 1998, Sannier et al. 2002, Wagenseil and Samimi 2006). Previous use of satellite data for vegetation measurement in Etosha focused on the use of Advanced Very High Resolution Radiometer (AVHRR) derived NDVI, for vegetation cover and fire risk assessment.

The objective of this study is to predict the density, cover, biomass, and greenness of the main vegetation forms in Etosha: trees, shrubs, and grasses, through time series analysis of MODIS VIs. I develop an extensive field methodology that can be used to measure vegetation parameters in vast savanna landscapes. I evaluate the importance of integrating VI information through time to improve prediction. I compare the ability of four VIs - NDVI, EVI, LAI, and FPAR - to accurately predict these vegetation parameters. Based on this information, I assess the transferability of the prediction model across space and time. Finally, I create full cover maps for each vegetation measurement for the whole of Etosha National park.

2.2. Methods

Etosha National park is a 22,270 km^2 reserve, located in north-central Namibia (18º45′ S, 15º30′ E) (Fig. 1). It is a semi-arid savanna with a gradient of 200- 450 millimeter of rainfall per year. Etosha experiences three main seasons: cold-dry (May – August), warm- dry (September – December), and warm- wet (January – April) season (Alleaume et al. 2005). The main vegetation types in Etosha are grassland, steppe, Acacia woodland and Mopani tree savanna. Etosha has been fully fenced since the early 1970s. To compensate for creating barriers along historical herbivore paths to water, the park management provides artificial watering sources for wildlife.

2.2.1. Vegetation measurement

I collected vegetation data over two field seasons. I sampled 348 sites across Etosha in the dry season, June to August 2011. In the dry season the differences between vegetation types are most pronounced and, hence, it is the preferred time to perform ground truthing for remote sensing data (McCoy 2005). I resampled 110 of these 348 sites during the wet season of March-April 2012, to evaluate contrasts between wet and dry season sites. Moreover, I wanted to evaluate how well remote sensing based models developed in the wet season could apply to predict vegetation in the dry season. Note that not all dry sites were accessible during the wet season due to restrictions placed on driving in areas where the ground was too muddy for safe passage.

2.2.2. Field sampling

My field sampling design used a vegetation classification map created in 1996, based on Landsat 5 TM data (Taylor et al. 1996). This is a physiognomic classification based on main cover types: water, soil, grass, steppe, shrub, low and high trees. Each class is further divided into total of sixteen classes according to the relative cover of each vegetation form: Dwarfed shrubs < 0.5 m; shrubs 0.5 – 2 m; low trees 2 – 5 m; high trees > 5 m (Sannier et al. 1996). I performed stratified random sampling to ensure equitable representation in my samples for each of the sixteen classes, with at least 20 points sampled in each predicted cover type. Sampling was made 50- 300 meters away from roads and at least one kilometer away from water.

At each of the 348 sampling sites I recorded the GPS location, elevation (using eTrex Vista HCX Garmin GPS), and the cover type. I took four photographs, one in each compass direction. I visually estimated the percent cover of grass, soil, shrubs and trees.

Woody vegetation measurements. I used the plot-less point-centered quarter (PCQ) method for woody vegetation measurements, which is an accurate and labor efficient method for woody vegetation measurement that does not assume that trees are randomly distributed (Engeman et al. 1994, White et al. 2008). At each random sampling point I divided the area into four equal quarters. In each quarter I measured the two shrubs and the two trees that were closest to the central point (eight trees and eight shrubs in total). I measured the distance from the central point to the trunk, the canopy area, the height, and the diameter of each individual plant. Short distances were measured when possible with a transect meter, while a Nikon ProStaft b50 range finder was used to measure large distances. Diameter of trees was measured at breast height (DBH, 1.37 meters); while for shrubs the widest part of the main stem was measured. Shrub height was measured using a measuring pole; for tree height I used a VertexIII hypsometer and Transponder T3 (Haglȍf Sweden AB). I identified the species of each measured plant. Unrecognized species were sent for identification in the National Herbarium of Namibia, Windhoek. The percent greenness of each measured plant was estimated visually. I measured the two closest individuals at each quarter up to a distance of 200 meters from the central point to obtain a set of eight distance values R_1 to R_8.

Tree density D (number per hectare) at each sampling site was estimated using the following equation (Pollard 1971) in terms of a correction factor (CF) and the eight distances R_1 to R_8:

$$D = \frac{28 * \mathrm{CF} * 10^4}{\pi * \sum_{i=1}^{8} R_i^2} \qquad (1)$$

The correction factor, *CF* accounts for the proportion of missing individuals in each point (Warde and Petranka 1981), while the factor 10^4 converts density measurement from per square meter to per hectare.

Canopy cover C (meter/ hectare) at each sampling site was calculated as the average of eight measured canopy sizes times the density.

Woody biomass B (in metric tons) at each sampling area was estimated, separately for trees and for shrubs, using the following equation formulated by Henry et al. (Henry et al. 2011) in terms trunk radius r_i, tree height h_i, and tree D (as determined by Eq. 1.):

$$B = \sum_{i=1}^{8} \frac{\pi {r_i}^2 * h_i * 0.5 * 0.7 * 10^3}{8} * D \qquad (2)$$

I used 0.7 $\mathrm{Mg*m^{-3}}$ is the average wood specific gravity suggested for Etosha (Alleaume et al. 2005), and 0.5 as an average coefficient form for trees suggested by (Henry et al. 2011).

Grass measurement. In order to measure herbaceous vegetation I used a 1x1 m frame that was divided into sixteen subsections. In each sampling area, I measured grasses at the central point, and at four points, 15 m away from the center, one in each compass direction. I recorded percent cover of grass, soil, and forbs, and the percent greenness in within the whole square. I identified the two dominant grass species and their cover in each square.

I used two complementary methods to measure grass biomass at each $1\mathrm{m}^2$ frame: assigning a visual class of 1-7 (C) and measuring the height h (cm) of a disc pasture meter (DPM) (Trollope and Potgieter 1986). I calibrated each method, by clipping and weighting grass in a subsample of 75 1x1 m frames, for the visual class method, or by clipping the grass directly under the DPM. Calibration was performed separately for the dry and the wet season. Dry biomass was measured by oven-drying the samples in 100° Celsius for 48 hours. I used linear regressions to estimate correlates between each type of measurement and grass biomass.

Calibration of the grass biomass measurements showed strong and significant correlations between DPM measurements and field biomass measurements (Equation (3) (R^2=0.94, $p < 0.001$, n=75). There was also strong relationship between visual class estimation C and field measurement (Equation (4). R^2=0.87, $p < 0.001$, n=75). Wet season calibration yielded good predictions as well for the DPM calibration (Equation (5). R^2=0.96, $p < 0.001$, n=13), and for the visual class estimation C (Equation (6). R^2=0.91, $p < 0.001$, n=13). The average of both methods and the five measurements at each sampling site was used to determine grass biomass density B (grams per square meter) in each location.

$$B_{\mathrm{DPM}} = 6.915\, h \qquad (3)$$

$$B_{\mathrm{visual}} = 58.43\, C \qquad (4)$$

$$B_{\mathrm{wet,\,DPM}} = 11.288\, h \qquad (5)$$

$$B_{\mathrm{wet,\,visual}} = 192.4\, h \qquad (6)$$

2.2.3. MODIS vegetation indices

My goal was to find the best MODIS-based vegetation index that correlated with each of the four vegetation parameters—cover, density, biomass and greenness, for each of the three main vegetation forms—trees, shrubs, and grasses (twelve parameters in total). I acquired MODIS data from the Reverb website (EODIS 2013), and extracted data for each VI, at each sampling point, using the Spatial Analyst Tools in ArcGIS 10.2 (ESRI 2011). I used four MODIS-based VIs: Normalized Difference Vegetation Index (NDVI), Enhanced Vegetation Index (EVI), Leaf Area Index (LAI), and Fraction of Photosynthetically Active Radiation (FPAR).

NDVI is calculated in terms of ρ_{red} and, ρ_{NIR} which are the reflectance measured by the satellite sensor in the red (620-670 nm) and near infrared (841-876 nm) wavelengths respectively, using the formula (Tucker et al. 1981):

$$\mathrm{NDVI} = \frac{\rho_{\mathrm{NIR}} - \rho_{\mathrm{red}}}{\rho_{\mathrm{NIR}} + \rho_{\mathrm{red}}} \qquad (7)$$

In addition to the above wavelengths, EVI is calculated in terms of ρ_{blue} which is the reflectance measure at the blue wavelength (459-479 nm), as well as in terms of L, the canopy background adjustment, and aerosol correction factors C_1 and C_2 (corrects the blue and red bands relative to the NIR band). The correction and adjustment factors used in the MODIS EVI algorithm are, C_1=6, C_2 = 7.5, and L =1, using the formula (Huete et al. 2002):

$$\mathrm{EVI} = \frac{\rho_{\mathrm{NIR}} - \rho_{\mathrm{red}}}{\rho_{\mathrm{NIR}} + C_1\, x\, \rho_{\mathrm{red}} - C_2\, x\, \rho_{\mathrm{blue}} + L} \qquad (8)$$

MODIS samples the earth daily. The NDVI and EVI data is a 16-days average provided in a 250 X 250 meter resolution, while LAI and FPAR are 8-day average with 1 km × 1 km resolution (Table 1). I resampled FPAR and LAI data to match NDVI's 250m resolution and removed null values (249-255).

Spatial Statistics. To incorporate inter- and intra-annual variation that can inform vegetation measurements prediction, I constructed a time series course for six years: October 2006 –

October 2012. To identify the growth pattern in Etosha I plotted the six years of MODIS VIs over time, for each of the seven main cover types, separately. The minimum value of all four vegetation indices occurs around end of September – Mid October. Therefore, I calculated each "growth year" as the VI data from October 16th of the previous year to middle October of the current year. For each growth year and for each VI I calculated nine summary statistics values. Each summary statistics was calculated on all data points provided by MODIS for the VI for one year; hence, the calculation was made on 23 data points per year for NDVI and EVI, or 46 data points per year for LAI and FPAR. These summary statistics values included the annual minimum, maximum, average, sum and standard deviation. Additionally, the date of minimum and date of maximum values occurrence were identified. I calculated the length of the growing season as the number of the days that VI values were above the 50th percentile of the VI value for that year. An average of each summary statistics value for the six years was calculated. Additionally, for each sampling point, I extracted the VI value at the closest date to the field sampling.

2.2.4. Statistical analysis

I predicted that including time series of remote sensing data would encompass more of the temporal variability in savanna vegetation, and therefore provide a better prediction of vegetation measurements. Therefore, I compared the relationship between VI data and each vegetation measurement at three time scales: one VI data point, summery statistics of one year of VI, and multitemporal VI data over six years. Woody vegetation had a log-normal distribution; therefore I used the natural log of these measurements as the response variable. For grass and shrub measurements, I performed regression only for the sample points with open cover types (grassland, grass savanna, steppe, and shrub savanna).

As a baseline, I performed univariate regressions between each of the twelve vegetation parameters (density, cover, biomass and greenness of trees, shrubs, and grasses) and the VI value at the closest date to the field measurement. Further, I calculated the correlation, over all sites during one year, between each field measurement and each summary statistic, for each VI. These summary statistics values therefore encompassed summary information of 23 or 46 dates (see Spatial Statistics subsection above), for NDVI/EVI or LAI/FPAR, respectively.

To create predictive models that incorporate six years of VI data and to reduce the dimensionality of the data I used Partial Least Square Regression (PLSR) (Hansen and Schjoerring 2003, Huang et al. 2004). PLSR is a powerful regression technique that is able to handle datasets with multiple predictor variables exhibiting high levels of multicollinearity (package *pls* in R. (Mevik and Wehrens 2007). The method generates orthogonal components which are linear combinations of the standardized predictor variables, such that each component explains the maximum covariance between the response and the predictor variables (Mevik and Wehrens 2007). PLSR is often used to analyze hyperspectral data (Hansen and Schjoerring 2003, Schmidtlein and Sassin 2004) and was demonstrated to be a good dimensions reduction technique for multitemporal MODIS data (Lazaridis et al. 2011).

I compared five multivariate PLSR model to assess the ability of each of the four VIs to predict vegetation measurements. I used a separate model for each of the four VIs. Each of these four models contained all VI data for six years in addition to the summary statistics for each year. The fifth model included only summary statistics for the four VIs together. For each PLSR model I performed leave-one-out cross-validation and used the resulting root mean square error of prediction (RMSEP) as the measures of model quality (Mevik and Cederkvist 2004). This method was suggested to be the best estimation of error and model quality in PLSR, while avoiding over-fitting the model (Mevik and Cederkvist 2004, Lazaridis et al. 2011). I used the same number of components for each model, to be able to compare between the models. I chose to use the 25 first components of each model. This number minimized the model RMSEP, while optimizing the percent of variance explained of the vegetation measurement (equivalent to R^2). I further confirmed the model quality by training the model on two thirds of the data selected at random, and testing the model on the remaining one third. I compared the resulting predicted versus measured data and compared the RMSEP to the RMSEP from the leave-one-out cross-validation. To calculate percent error I divided the exponent of the RMSEP (for log models) by the average value of the vegetation measurement.

2.2.5. Transferability

I assessed how my models could be transferred across space and time by using a predictive model build on a training dataset, to predict vegetation measurement of a test dataset. I then compared the RMSEP of predicted versus measured vegetation variables. To examine transferability in *space* I divided my sample sites into sites that occurred in drier versus wetter parts of the reserve. I chose these areas by assessing if they had annual rainfall below or above the average of the annual rainfall of ten years for Etosha (360 mm/year). This roughly separated the sites into the east versus the central/west parts of the reserve. I applied a model trained in the wetter area to sites in a dried area and vice versa, in order to examine whether precipitation had an effect on model prediction ability. To test model transferability in *time*, I applied the models built using the 2011 dry season data, to the 2012 wet season data.

2.3. Results

2.3.1. Field methodology for vegetation measurement

I sampled 348 points over a large area of 22,750 km^2, and compared between visual and measured information as two complementary methods to estimate vegetation cover and biomass. The vegetation cover type, based on 16 physiognomic classes, showed a good relationship to the visually estimated cover of each vegetation form (grass, dwarf shrubs, shrub, low/high trees) (Fig. 2A). Furthermore, there was good agreement between percent cover assessed by visual estimation and percent cover measured in the field (Fig. 2B). Only 31% of the points I sampled had a vegetation cover type that matched the previous classification created for Etosha.

2.3.2. Prediction of vegetation measurements using MODIS

Each vegetation cover type showed a distinctive time series pattern for each vegetation index (VI) (Fig. 3). All VIs showed an annual unimodal pattern, where the maximum value occurred around early February and minimum value occurred around mid-October. Different vegetation cover types had distinct maximum annual values and different length of growing season (Fig. 3).

Univariate regressions between vegetation measurements and MODIS provided weak but significant predictions. When I used only one VI value from the date closest to field measurement, the best results were obtained with NDVI as predictor variable. Although this model gave best results relative to the other univariate regressions, NDVI showed weak correlation with tree density, tree cover (R^2=0.34, $p < 0.001$), and tree biomass (R^2=0.37, $p < 0.001$). When I performed univariate regressions using summary statistics values of one year

(2011) it improved the results. Here, again, NDVI as a predictor gave the best model. The annual mean was the summary statistics value that provided the best prediction of tree density (R^2=0.44, $p < 0.001$), tree cover (R^2=0.42), and tree biomass (R^2=0.37). NDVI annual mean gave the best prediction of grass cover (R^2=0.43, $p < 0.001$). See Appendix 1 for a complete summary of values for univariate models.

Partial Least Square Regression (PLSR) significantly improved the model ability to predict measured vegetation parameters. PLSR models with 25 components predicted up to 88% of variability in grass cover (RMSEP = 23%) and 86% of variability in grass biomass. However, the error margins of predicted grass levels was rather high (RMSEP = 45 kg/ha) (Table 2A). The prediction ability of shrub measurement, using multi-temporal PLSR models, was very high. LAI based model explained 88% of variability in shrub density (RMSEP = 2.3 shrub/ ha) and 87% of variability in shrub cover (RMSEP = 2.3 m^2/ha, or 0.023% cover) (Table 2B). NDVI based models gave the best prediction of shrub biomass (87% of variability explained), but the error was rather high (22%). FPAR based model explained 81% of variability in shrub greenness with 37% error. While the RMSEP of shrub greenness was quite low (2-5%) the total error was high because of the low average greenness in the dry season (37-157% error).

NDVI based models gave the best prediction of tree density (78%, RMSEP=1.6 tree/ha), tree canopy cover (78%, RMSEP= 1.6 m^2/ha), and tree biomass (76%, RMSEP=2.11 kg/ha). The percent error on these measurements was very low and did not exceed 4% (Table 2C). Models explained 41-66% of variability in tree greenness, and FPAR explained the highest percent of the variance (66%, RMSEP =1.66 % greenness).

For the majority of the prediction models, the test model predicted on random subset of a third of the data resulted in slightly higher RMSEP than the cross-validation RMSEP (Table 2).

2.3.3. Comparing optimal time span for vegetation measurement

I compared the predicted versus measured plots of three models built for different time spans, to assess the importance of time integrated data for the quality of vegetation measurement prediction. In Figure 4 I present tree density as an example, but the results apply to all vegetation measures (see Table 2 and Appendix 1). Mean NDVI values for a whole year (2011) better predict tree density than NDVI acquired at a single date, closest to the date of field measurement (R^2 = 0.53 versus R^2 = 0.4, respectively; $p < 0.001$). Furthermore, the model built with six years of NDVI data provides considerable improvement (R^2 = 0.89) (Fig. 4).

I determined which summery statistics and individual dates were important for prediction by examining the loadings on each VI value for each model. My results varied across the different vegetation measurements, but I observed the following patterns. Summary statistics had much stronger influence on the prediction than individual VI dates. Interestingly, the Julian date of occurrence of annual minimum and annual maximum VI values had a stronger influence on the model prediction than the VI value itself at these dates. Additionally, the length of the growing season had a strong influence in most prediction models. Individual VI values measured during the rainy season (January – April) had an influence on the prediction models as well (Fig. 5A). In the model containing all VIs summary statistics, the date of occurrence of annual maximum repeatedly appeared to have a strong influence on model prediction (Fig. 5B).

2.3.4. Comparing vegetation indices

Next, I determined which VIs were the most effective in predicting vegetation measurements. First, I compared the number of components it took for each of the four VI models to achieve a given percent of explained variance. FPAR and LAI required fewer components than NDVI or EVI. Further, FPAR and LAI explained more variance for a given number of components, when predicting tree density, cover, and biomass (Fig. 6A-C) than NDVI/EVI. There was only slight difference between the VIs in their ability to predict tree greenness (Fig. 6D). Similarly, in the model which used the summary statistics values of all four VIs, FPAR had the highest loadings in the models (Fig. 5B).

When comparing between the models for vegetation measurements – each vegetation form had a different VI that gave the best prediction. EVI yielded the best prediction model for grass cover, while FPAR gave the best results for grass biomass (Table 2A). LAI was the best predictor of shrub density and cover, while NDVI gave the best results for shrub biomass. NDVI explained the highest percent variance for shrub greenness but had a very high error (157%). In terms of smallest error, FPAR had the best results for shrub greenness (Table 2). NDVI was the best predictor of tree density, tree canopy cover, and tree biomass, both in terms of highest variance explained and the smallest error. FPAR had the smallest error for predicting tree greenness (Table 2C).

2.3.5. Model transferability

I examined model transferability: how well a VI model for each vegetation measurement could be transferred to predict vegetation measurement in a different area or time. Based on the models selected in the prediction section (Table 2B), I used NDVI to assess transferability for the tree models, and FPAR for transferability of grass models.

<u>Transferability in space.</u> When applying a model built in the wet area of Etosha to the dry area, I achieved good correlation between predicted and measured for models for tree canopy cover, tree biomass, and tree greenness (Fig. 7A). However, the model for tree density tended to overestimate the lower range of values in the dry season. I attained similar results when I build the model for the dry part of Etosha and applying it to predict tree measurements in the wet part (Fig. 7B). Generally, there was a good fit between predicted and measured values for all for tree measurements, specifically for tree biomass. However, several high values of tree density and tree cover were overestimates (Fig. 7B).

For grass measurements, model trained in the drier area gave fair results when predicting grass cover and biomass in the wet area (Fig. 8B). However, transferring model for grass biomass from the wet to the dry area in Etohsa gave poor result with high RMSEP values. (Table 2A). The RMSEP of predicted values were generally lower for models trained on the dry part of Etosha and examined in the wetter part (Table 2).

<u>Transferability in time.</u> I achieved good model transferability in time; prediction models that were built for field data from the dry season of 2011 gave excellent prediction of tree density, canopy cover, and biomass in the wet season of the following year, 2012 (Fig. 7C). The RMSEP was less than 4 for the transferred predictions models for shrubs and most of the models for trees (Tables 2B and 2C). As expected, the model for tree greenness gave very poor prediction in the wet season (Fig. 7C). The prediction models created in 2011 for grass biomass and cover did not yield good prediction in the wet season (Fig. 8C).

2.3.6. Vegetation maps

Using the best PLSR model for each vegetation type (see section 3.2.) I created a series of maps of vegetation parameters for Etosha National Park. Figure 9 is an example of percent tree cover for the reserve, based on the NDVI PLSR model.

2.4. Discussion and conclusions

Predicting vegetation measurements with remote sensing in savanna ecosystems is challenging due to high variability of vegetation cover and phenology through space and time. Creating successful and transferable predictive models is further challenged by limited availability of field data and by the reflectance properties of savanna ecosystems. In this chapter, I have addressed these challenges by combining three key components: (1) developing methodology for extensive field sampling, (2) using time series data to account for vegetation temporal variability, and (3) comparing between four MODIS VIs that contain different radiometric information. I also showed that these methods are robust as they have spatial and temporal transferability.

2.4.1. Field sampling methodology

Measuring vegetation parameters for remote sensing validation in savanna ecosystems is often challenging and time consuming due to the vast landscapes and limited accessibility to these areas. Here, I demonstrated an extensive and relatively rapid field methodology to measure multiple vegetation parameters for ground truthing remote sensing data. I showed that there is a strong relationship between visual estimation and measured cover of different vegetation forms, which suggests that visual estimation might be a sufficient method for validating cover for remote sensing studies. The point centered quarter (PCQ) method I used here to measure woody vegetation proved to be a rapid and efficient technique for collecting large amount of data points. Indeed, PCQ was suggested as a good method that combines accuracy and efficiency (Engeman et al. 1994).

Only in 31% of the points I sampled the vegetation cover type matched the Landsat based classification done for Etosha in 1996. A possible explanation is that the old classification was mainly validated using an aerial survey and was a preliminary product (Taylor et al. 1996, Sannier et al. 1996). Otherwise, the discrepancy between my field samples and the past classification could be explained by rapid changes in vegetation structure in Etosha over the 15 years between surveys. Indeed, a study based on terrestrial photography showed that 80% of the sampled sites had changed in vegetation structure or composition over a time span of fifteen years (Du Plessis et al. 1998b). My results further confirm the need for frequent and extensive monitoring of savanna vegetation.

My extensive field sampling methodology enabled me to use remote sensing to predict four key vegetation parameters: density, cover, biomass, and greenness. While these measures were correlated, each parameter adds important information for the understanding of the overall community structure. Moreover, I sampled three different vegetation forms: grass, shrubs, and trees. Each one of these forms has a different ecosystem function by affecting distribution of grazers and browsers, influencing fire intensity, and protecting soil and water retention. Therefore, the ability of this methodology to predict all three components adds valuable remote sensing tool for savanna vegetation monitoring.

There was variation in the ability to predict different vegetation forms. Models for shrub density and canopy cover yielded the highest explained variance with low errors. This might be attributed to the fact that during the dry season shrubs are clearly distinct from the surrounding grass and soil by maintaining moisture and photosynthetic activity, which can be detected by VIs. While models for grass explained high percent of the variability, the error was quite high. This might be explained by the large variation of grass cover in different parts of Etosha. As expected, vegetation greenness prediction yielded high error for the dry season models, since most of the vegetation was dry. Indeed, models for predicting greenness based on the 2012 wet season resulted in much lower error.

2.4.2. Temporal variation

Predictive models based on summary statistics of one year of VI data performed much better than a model based on only single date value. This coincided with large body of research which demonstrated that integrated or maximum VI values allow better mapping of biomass and tree cover (Du Plessis 1999, Sannier et al. 2002). Here, I further show that the including time series data of six years significantly improves ability to predict vegetation measures. Interestingly, the dates of the minimum and the maximum occurrence had important part in the prediction. Indeed, previous research has shown that transition dates of vegetation phenology can be useful in MODIS-based vegetation monitoring (Zhang et al. 2003, Hmimina et al. 2013). While the summary statistic values had a prominent role in the final predictive model, the individual VI values considerably improved the overall prediction ability. This suggests that fine scale temporal VI information improves prediction ability beyond the averaged data. Overall, my results suggest that predictive models based on times series of MODIS data can significantly improve model prediction of vegetation measurements.

2.4.3. Comparison of prediction power of four VIs

While NDVI gave the best results for tree measurements, FPAR and LAI explained a large proportion of variability in tree measures for a given number of components. Moreover, LAI was the best predictor of shrub density and cover, while FPAR was the best predictor for grass biomass. A possible explanation is that while NDVI/EVI are good measures of vegetation greenness, LAI and FPAR measure structural and functional properties of vegetation, which are more relevant for measuring senesced vegetation prevalent in savanna ecosystems (Knyazikhin et al. 1999; Myneni et al. 2002). LAI and FPAR have a strong relationship with grassland biomass, both green and senescent, in variety of ecosystems (Asner et al. 1998, Malmstrom et al. 2009). LAI describes the canopy structure of the number of equivalent layers of leaves relative to a unit ground area, which may explain its superiority at predicting shrub cover and biomass.

Fensholt et al. (Fensholt et al. 2004) demonstrated that MODIS LAI reproduces ground measured LAI in semiarid savanna. FPAR measures the photosynthetic capacity of vegetation. This capacity continues, to some degree, in dry vegetation as well (Butterfield and Malmstrom 2009). Additionally, the model that MODIS uses to calculate LAI and FPAR includes NDVI as well as canopy reflectance data, sun-view geometry, a cover radiance transfer model specific for each land cover type, and extensive ground validation (Knyazikhin et al. 1999). These additional data sets may improve the correlation between LAI and FPAR and the ground-based measure of vegetation (Fensholt et al. 2004). While LAI and FPAR are important vegetation structural parameters which are often collected in the field (Baret and Guyot 1991), the MODIS –based indices for these parameters are not widely applied. Here, I demonstrate the utility of FPAR and LAI in improving measurement of vegetation in savanna ecosystems, beyond the traditional use of NDVI.

2.4.4. Transferability

One of the challenges in using remote sensing for vegetation measurements in semiarid environments is the ability to use models created in one place for vegetation measurement in another (Eisfelder et al. 2012). Here, I address the challenge of transferability between areas with different environmental conditions and between seasons. I achieved excellent results with good alignment between predicted and measured data. This demonstrates the prediction robustness of my models. Interestingly, transferring a model from drier to a wetter area provided better prediction than the other way around. A possible explanation might be that the drier part have lower variability of vegetation parameters. This suggests that it might be advisable to use a training dataset in an area with smaller rainfall gradient when calibrating remote sensing based models.

An exciting result I show here is the ability to use remote sensing models built for one year to predict vegetation measurement in the next. The use of integrated multiyear VI data incorporates temporal variability in vegetation conditions and therefore allows better prediction in a different time period. In order to apply this method to quantify change over time, it should be further investigated if temporal transferability can persist between areas with larger variations in vegetation condition.

Based on my results I have created full cover maps for density, cover, and biomass of grass, shrubs and trees for Etosha National park. These maps and can be used to further understand and key ecological processes in savanna ecosystems such as wildlife movement and distribution patterns, fire-vegetation dynamics, and understand soil and vegetation degradation processes. Moreover, the rich vegetation information acquired by my prediction models is extremely valuable for Etosha’s management and can improve vegetation and wildlife conservation in the reserve.

Using the method described here I demonstrate low cost and rapid methodology to measure savanna vegetation using freely available MODIS satellite data. I demonstrate that time series data and a combination of MODIS based VIs, including LAI and FPAR, can produce reliable and robust models to measure large suite of vegetation parameters. Furthermore, this methodology enables me to address a key challenge in remote sensing of semiarid environments by demonstrating model transferability through space and time. The ability to monitor large savanna landscapes in a timely cost efficient way is crucial for management and conservation of savanna ecosystems which the livelihood of millions of people and rich biodiversity depend on.

2.5. Acknowledgements

I thank the Namibian Ministry of Environment and Tourism (MET) for permission to conduct field work and for providing facility resources for this work. I am grateful to the staff at the Etosha Ecological Institute (EEI) for scientific and technical assistance, particularly Werner Killian, Shayne Kὸtting, Wilferd Versfeld, Marthin Kasaona, Birgit Kὸtting, Ndapanda Kanime, and Erastus Ithana. I thank Etosha’s wardens and rangers, and the staff of Namibia Wildlife Resorts (NWR) in Etosha. Emilia Haimbili and Maria Johannes provided dedicated assistance in field work. Audrey Taylor, Janelle Dorcy, Ashley Poggio, Angie Pettenato and Jake Toy helped in data digitizing. National Herbarium of Namibia performed excellent work identifying species samples. The Geospatial Innovation Facility at the University of California, Berkeley provided state of the art facilities and geospatial support. Professor Maureen Lahiff gave statistical assistance. This research was funded by the Science and Engineering fellowship from the Center for Emerging and Neglected diseases (CEND), by the Andrew and Mary Thomson Rocca dissertation research fellowship, and by the NIH Grant GM083863 and a USFWS Grant to WMG. Sponsors did not have a role in planning, executing or writing this research.

2.6. Tables

Table 1. Moderate Resolution Imaging Spectroradiometer (MODIS) vegetation indices used in this research and the parameters of each index.

Veg. index	MODIS product	Temporal resolution	Spatial resolution	Boolean dates used	Data Range	Scale factor
NDVI	MOD13Q1	16-days	250 m	289/2006 – 273/2012	–2000, 10000 Fill value: –3000	0.0001
EVI	MOD13Q1	16-days	250 m	289/2006 – 273/2012	–2000, 10000 Fill value: –3000	0.0001
FPAR	MOD15A2	8- days	1 km	289/2006 – 281/2012	0–100 Null values: 249–255	0.01
LAI	MOD15A2	8-days	1 km	289/2006 – 281/2012	0-100 Null values: 249–255	0.1

Table 2A. Partial Least square results for grass measurements

Vegetation Index	Measurement	RMSEP	Percent Error	R^2	RMSEP random[1]	RMSEP wet to dry[2]	RMSEP dry to wet[3]	RMSEP 2012[4]	RMSEP 2011 to 2012[5]
NDVI	Cover	0.29	61.28	0.86	0.42	0.68	0.34	0.27	0.24
EVI	Cover	0.23	49.67	0.88	0.30	0.36	0.22	0.26	0.23
LAI	Cover	0.29	62.51	0.84	0.37	1.22	0.27	0.19	0.23
FPAR	Cover	0.29	61.41	0.86	0.27	0.53	0.32	0.26	0.24
All four VIs	Cover	0.34	73.36	0.85	0.50	0.41	0.46	0.46	0.24
NDVI	Biomass	54.73	61.56	0.86	60.44	286.58	72.17	170.48	161.59
EVI	Biomass	54.85	61.69	0.86	65.68	140.39	65.75	146.06	170.77
LAI	Biomass	68.26	76.78	0.84	73.47	281.57	64.03	198.56	186.96
FPAR	Biomass	45.49	51.16	0.87	42.89	135.04	81.62	123.01	181.76
All four VIs	Biomass	102.43	115.22	0.72	100.13	141.16	100.10	120.24	181.38

Best results are greyed out. [1]Root mean square error of predicted (RMSEP) of sample of random 33% of all samples; [2]RMSEP of test samples in dry area, on training models built in the wet area; [3] RMSEP of test samples in wet area, on training models built in the dry area; [4]RMSEP of model for 2012 wet season data. [5] RMSEP of test samples in wet season of 2012, on training models built in the dry season of 2011.

Table 2B. Partial Least square results for shrub measurements

Vegetation Index	Measurement	RMSEP	Percent Error	R^2	RMSEP random[1]	RMSEP wet to dry[2]	RMSEP dry to wet[3]	RMSEP 2012[4]	RMSEP 2011 to 2012[5]
NDVI	Density	2.60	0.42	0.87	3.18	4.74	3.25	4.62	2.12
EVI	Density	2.89	0.57	0.87	3.73	3.35	3.21	4.08	1.84
LAI	Density	2.31	0.32	0.88	3.75	4.78	3.11	3.29	2.00
FPAR	Density	2.91	0.58	0.86	2.38	3.85	5.04	3.22	2.02
All four VIs	Density	3.19	0.76	0.78	4.26	5.56	4.24	5.29	2.01
NDVI	Canopy cover	2.48	1.04	0.86	3.13	4.24	2.97	3.71	1.98
EVI	Canopy cover	2.97	1.70	0.86	2.32	3.79	3.08	2.73	1.76
LAI	Canopy cover	2.47	1.03	0.87	3.62	5.63	3.88	3.08	1.94
FPAR	Canopy cover	2.86	1.52	0.84	2.99	3.66	3.87	3.50	1.83
All four VIs	Canopy cover	3.49	2.85	0.71	5.76	5.06	3.93	4.63	1.67
NDVI	Biomass	2.70	22.58	0.87	2.64	3.69	3.31	3.99	2.17
EVI	Biomass	3.17	35.90	0.86	2.79	3.34	3.31	3.43	1.87
LAI	Biomass	3.12	34.11	0.84	3.07	6.24	4.61	3.58	2.24
FPAR	Biomass	2.92	28.00	0.85	2.80	4.33	3.47	3.18	2.17
All four VIs	Biomass	4.16	96.98	0.71	5.05	4.92	4.18	6.28	2.02
NDVI	Greenness (%)	3.57	157.35	0.91	2.91	10.10	2.97	0.25	3.16
EVI	Greenness (%)	2.97	86.41	0.90	3.75	6.11	2.89	0.33	2.89
LAI	Greenness (%)	2.36	46.97	0.80	2.07	3.73	2.71	0.41	2.91
FPAR	Greenness (%)	2.13	37.41	0.81	1.57	3.02	3.67	0.31	3.06
All four VIs	Greenness (%)	4.95	624.53	0.80	4.68	3.65	4.46	0.47	3.70

Table 2C. Partial Least square results for tree measurements

Vegetation Index	Measurement	RMSEP	Percent Error	R^2	RMSEP random[1]	RMSEP wet to dry[2]	RMSEP dry to wet[3]	RMSEP 2012[4]	RMSEP 2011 to 2012[5]
NDVI	Density	1.65	2.50	0.78	1.93	2.50	2.23	1.77	1.13
EVI	Density	1.87	3.11	0.75	1.99	2.74	2.32	2.42	1.24
LAI	Density	2.07	3.80	0.71	2.20	2.99	2.46	2.18	1.39
FPAR	Density	1.95	3.35	0.74	1.96	2.75	2.57	1.90	1.32
All four VIs	Density	1.95	3.35	0.63	2.67	2.68	2.30	3.90	1.48
NDVI	Canopy cover	1.58	0.35	0.79	1.57	2.11	2.29	1.78	1.18
EVI	Canopy cover	1.62	0.36	0.76	1.57	2.30	1.96	2.12	1.20
LAI	Canopy cover	2.12	0.60	0.75	2.04	2.47	2.43	2.11	1.32
FPAR	Canopy cover	1.78	0.43	0.76	1.89	2.44	2.35	1.92	1.31
All four VIs	Canopy cover	1.85	0.45	0.65	2.14	2.57	2.04	3.96	1.47
NDVI	Biomass	2.11	0.65	0.76	2.78	2.57	2.62	2.45	1.66
EVI	Biomass	2.19	0.71	0.74	2.52	2.98	2.95	2.15	1.39
LAI	Biomass	2.73	1.21	0.72	2.89	3.56	4.06	2.62	1.68
FPAR	Biomass	2.42	0.89	0.76	2.29	3.40	3.28	2.67	1.62
All four VIs	Biomass	2.48	0.95	0.64	2.76	3.76	3.06	3.39	1.74
NDVI	Greenness (%)	1.53	19.53	0.53	1.60	2.55	1.79	0.63	1.42
EVI	Greenness (%)	1.52	19.36	0.61	1.74	2.80	1.87	0.69	2.08
LAI	Greenness (%)	1.63	21.58	0.66	1.72	5.20	1.97	0.67	1.69
FPAR	Greenness (%)	1.66	22.15	0.66	1.65	2.46	1.69	0.53	1.92
All four VIs	Greenness (%)	1.64	21.80	0.41	2.12	3.52	2.38	0.84	1.98

Best results are greyed out. [1] Root mean square error of predicted (RMSEP) of sample of random 33% of all samples; [2] RMSEP of test samples in dry area, on training models built in the wet area; [3] RMSEP of test samples in wet area, on training models built in the dry area; [4] RMSEP of model for 2012 wet season data. [5] RMSEP of test samples in wet season of 2012, on training models built in the dry season of 2011.

2.7. Figures

Figure 1. Map of study site, Etosha National Park. The location of sampling sites (brown) and watering points (blue) are marked

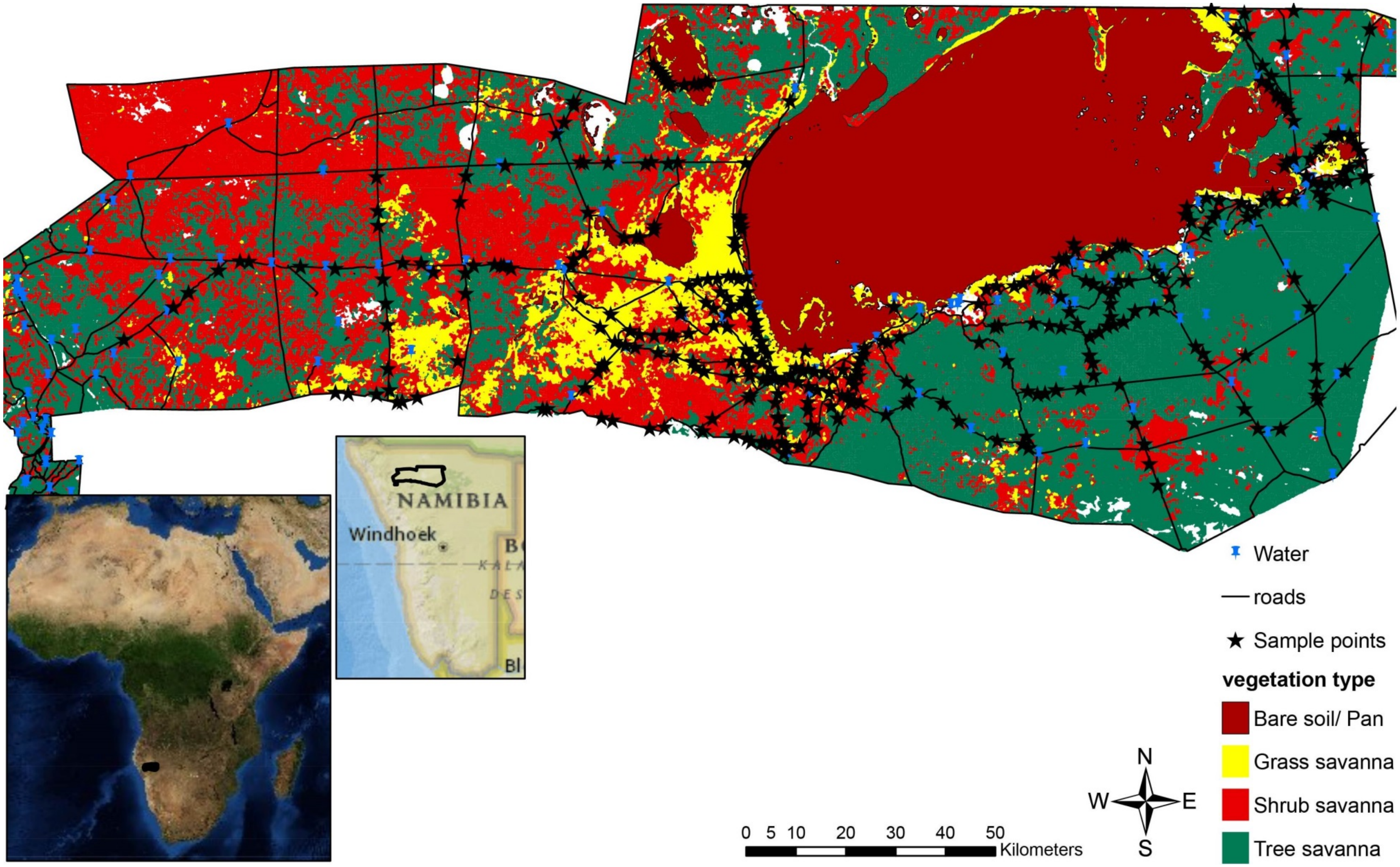


Figure 2. A. Visual estimation of the percent cover of the main vegetation forms in different vegetation cover classes. **B.** Tree cover measured in the field in different vegetation cover classes.

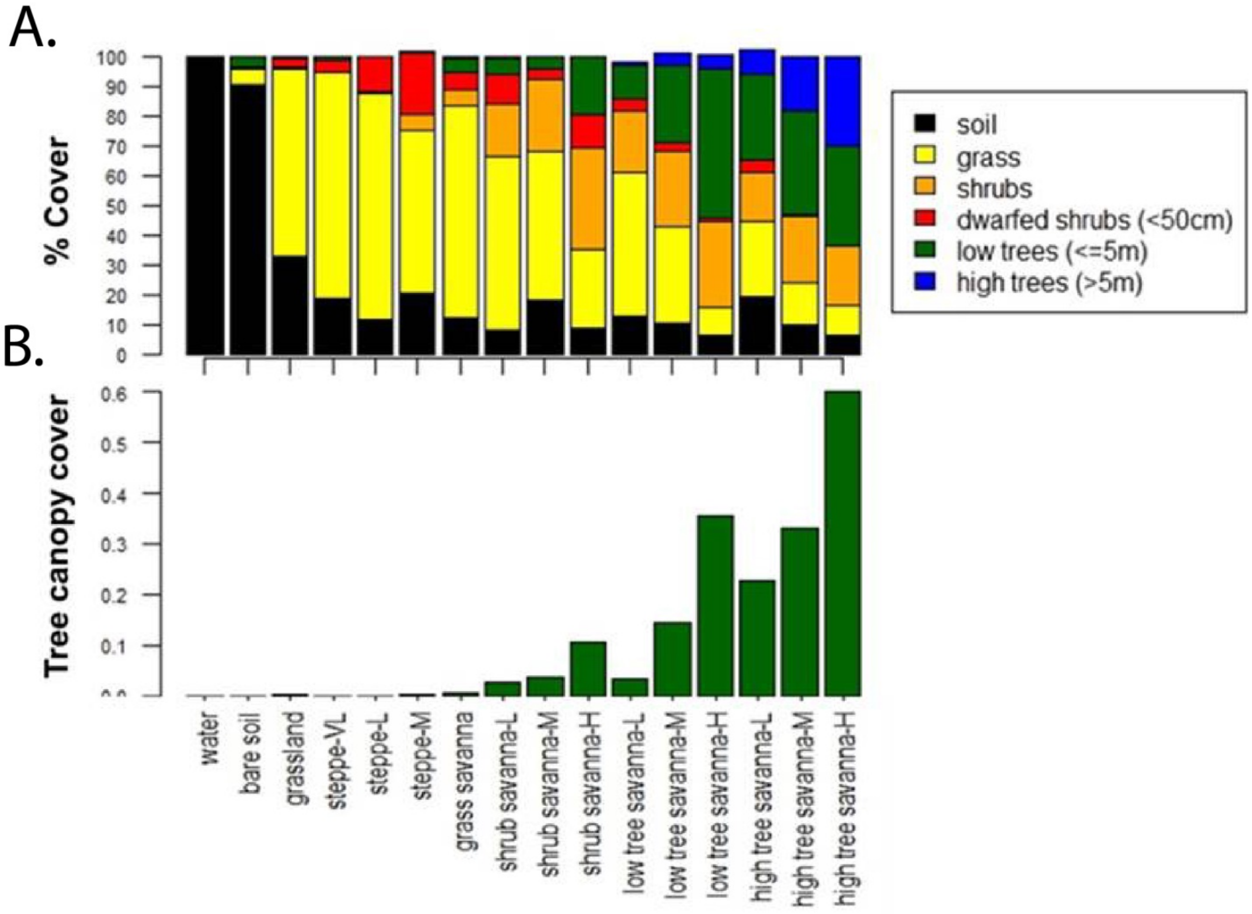


Figure 3. Vegetation Index time series profile (2007 – 2012) for different vegetation cover classes. **A.** NDVI. **B.** FPAR

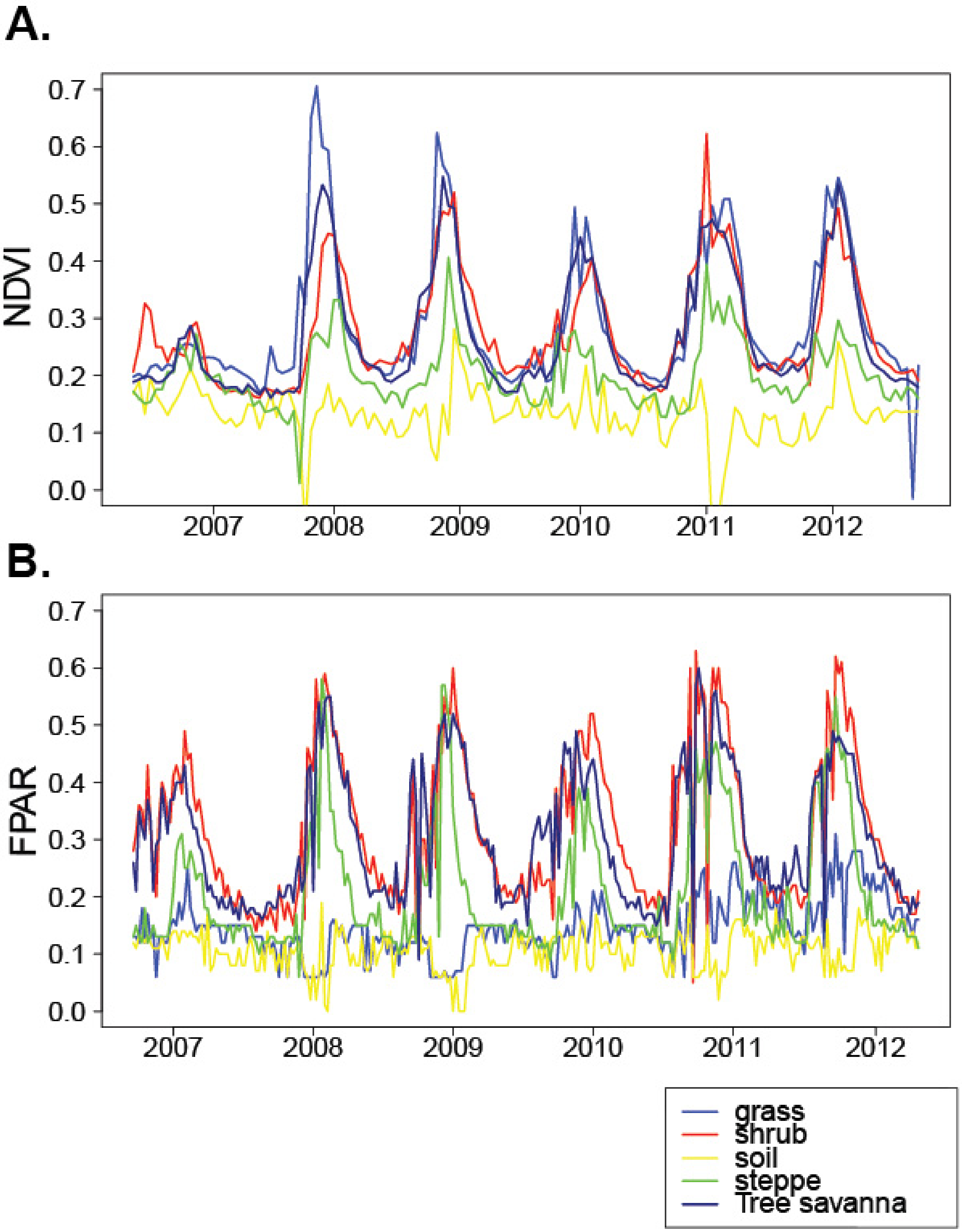


Figure 4. Predicted versus measured tree density built with NDVI models of: **A.** Closest date to field measurement. **B.** Mean annual NDVI for 2011. **C.** PLSR model for five years of NDVI data. * Note that the values in this figure are somewhat higher than the results for the overall model, since the models here were built on a training set of random 50% of the data.

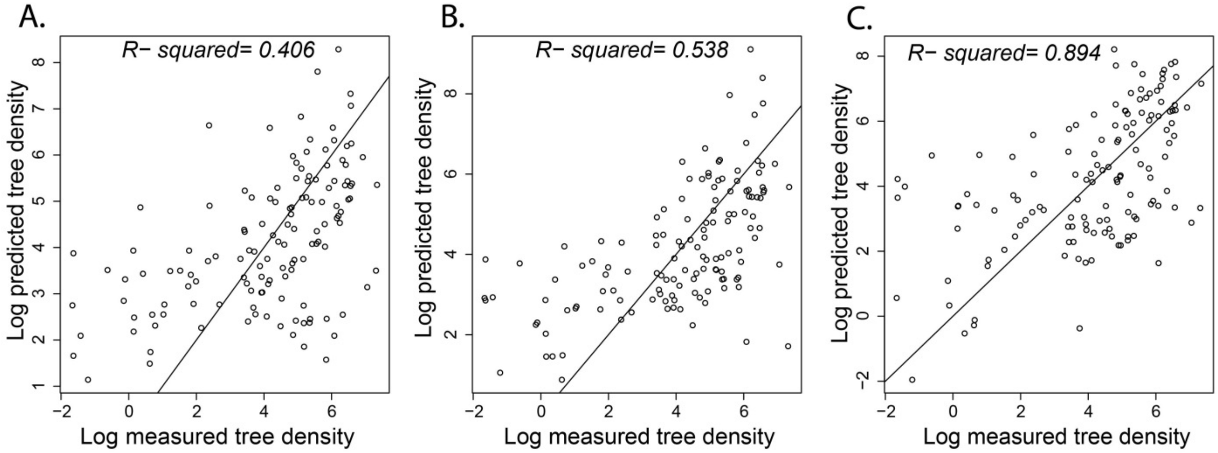


Figure 5. A. Loadings of NDVI prediction model for tree density. Highest loadings are marked. **B.** Loadings for tree density model based on summery statistics values of all four VIs.

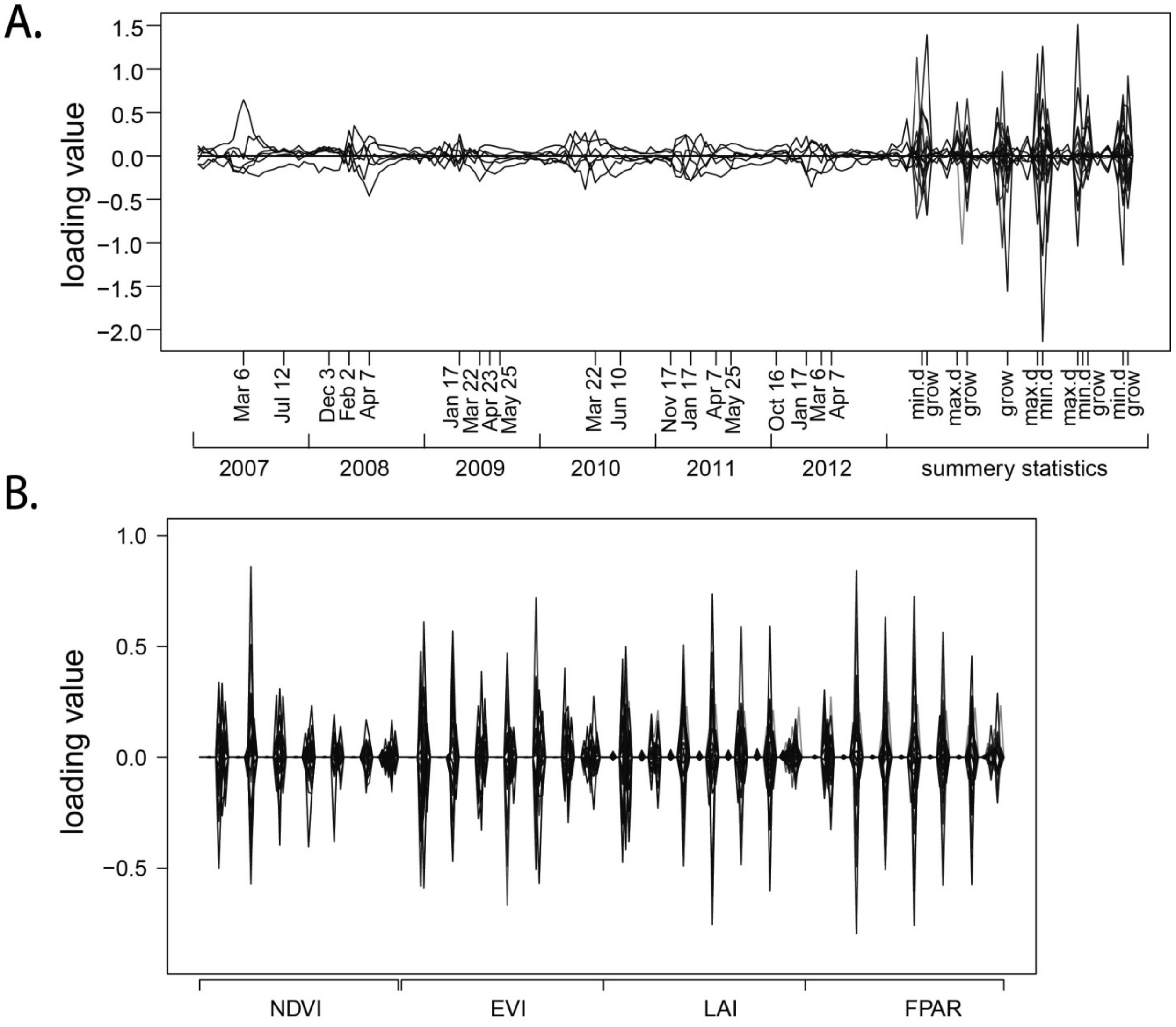


Figure 6. Comparing prediction ability of four vegetation index to predict: **A.** Tree density. **B.** Tree cover. **C.** Tree biomass. **D.** Tree greenness.

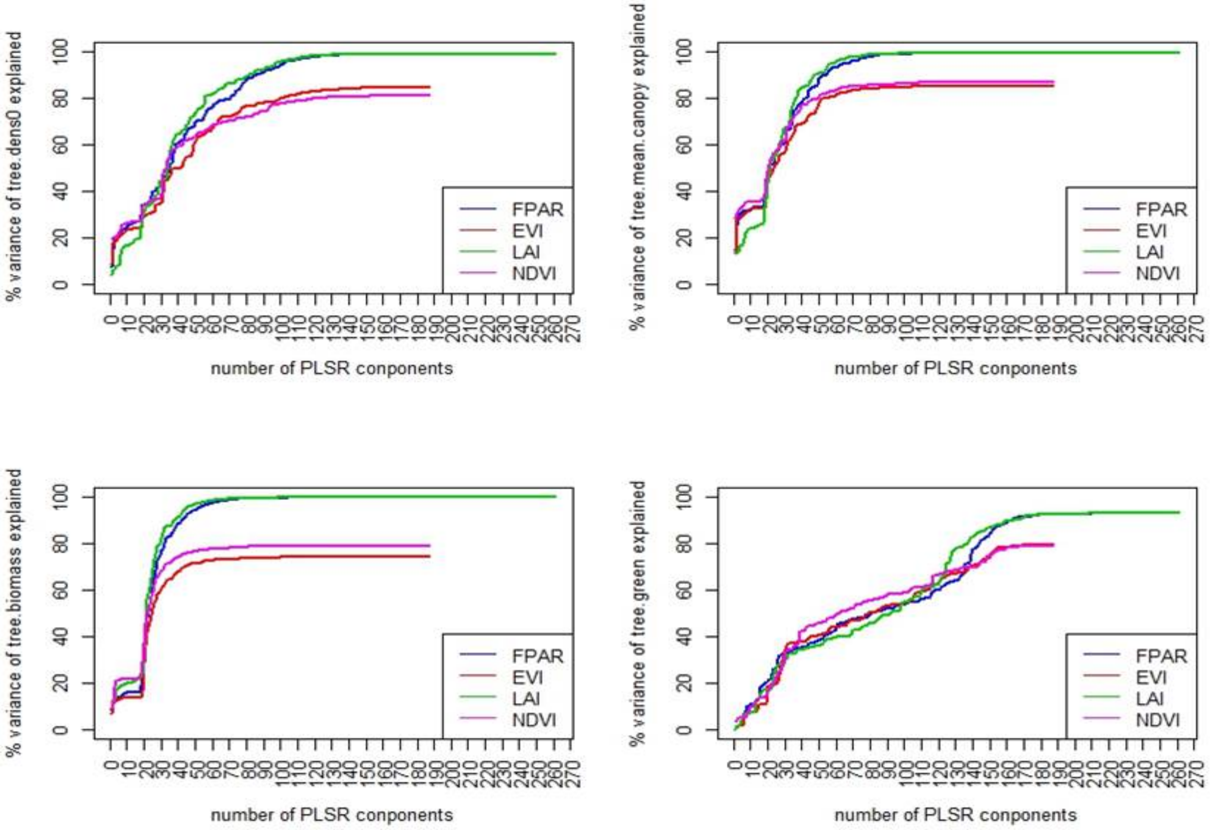


Figure 7A. Transferability of NDVI-based models for tree measurements. Predicted versus measured of log tree measurements. Transferability in space: from wet to dry areas. Diagonal lines have an aspect ratio of 1.

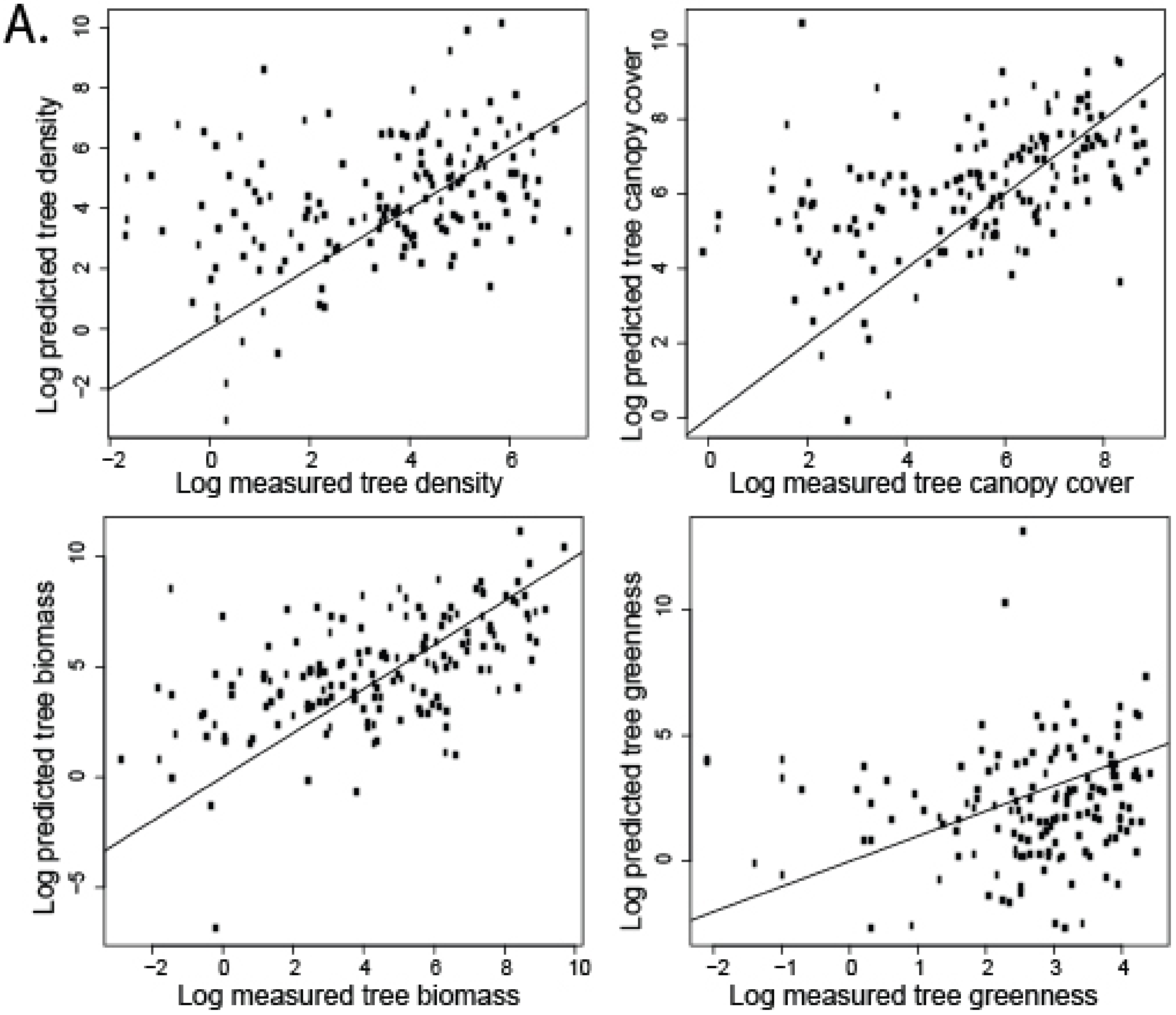


Figure 7B. Transferability of NDVI-based models for tree measurements. Predicted versus measured of log tree measurements. Transferability in space: from dry to wet areas. Diagonal lines have an aspect ratio of 1.

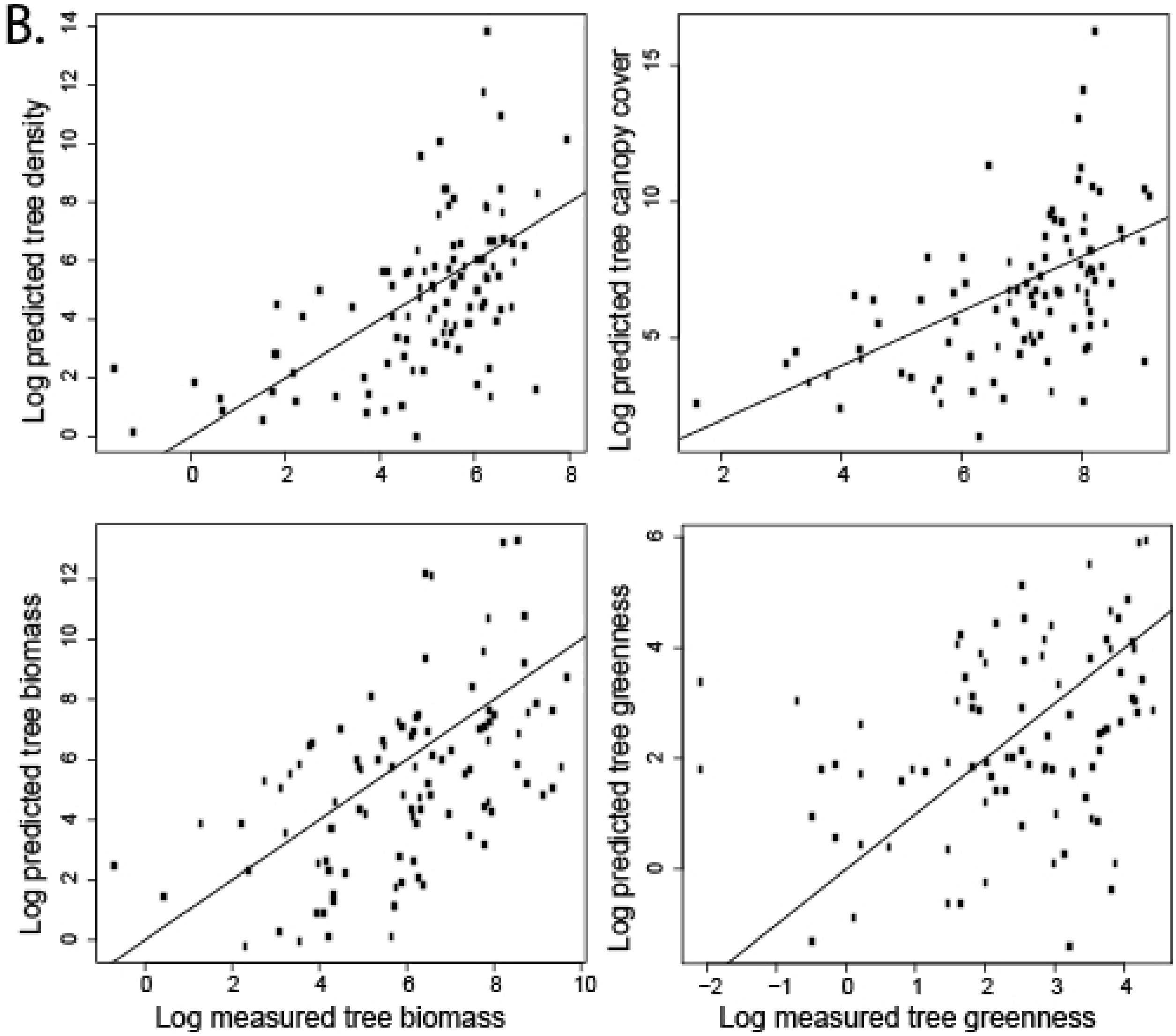


Figure 7C. Transferability of NDVI-based models for tree measurements. Predicted versus measured of log tree measurements. Transferability in time (from 2011 to 2012). Diagonal lines have an aspect ratio of 1.

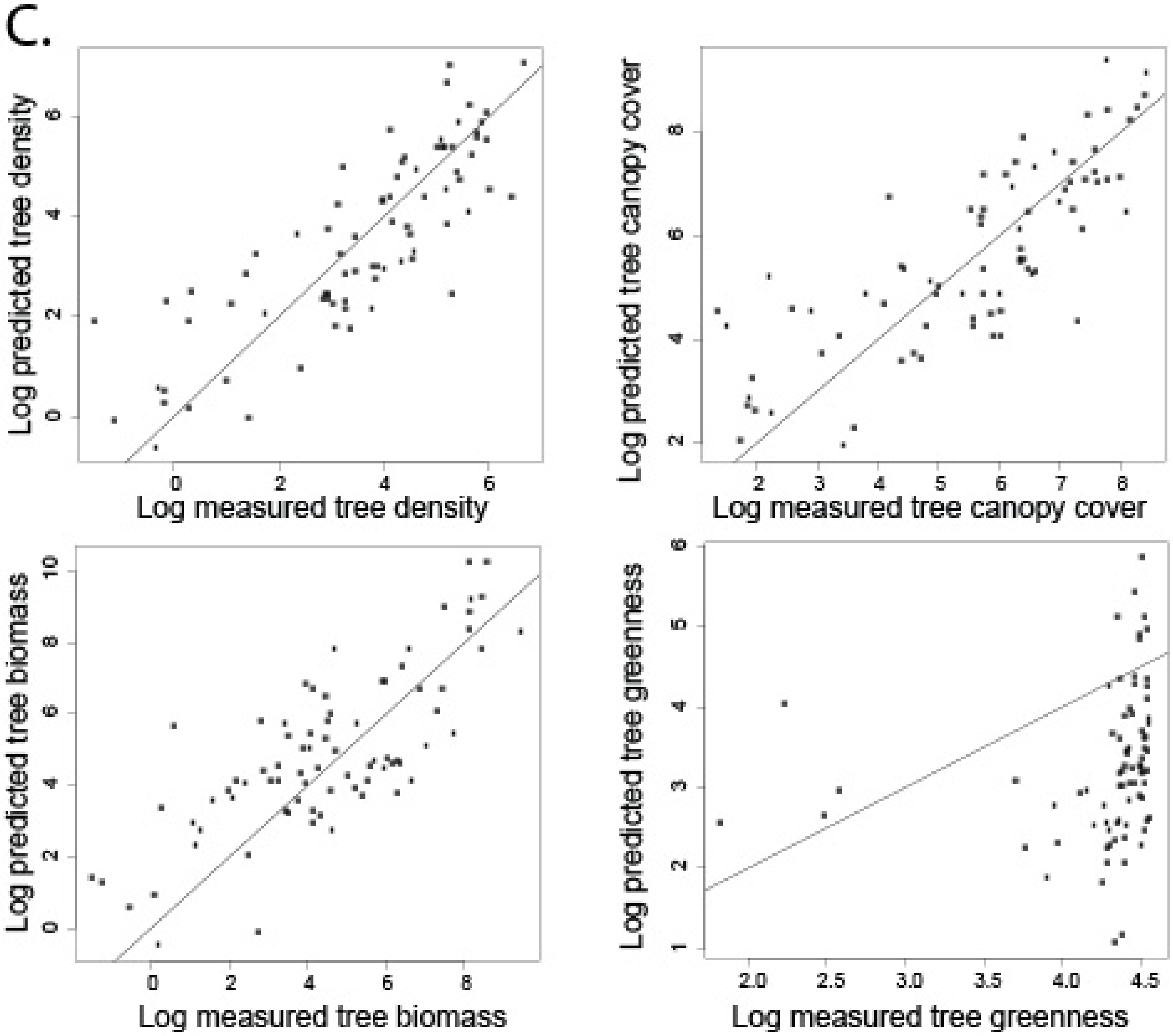


Figure 8. Transferability of FPAR based models for grass measurements. **A.** Transferability in space: from wet to dry areas. **B.** Transferability in space: from dry to wet areas. **C.** Transferability in time (from 2011 to 2012). Upper panel shows grass cover, lower panel shows grass biomass. Diagonal lines have an aspect ratio of 1.

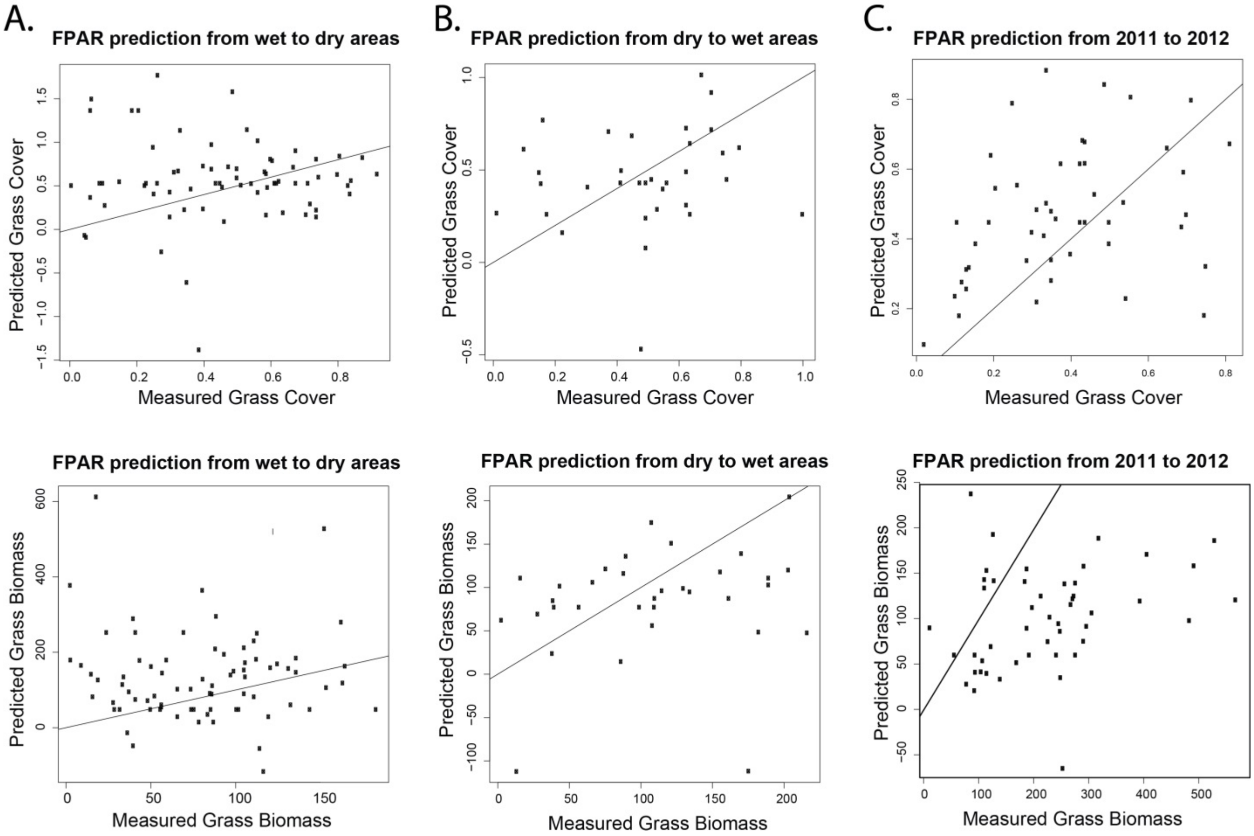
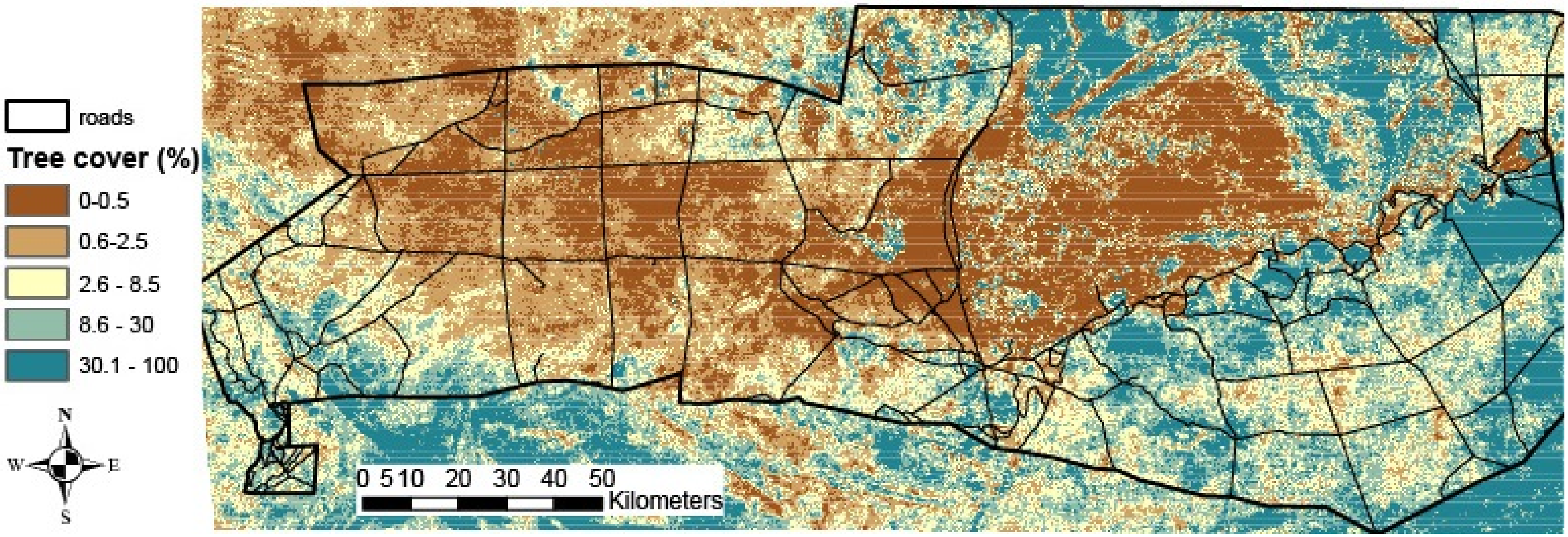


Figure 9. Predicted percent tree canopy cover in Etosha based on NDVI model.



Appendix 1. Results from univariate regressions

Appendix 1A. Results of univariate regression for grass measurements

$R^2 > 0.3$ and $p < 0.05$ are highlighted

Vegetation Index	Vegetation Measurement	Summary Statistics	R-square	*p value*	coefficient	coefficient *p value*
NDVI	Grass Cover	Closest date	0.16	0.00	3.04	0.00
NDVI	Grass Cover	Mean	0.43	0.00	2.51	0.00
NDVI	Grass Cover	Median	0.22	0.00	2.50	0.00
NDVI	Grass Cover	Sum	0.43	0.00	0.11	0.00
NDVI	Grass Cover	Maximum	0.38	0.00	1.23	0.00
NDVI	Grass Cover	Minimum	0.29	0.00	1.75	0.00
NDVI	Grass Cover	Growing season	0.12	0.00	0.00	0.00
NDVI	Grass Biomass	Closest date	0.23	0.00	748.63	0.00
NDVI	Grass Biomass	Mean	0.21	0.00	352.99	0.00
NDVI	Grass Biomass	Median	0.24	0.00	534.35	0.00
NDVI	Grass Biomass	Sum	0.21	0.00	15.35	0.00
NDVI	Grass Biomass	Maximum	0.16	0.00	162.19	0.00
NDVI	Grass Biomass	Minimum	0.14	0.00	239.78	0.00
NDVI	Grass Biomass	Growing season	0.05	0.02	-0.20	0.02
NDVI	Grass Greenness %	Closest date	0.04	0.06	10.00	0.06
NDVI	Grass Greenness %	Mean	0.00	0.66	1.20	0.66
NDVI	Grass Greenness %	Median	0.04	0.07	6.51	0.07
NDVI	Grass Greenness %	Sum	0.00	0.66	0.05	0.66
NDVI	Grass Greenness %	Maximum	0.00	0.64	-0.68	0.64
NDVI	Grass Greenness %	Minimum	0.01	0.50	1.60	0.50
NDVI	Grass Greenness %	Growing season	0.00	0.83	0.00	0.83
EVI	Grass Cover	Closest date	0.04	0.03	3.37	0.03
EVI	Grass Cover	Mean	0.30	0.00	3.69	0.00
EVI	Grass Cover	Median	0.15	0.00	3.63	0.00
EVI	Grass Cover	Sum	0.30	0.00	0.16	0.00
EVI	Grass Cover	Maximum	0.17	0.00	1.37	0.00
EVI	Grass Cover	Minimum	0.22	0.00	1.95	0.00
EVI	Grass Cover	Growing season	0.09	0.00	0.00	0.00
EVI	Grass Biomass	Closest date	0.04	0.04	679.56	0.04
EVI	Grass Biomass	Mean	0.11	0.00	451.66	0.00
EVI	Grass Biomass	Median	0.13	0.00	711.93	0.00
EVI	Grass Biomass	Sum	0.11	0.00	19.64	0.00
EVI	Grass Biomass	Maximum	0.05	0.02	155.78	0.02
EVI	Grass Biomass	Minimum	0.09	0.00	247.72	0.00
EVI	Grass Biomass	Growing season	0.07	0.01	-0.21	0.01
EVI	Grass Greenness %	Closest date	0.03	0.09	18.83	0.09
EVI	Grass Greenness %	Mean	0.00	0.64	2.30	0.64
EVI	Grass Greenness %	Median	0.04	0.09	11.36	0.09
EVI	Grass Greenness %	Sum	0.00	0.64	0.10	0.64
EVI	Grass Greenness %	Maximum	0.00	0.88	0.39	0.88
EVI	Grass Greenness %	Minimum	0.00	0.70	1.22	0.70
EVI	Grass Greenness %	Growing season	0.00	0.83	0.00	0.83

Appendix 1A.(*continue*). Results of univariate regression for grass measurements
$R^2 > 0.3$ and $p < 0.05$ are highlighted

Vegetation Index	Vegetation Measurement	Summary Statistics	R-square	*p value*	coefficient	coefficient *p value*
FPAR	Grass Cover	Closest date	0.03	0.09	0.66	0.09
FPAR	Grass Cover	Mean	0.08	0.00	0.79	0.00
FPAR	Grass Cover	Median	0.03	0.06	0.68	0.06
FPAR	Grass Cover	Sum	0.08	0.00	0.02	0.00
FPAR	Grass Cover	Maximum	0.10	0.00	0.41	0.00
FPAR	Grass Cover	Minimum	0.01	0.33	0.63	0.33
FPAR	Grass Cover	Growing season	0.00	0.95	0.00	0.95
FPAR	Grass Biomass	Closest date	0.04	0.03	185.47	0.03
FPAR	Grass Biomass	Mean	0.05	0.02	140.97	0.02
FPAR	Grass Biomass	Median	0.05	0.01	192.30	0.01
FPAR	Grass Biomass	Sum	0.05	0.02	3.06	0.02
FPAR	Grass Biomass	Maximum	0.05	0.02	62.50	0.02
FPAR	Grass Biomass	Minimum	0.01	0.22	169.08	0.22
FPAR	Grass Biomass	Growing season	0.00	0.49	-0.04	0.49
FPAR	Grass Greenness %	Closest date	0.00	0.97	0.11	0.97
FPAR	Grass Greenness %	Mean	0.00	0.74	-0.67	0.74
FPAR	Grass Greenness %	Median	0.00	0.66	1.16	0.66
FPAR	Grass Greenness %	Sum	0.00	0.74	-0.01	0.74
FPAR	Grass Greenness %	Maximum	0.01	0.47	-0.67	0.47
FPAR	Grass Greenness %	Minimum	0.00	0.58	-2.55	0.58
FPAR	Grass Greenness %	Growing season	0.00	0.63	0.00	0.63
LAI	Grass Cover	Closest date	0.01	0.43	0.17	0.43
LAI	Grass Cover	Mean	0.10	0.00	0.41	0.00
LAI	Grass Cover	Median	0.03	0.08	0.33	0.08
LAI	Grass Cover	Sum	0.10	0.00	0.01	0.00
LAI	Grass Cover	Maximum	0.14	0.00	0.15	0.00
LAI	Grass Cover	Minimum	0.01	0.26	0.37	0.26
LAI	Grass Cover	Growing season	0.02	0.16	0.00	0.16
LAI	Grass Biomass	Closest date	0.02	0.13	70.72	0.13
LAI	Grass Biomass	Mean	0.05	0.01	67.24	0.01
LAI	Grass Biomass	Median	0.04	0.04	84.19	0.04
LAI	Grass Biomass	Sum	0.05	0.01	1.46	0.01
LAI	Grass Biomass	Maximum	0.06	0.01	21.76	0.01
LAI	Grass Biomass	Minimum	0.02	0.13	105.46	0.13
LAI	Grass Biomass	Growing season	0.02	0.15	-0.08	0.15
LAI	Grass Greenness %	Closest date	0.00	0.64	0.72	0.64
LAI	Grass Greenness %	Mean	0.00	0.84	-0.19	0.84
LAI	Grass Greenness %	Median	0.01	0.43	1.07	0.43
LAI	Grass Greenness %	Sum	0.00	0.84	0.00	0.84
LAI	Grass Greenness %	Maximum	0.01	0.49	-0.20	0.49
LAI	Grass Greenness %	Minimum	0.00	0.77	-0.69	0.77
LAI	Grass Greenness %	Growing season	0.00	0.56	0.00	0.56

Appendix 1B. Results of univariate regression for trees measurements

$R^2 > 0.3$ and $p < 0.05$ are highlighted

Vegetation Index	Tree Measurement	Summary Statatistics	R-square	*p value*	coefficient	coefficient *p value*
NDVI	Density	Closest date	0.34	0.00	40.18	0.00
NDVI	Density	Mean	0.44	0.00	26.71	0.00
NDVI	Density	Median	0.40	0.00	15.30	0.00
NDVI	Density	Sum	0.44	0.00	1.16	0.00
NDVI	Density	Maximum	0.19	0.00	14.19	0.00
NDVI	Density	Minimum	0.33	0.00	32.38	0.00
NDVI	Density	Growing season	0.27	0.00	0.04	0.00
NDVI	Canopy Cover	Closest date	0.34	0.00	38.57	0.00
NDVI	Canopy Cover	Mean	0.42	0.00	25.46	0.00
NDVI	Canopy Cover	Median	0.39	0.00	14.73	0.00
NDVI	Canopy Cover	Sum	0.42	0.00	1.11	0.00
NDVI	Canopy Cover	Maximum	0.21	0.00	14.29	0.00
NDVI	Canopy Cover	Minimum	0.34	0.00	31.74	0.00
NDVI	Canopy Cover	Growing season	0.24	0.00	0.03	0.00
NDVI	Biomass	Closest date	0.37	0.00	52.87	0.00
NDVI	Biomass	Mean	0.37	0.00	31.35	0.00
NDVI	Biomass	Median	0.33	0.00	17.78	0.00
NDVI	Biomass	Sum	0.37	0.00	1.36	0.00
NDVI	Biomass	Maximum	0.16	0.00	16.41	0.00
NDVI	Biomass	Minimum	0.37	0.00	43.31	0.00
NDVI	Biomass	Growing season	0.19	0.00	0.04	0.00
NDVI	Greenness %	Closest date	0.00	0.95	-0.20	0.95
NDVI	Greenness %	Mean	0.05	0.00	-6.14	0.00
NDVI	Greenness %	Median	0.03	0.00	-3.01	0.00
NDVI	Greenness %	Sum	0.05	0.00	-0.27	0.00
NDVI	Greenness %	Maximum	0.05	0.00	-5.07	0.00
NDVI	Greenness %	Minimum	0.01	0.22	-2.98	0.22
NDVI	Greenness %	Growing season	0.04	0.00	-0.01	0.00
EVI	Density	Closest date	0.05	0.00	28.32	0.00
EVI	Density	Mean	0.24	0.00	40.85	0.00
EVI	Density	Median	0.32	0.00	31.66	0.00
EVI	Density	Sum	0.24	0.00	1.78	0.00
EVI	Density	Maximum	0.04	0.00	7.35	0.00
EVI	Density	Minimum	0.03	0.01	16.59	0.01
EVI	Density	Growing season	0.12	0.00	0.02	0.00
EVI	Canopy Cover	Closest date	0.05	0.00	27.96	0.00
EVI	Canopy Cover	Mean	0.25	0.00	39.61	0.00
EVI	Canopy Cover	Median	0.33	0.00	31.04	0.00
EVI	Canopy Cover	Sum	0.25	0.00	1.72	0.00
EVI	Canopy Cover	Maximum	0.05	0.00	7.75	0.00
EVI	Canopy Cover	Minimum	0.03	0.00	18.27	0.00
EVI	Canopy Cover	Growing season	0.09	0.00	0.02	0.00
EVI	Biomass	Closest date	0.07	0.00	43.30	0.00
EVI	Biomass	Mean	0.22	0.00	49.27	0.00
EVI	Biomass	Median	0.30	0.00	38.98	0.00
EVI	Biomass	Sum	0.22	0.00	2.14	0.00
EVI	Biomass	Maximum	0.03	0.00	8.15	0.00
EVI	Biomass	Minimum	0.07	0.00	33.00	0.00
EVI	Biomass	Growing season	0.08	0.00	0.02	0.00
EVI	Greenness %	Closest date	0.00	0.38	-4.79	0.38
EVI	Greenness %	Mean	0.04	0.00	-10.30	0.00
EVI	Greenness %	Median	0.02	0.02	-5.64	0.02
EVI	Greenness %	Sum	0.04	0.00	-0.45	0.00
EVI	Greenness %	Maximum	0.03	0.01	-3.81	0.01
EVI	Greenness %	Minimum	0.00	0.43	3.43	0.43
EVI	Greenness %	Growing season	0.02	0.01	-0.01	0.01

Appendix 1B. (*continue*) Results of univariate regression for trees measurements

$R^2 > 0.3$ and $p < 0.05$ are highlighted

Vegetation Index	Tree Measurement	Summary Statatistics	R-square	*p value*	coefficient	coefficient *p value*
FPAR	Density	Closest date	0.11	0.00	15.46	0.00
FPAR	Density	Mean	0.24	0.00	15.39	0.00
FPAR	Density	Median	0.32	0.00	16.49	0.00
FPAR	Density	Sum	0.24	0.00	0.33	0.00
FPAR	Density	Maximum	0.14	0.00	6.34	0.00
FPAR	Density	Minimum	0.11	0.00	18.55	0.00
FPAR	Density	Growing season	0.00	0.70	0.00	0.70
FPAR	Canopy Cover	Closest date	0.12	0.00	15.99	0.00
FPAR	Canopy Cover	Mean	0.25	0.00	15.48	0.00
FPAR	Canopy Cover	Median	0.32	0.00	16.34	0.00
FPAR	Canopy Cover	Sum	0.25	0.00	0.34	0.00
FPAR	Canopy Cover	Maximum	0.16	0.00	6.75	0.00
FPAR	Canopy Cover	Minimum	0.10	0.00	17.51	0.00
FPAR	Canopy Cover	Growing season	0.00	0.84	0.00	0.84
FPAR	Biomass	Closest date	0.11	0.00	20.72	0.00
FPAR	Biomass	Mean	0.23	0.00	19.47	0.00
FPAR	Biomass	Median	0.29	0.00	20.16	0.00
FPAR	Biomass	Sum	0.23	0.00	0.42	0.00
FPAR	Biomass	Maximum	0.16	0.00	8.84	0.00
FPAR	Biomass	Minimum	0.12	0.00	24.69	0.00
FPAR	Biomass	Growing season	0.00	0.95	0.00	0.95
FPAR	Greenness %	Closest date	0.00	0.63	-0.96	0.63
FPAR	Greenness %	Mean	0.03	0.01	-3.46	0.01
FPAR	Greenness %	Median	0.02	0.03	-2.80	0.03
FPAR	Greenness %	Sum	0.03	0.01	-0.08	0.01
FPAR	Greenness %	Maximum	0.02	0.05	-1.43	0.05
FPAR	Greenness %	Minimum	0.00	0.85	-0.45	0.85
FPAR	Greenness %	Growing season	0.01	0.24	0.00	0.24
LAI	Density	Closest date	0.10	0.00	7.70	0.00
LAI	Density	Mean	0.24	0.00	5.61	0.00
LAI	Density	Median	0.27	0.00	6.11	0.00
LAI	Density	Sum	0.24	0.00	0.12	0.00
LAI	Density	Maximum	0.12	0.00	1.52	0.00
LAI	Density	Minimum	0.11	0.00	9.68	0.00
LAI	Density	Growing season	0.01	0.21	0.00	0.21
LAI	Canopy Cover	Closest date	0.13	0.00	8.34	0.00
LAI	Canopy Cover	Mean	0.26	0.00	5.68	0.00
LAI	Canopy Cover	Median	0.29	0.00	6.10	0.00
LAI	Canopy Cover	Sum	0.26	0.00	0.12	0.00
LAI	Canopy Cover	Maximum	0.15	0.00	1.62	0.00
LAI	Canopy Cover	Minimum	0.11	0.00	9.52	0.00
LAI	Canopy Cover	Growing season	0.01	0.15	0.00	0.15
LAI	Biomass	Closest date	0.11	0.00	10.22	0.00
LAI	Biomass	Mean	0.21	0.00	6.75	0.00
LAI	Biomass	Median	0.24	0.00	7.40	0.00
LAI	Biomass	Sum	0.21	0.00	0.15	0.00
LAI	Biomass	Maximum	0.12	0.00	1.94	0.00
LAI	Biomass	Minimum	0.13	0.00	13.41	0.00
LAI	Biomass	Growing season	0.01	0.14	0.00	0.14
LAI	Greenness %	Closest date	0.00	0.56	-0.58	0.56
LAI	Greenness %	Mean	0.04	0.00	-1.45	0.00
LAI	Greenness %	Median	0.03	0.01	-1.23	0.01
LAI	Greenness %	Sum	0.04	0.00	-0.03	0.00
LAI	Greenness %	Maximum	0.03	0.01	-0.52	0.01
LAI	Greenness %	Minimum	0.00	0.99	0.01	0.99
LAI	Greenness %	Growing season	0.00	0.59	0.00	0.59

Appendix 1B. (*continue*) Results of univariate regression for shrub measurements

$R^2 > 0.3$ and $p < 0.05$ are highlighted

Vegetation Index	Shrub Measurement	Summary Statatistics	R-square	*p value*	coefficient	coefficient *p value*
NDVI	Density	Closest date	0.11	0.00	32.15	0.00
NDVI	Density	Mean	0.30	0.00	27.09	0.00
NDVI	Density	Median	0.10	0.00	18.43	0.00
NDVI	Density	Sum	0.30	0.00	1.18	0.00
NDVI	Density	Maximum	0.23	0.00	13.11	0.00
NDVI	Density	Minimum	0.29	0.00	24.52	0.00
NDVI	Density	Growing season	0.04	0.03	-0.01	0.03
NDVI	Canopy Cover	Closest date	0.10	0.00	29.87	0.00
NDVI	Canopy Cover	Mean	0.28	0.00	26.43	0.00
NDVI	Canopy Cover	Median	0.10	0.00	17.84	0.00
NDVI	Canopy Cover	Sum	0.28	0.00	1.15	0.00
NDVI	Canopy Cover	Maximum	0.15	0.00	10.74	0.00
NDVI	Canopy Cover	Minimum	0.26	0.00	25.88	0.00
NDVI	Canopy Cover	Growing season	0.00	0.73	0.00	0.73
NDVI	Biomass	Closest date	0.14	0.00	37.79	0.00
NDVI	Biomass	Mean	0.33	0.00	31.01	0.00
NDVI	Biomass	Median	0.17	0.00	25.43	0.00
NDVI	Biomass	Sum	0.33	0.00	1.35	0.00
NDVI	Biomass	Maximum	0.16	0.00	11.69	0.00
NDVI	Biomass	Minimum	0.31	0.00	30.79	0.00
NDVI	Biomass	Growing season	0.00	0.99	0.00	0.99
NDVI	Greenness %	Closest date	0.03	0.14	-11.04	0.14
NDVI	Greenness %	Mean	0.06	0.03	-8.73	0.03
NDVI	Greenness %	Median	0.06	0.03	-10.18	0.03
NDVI	Greenness %	Sum	0.06	0.03	-0.38	0.03
NDVI	Greenness %	Maximum	0.05	0.06	-4.31	0.06
NDVI	Greenness %	Minimum	0.02	0.20	-5.01	0.20
NDVI	Greenness %	Growing season	0.01	0.38	-0.01	0.38
EVI	Density	Closest date	0.04	0.02	35.35	0.02
EVI	Density	Mean	0.29	0.00	47.81	0.00
EVI	Density	Median	0.06	0.00	27.38	0.00
EVI	Density	Sum	0.29	0.00	2.08	0.00
EVI	Density	Maximum	0.11	0.00	13.90	0.00
EVI	Density	Minimum	0.31	0.00	34.29	0.00
EVI	Density	Growing season	0.03	0.04	-0.01	0.04
EVI	Canopy Cover	Closest date	0.01	0.31	14.97	0.31
EVI	Canopy Cover	Mean	0.21	0.00	42.15	0.00
EVI	Canopy Cover	Median	0.04	0.02	21.70	0.02
EVI	Canopy Cover	Sum	0.21	0.00	1.83	0.00
EVI	Canopy Cover	Maximum	0.05	0.02	8.93	0.02
EVI	Canopy Cover	Minimum	0.23	0.00	32.82	0.00
EVI	Canopy Cover	Growing season	0.00	0.49	0.00	0.49
EVI	Biomass	Closest date	0.01	0.35	15.00	0.35
EVI	Biomass	Mean	0.21	0.00	45.35	0.00
EVI	Biomass	Median	0.07	0.00	29.22	0.00
EVI	Biomass	Sum	0.21	0.00	1.97	0.00
EVI	Biomass	Maximum	0.04	0.04	8.50	0.04
EVI	Biomass	Minimum	0.21	0.00	34.14	0.00
EVI	Biomass	Growing season	0.00	0.57	0.00	0.57
EVI	Greenness %	Closest date	0.01	0.45	-9.76	0.45
EVI	Greenness %	Mean	0.04	0.07	-13.00	0.07
EVI	Greenness %	Median	0.04	0.08	-14.60	0.08
EVI	Greenness %	Sum	0.04	0.07	-0.57	0.07
EVI	Greenness %	Maximum	0.06	0.04	-7.24	0.04
EVI	Greenness %	Minimum	0.01	0.41	-4.35	0.41
EVI	Greenness %	Growing season	0.00	0.67	0.00	0.67

Appendix 1B. (*continue*) Results of univariate regression for shrub measurements

R^2 > 0.3 and $p < 0.05$ are highlighted

Vegetation Index	**Shrub Measurement**	**Summary Statatistics**	**R-square**	***p value***	**coefficient**	**coefficient *p value***
FPAR	Density	Closest date	0.00	0.52	2.62	0.52
FPAR	Density	Mean	0.04	0.03	6.25	0.03
FPAR	Density	Median	0.01	0.26	4.27	0.26
FPAR	Density	Sum	0.04	0.03	0.14	0.03
FPAR	Density	Maximum	0.05	0.01	3.46	0.01
FPAR	Density	Minimum	0.00	0.57	3.45	0.57
FPAR	Density	Growing season	0.00	0.48	0.00	0.48
FPAR	Canopy Cover	Closest date	0.00	0.51	2.49	0.51
FPAR	Canopy Cover	Mean	0.04	0.02	6.33	0.02
FPAR	Canopy Cover	Median	0.02	0.12	5.48	0.12
FPAR	Canopy Cover	Sum	0.04	0.02	0.14	0.02
FPAR	Canopy Cover	Maximum	0.04	0.02	2.96	0.02
FPAR	Canopy Cover	Minimum	0.01	0.25	6.55	0.25
FPAR	Canopy Cover	Growing season	0.00	0.45	0.00	0.45
FPAR	Biomass	Closest date	0.01	0.18	5.38	0.18
FPAR	Biomass	Mean	0.07	0.00	8.76	0.00
FPAR	Biomass	Median	0.05	0.02	9.01	0.02
FPAR	Biomass	Sum	0.07	0.00	0.19	0.00
FPAR	Biomass	Maximum	0.06	0.01	3.78	0.01
FPAR	Biomass	Minimum	0.04	0.03	13.50	0.03
FPAR	Biomass	Growing season	0.00	0.91	0.00	0.91
FPAR	Greenness %	Closest date	0.00	0.74	-1.34	0.74
FPAR	Greenness %	Mean	0.01	0.33	-2.71	0.33
FPAR	Greenness %	Median	0.01	0.50	-2.39	0.50
FPAR	Greenness %	Sum	0.01	0.33	-0.06	0.33
FPAR	Greenness %	Maximum	0.02	0.27	-1.47	0.27
FPAR	Greenness %	Minimum	0.00	0.64	-2.69	0.64
FPAR	Greenness %	Growing season	0.00	0.71	0.00	0.71
LAI	Density	Closest date	0.00	0.79	0.57	0.79
LAI	Density	Mean	0.05	0.02	3.09	0.02
LAI	Density	Median	0.01	0.36	1.68	0.36
LAI	Density	Sum	0.05	0.02	0.07	0.02
LAI	Density	Maximum	0.07	0.00	1.20	0.00
LAI	Density	Minimum	0.00	0.51	2.07	0.51
LAI	Density	Growing season	0.01	0.27	0.00	0.27
LAI	Canopy Cover	Closest date	0.00	0.88	0.29	0.88
LAI	Canopy Cover	Mean	0.05	0.01	2.95	0.01
LAI	Canopy Cover	Median	0.01	0.27	1.87	0.27
LAI	Canopy Cover	Sum	0.05	0.01	0.06	0.01
LAI	Canopy Cover	Maximum	0.05	0.02	0.94	0.02
LAI	Canopy Cover	Minimum	0.01	0.30	3.10	0.30
LAI	Canopy Cover	Growing season	0.01	0.39	0.00	0.39
LAI	Biomass	Closest date	0.01	0.36	1.99	0.36
LAI	Biomass	Mean	0.08	0.00	4.18	0.00
LAI	Biomass	Median	0.03	0.05	3.55	0.05
LAI	Biomass	Sum	0.08	0.00	0.09	0.00
LAI	Biomass	Maximum	0.06	0.01	1.17	0.01
LAI	Biomass	Minimum	0.04	0.03	6.87	0.03
LAI	Biomass	Growing season	0.02	0.17	0.00	0.17
LAI	Greenness %	Closest date	0.01	0.29	-2.18	0.29
LAI	Greenness %	Mean	0.01	0.29	-1.24	0.29
LAI	Greenness %	Median	0.01	0.44	-1.28	0.44
LAI	Greenness %	Sum	0.01	0.29	-0.03	0.29
LAI	Greenness %	Maximum	0.03	0.12	-0.61	0.12
LAI	Greenness %	Minimum	0.01	0.52	-1.95	0.52
LAI	Greenness %	Growing season	0.00	0.94	0.00	0.94

Chapter 3. African elephant movement in response to spatial and temporal landscape correlates

Abstract

Elucidating the effect of landscape variables on wildlife movement is critical for implementing conservation measures to protect species. However, it is not well understood how individual animal responds to landscape variables with their movement decisions. Moreover, it is not clear how the relationship between the movement path and the underlying landscape varies over time. Here, I examine the relative importance of detailed landscape variables in determining the movement direction and speed of African elephants (*Loxodonta africana*). I fitted fifteen elephants in Etosha National Park, Namibia, with GPS-GSM collars. Through extensive fieldwork and satellite imagery, I also collected detailed information on vegetation density, cover, productivity, and temporal variability. Movement passes were also assessed with regard to linear distances to roads, fences, and water sources. I used a step selection function to measure the relative importance of these landscape variables in determining an elephants' directional movement. I examined the effect of individual traits (sex, age), temporal variation, and temporal scale of analysis on the elephant resource selection. I also tested the hypothesis that movement speed is inversely related to the quality of the landscape, as perceived by the individual.

My results show that elephants choose areas with higher annual productivity, higher shrub and grass biomass, but lower tree biomass than the average in their surroundings. Elephants also chose to walk closer to water and, surprisingly, closer to roads and fences, when compared with alternatives available travel routes. Analysis of movement speed led to similar conclusions about elephant resource selection. Importantly, resource preference varied with time of day, providing insight into how elephants use the landscape on a diurnal cycle. Seasonal variation in resource selection further illustrated the ecological importance of each landscape factor. Finally, I show that the temporal scale of analysis has considerable impact on the results, and thus, the relative importance of various factors must be interpreted in the context of processes at different spatiotemporal scales.

3.1. Introduction

Elucidating the effect of underlying landscape structure on wildlife movement is central to the understanding of behavioral ecology and hence the impact of ecosystems management on species conservation. How animals choose environmental features has been explored at various spatiotemporal scales, from the geographic distribution of populations, through niche preference within individual home ranges, and the local foraging-patch scale (Schick et al. 2008, Soberon and Nakamura 2009). An animal incorporates information about its surrounding landscape when deciding on the direction and speed of its movement. The landscape can be described by different variables that provide information on availability of forage and cover (e.g. water, vegetation), ease of movement (e.g. topography, snow depth), and potential threats (e.g. human settlements and roads). However, it is not well understood how individuals' respond to these landscape variables with their movement decisions. Moreover, it is not clear how the relationship between the movement path and the underlying landscape varies over time. A movement ecology framework suggests that the movement path of an individual can be explained by the individual's movement capability, its internal state, its memory and navigation capabilities, and external factors such as time of day, the season, and the surrounding landscape (Nathan et al. 2008). In this chapter I combine essential elements of the movement ecology framework by analyzing the relative importance of landscape variables in determining movement decisions of African elephants (*Loxodonta africana*), while considering traits of individuals, temporal variation and the effect of temporal scale on the results.

A variety of methods have been proposed to examine how an landscape characteristic affect movement patterns. Resource selection functions (RSF) are used to characterize the resources an animal chooses relative to their availability on the surrounding landscape (Boyce and McDonald 1999). In RSF analysis, the 'domain of availability' is the proportion of selected resources that are available to the animal. Step selection function (SSF) has been proposed as a powerful way to characterize the relationship between individual directional movement and resource selection (Fortin et al. 2005, Forester et al. 2009, Thurfjell et al. 2014). This method examines the movement direction and step length of the animal at each user-defined time step. The landscape characteristic of the chosen direction are then compared to the landscape charachteristics of case control steps (Thurfjell et al. 2014).

The resources an animal selects may change, depending on the overall environmental and climatic condition in the animal's habitat. Therefore, I hypothesize that the relationship between the landscape and the emerging movement patterns will vary both with time and temporal scale of analysis, from diurnal to annual (Godvik et al. 2009, Polansky et al. 2010). Previous research has demonstrated that diurnal movement cycles vary with habitat suitability (Wittemyer et al. 2008). Similarly, habitat preference of elephant changes with season and region (Loarie et al. 2009a). For example, the proportion of grass in an elephant's diet increases in the rainy season (Sukumar 2003, Codron et al. 2006). Additionally, the size of an individual elephant's home range expands in the rainy season, when the individual is less restricted by water availability (van Aarde et al. 2006). Individual attributes such as sex and age are expected to further affect temporal variation in movement patterns. For example, female elephants in Kruger National Park prefer high herbaceous biomass and low tree cover, while males have the opposite response (de Knegt et al. 2011).

In addition to temporal variation, the spatial and temporal scales of analysis have considerable effect on the resulting response of animal movement to the surrounding landscape (Wiens 1989, Fryxell et al. 2008, Boyce 2006). In telemetry data, the temporal and spatial scales are interdependent, because the animal will walk a greater distance over a longer time interval (Swain et al. 2008). Furthermore, the resolution of underlying landscape information affects the relative importance of each variable for the animal (de Knegt et al. 2011). The temporal scale at which movement is sampled, or the Global Positioning System (GPS) fix rate, can lead to different conclusions about the movement patterns of an animal. GPS fix rates affect the estimation of movement measures, such as movement speed and step length (Laube and Purves 2011, Prichard et al. 2013, Frair et al. 2010). Furthermore, the temporal scale of analysis affects the conclusions about the relationship between the species and its environment (Fryxell et al. 2008). For example, the spatial and temporal scales at which a study was conducted affected conclusions regarding the influence of human infrastructure on reindeer and caribou distributions (Vistnes and Nellemann 2008). Similarly, correcting for acquisition probability of GPS fixes in different landscapes improved the prediction accuracy of species' resource selection (Webb et al. 2013, Heard et al. 2008). In this chapter I examine the effects of temporal scale and temporal variation on the resulting resource selection estimate.

An additional way to examine resource selection is to analyze the speed at which individuals move through landscapes of different types. I can examine the speed of movement across a gradient of landscape measurements, for example increasing vegetation biomass or tree cover. The underlying assumption is that wildlife exhibit different behaviors (feeding, running, walking, etc.) in different habitats and each of these behaviors has a characteristic movement speed. The animal will walk faster through a less favorable environment, while it will linger in a safer landscape that has richer resources (Owen-Smith et al. 2010, Roever et al. 2010). On the other hand, herbivores may move faster in a more erratic fashion to avoids detection by predators (Fischhoff et al. 2007). Therefore, I hypothesize that the speed of movement can be an indicator of habitat quality, as perceived by the individual. I predict that using the speed of movement, in conjunction with a step selection function will provide further insight into the fine scale aspects of resource selection.

In southern Africa, land use change and fencing of reserves influences the movement of elephants. The confinement of elephants to constrained areas leads to vegetation degradation and tree damage (Loarie et al. 2009b, de Beer et al. 2006, Franz et al. 2010). Furthermore, seasonal variation in elephant movement patterns leads to increased human-wildlife conflict around reserve boundaries. Understanding how elephant movement decisions respond to the landscape at different temporal scales, can be used to promote the conservation of African elephants and their habitats.

In this chapter, I use the step selection function to examine the relative importance of landscape variables in determining elephant movement decisions. I further explore what complementary insights can be gained on elephants' preference, by examining their speed movement through different landscapes. Additionally, I examine the interaction between individual traits (sex, age), diurnal and seasonal variation, and landscape characteristics in determining the movement direction of individuals. Finally, I explore the effect of temporal scales of analysis on the relationship between movement decisions and underlying landscape variables.

3.2. Methods

3.2.1. Study Area

Etosha National Park (ENP) is a 22,270 km^2 reserve located in north-central Namibia (19^{o}S, 16^{o}E). It is a semi-arid savanna with an east-west rainfall gradient of 200 - 450 millimeter per year. There are three main seasons in ENP: the cool dry season (May – August), hot dry season (September – December), and the hot wet season (January – April) (Du Plessis et al. 1998a). Peak rainfall occurs in January – February (Turner and Getz 2010). The main vegetation types in Etosha consist of grassland, steppe, Acacia woodland and Mopani tree savanna (Le Roux et al. 1988). Etosha has been fully fenced since 1973; the fence is restricting and altering ungulate movement. Etosha pan is a prominent feature in the reserve, spanning 4,410 km^2. It is a natural saline lake depression that is dry for most of the year and seasonally is partially filled with water. Animals use the pan for licking salt and minerals (de Beer et al. 2006).

3.2.2. Elephant movement data

The African elephant (*Loxodonta africana*) population in Etosha was estimated to be around 2,600 in a 2005 aerial census (de Beer et al. 2006, Turner et al. 2013). This population size is thought to be stable, although smaller than it used to be few decades ago (de Beer and van Aarde 2008). The elephant population size is thought to be regulated by restricted resource availability, due to the fencing of the reserve, and by the natural cycles of zoonotic anthrax (*Bacillus anthracis*) in the park. During the period 1968-2011, 522 cases of elephant mortality due to anthrax were recorded in ENP (Turner et al. 2013).

I fitted 15 elephants with GPS/GSM platform collars (Africa Wildlife Tracking), eight cows and seven bulls. Three of the females were young adults. Collaring was performed in the central part of ENP, around Okaukuejo station (15°55'20.156"E 19°10'49.736"S). Darting and collaring procedures were performed in compliance with the University of California Berkeley animal care and use protocol (#R217-0511B). Elephants were collared during two periods, October 2008 and July 2009. Data from collars was collected for two to four years, depending on the collar performance and battery life. Location information was recorded in alternating time intervals of one-minute and 19-minutes. GPS collars accuracy is ±3 meters, as was confirmed in the field. I sub-sampled the spatial extent of the GPS location by choosing data points within Etosha's boundaries. Additionally, I removed duplicated records. I compared analyses with different GPS sampling intervals and chose to use one hour sampling frequency for the analysis. I calculated the average hourly speed of individuals to be 554 meter/hour, using one hour sampling frequency. The available landscape data resolution of 231 X 231 meter (see below). Therefore, in order to match the temporal and spatial resolution of my data I used a sampling rate of one hour between consecutive location points. For each location I calculated the distance to the next step (step size), movement speed (km/hour), turning angle (degrees), and absolute angle (radians). To analyze the change in movement speed during the year I performed factorial Analysis of Variance (ANOVA) to compare the average movement speed of males versus females in each month. I used Tukey Honest Significant Differences (HSD) to correct for multiple comparisons (Yandell 1997).

3.2.3. Landscape information

Landscape vegetation information was created based on models that used extensive field sampling and satellite imagery, as described in Tsalyuk *et. al (Tsalyuk et al. In reviewa).* In short, I used multivariate models of time series data of Moderate Resolution Imaging Spectroradiometer (MODIS) based vegetation indices (VIs) to predict field vegetation measurement. Based on these models I created maps for Etosha that describe the cover, density, and biomass of woody and herbaceous vegetation (trees, shrubs and grasses). Models for tree cover, density, and biomass, and for shrub biomass were based on Normalized Difference Vegetation Index (NDVI). The model for shrub density was based on Leaf Area Index (LAI), while the models for grass cover and grass biomass were based on Fraction of Photosynthetic Active Radiation (FPAR). Model results were verified using root mean square error from leave-one-out cross validation (Mevik and Cederkvist 2004). For more details on the creation and selection of vegetation models refer to Tsalyuk *et. al.* (Tsalyuk et al. In reviewa).

In addition to the above vegetation measurement, I used MODIS vegetation indices directly as a measure of vegetation productivity and temporal variability. NDVI is a measure of vegetation productivity and green biomass (Tucker et al. 1983, Tucker 1979, Gamon et al. 1995). FPAR is a functional measure of vegetation photosynthetic activity. FPAR is related to both green and dry vegetation biomass, specifically of grasses since photosynthetic activity continues, to some degree, in dry vegetation as well (Butterfield and Malmstrom 2006). FPAR measures the proportion of sun radiation received by the plant, out of the total available radiation in the photosynthetically active wavelengths of the spectrum 400 - 700 nm (Knyazikhin et al. 1999, Asner et al. 1998). I acquired MODIS data from the Reverb website (EODIS 2013). MODIS NDVI is provided as a 16-day average and FPAR as an 8-day average. For each pixel, I calculated the mean and the variance of NDVI and of FPAR for 2008 - 2010.

I calculated linear distance to roads, water sources, and park fences, based on GIS layers for Etosha provided by the Etosha Ecological Institute (EEI). I created maps for the distance to the fence, roads, and water sources, using the “distance” function (package “raster”, R 3.0.1). I assumed distance from the fence will only influence elephant movement relatively close (within 10 km) to the fence. Since elephants remember the location of permanent landscape features and can walk as much as 20 km/hr I choose 10 km as maximum distance to the fence that might influence their movement. Therefore, I included distance from the fence as a covariate only within 10 km of a fence. All landscape variables were scaled to have a mean of 0 and standard deviation of ±1, so that the model coefficients associated with different variables could be directly compared. I calculated pixel-based Pearson correlation coefficient for every pair of variables. To reduce collinearity in the predictor variables, I included only variables that had $R^2 < 0.7$ (Dormann et al. 2013). All landscape covariates were created using the NDVI MODIS resolution of 231 x 231 meters.

Most roads in the reserve are gravel roads or fire breaks, and only few roads are paved. To further understand the effect of roads on elephant movement in Etosha, I estimated the effect of car density. I used the number of tourist cars entering daily at the Anderson gate (main entrance gate of Etosha, close to Okaukuejo) to calculate average monthly tourist travel in Etosha.

I calculated rainfall for Etosha by averaging three years of information at each of 168 rain gauges distributed around the reserve for 2009-2010. I used Kriging method (Spatial Analyst Tools, ArcGIS 10.2 (ESRI 2011)) to extrapolate these point data to the entire reserve. Monthly rainfall was acquired from an additional eight electronic rain stations that are distributed across Etosha and measure rainfall daily (EEI). I use data from the Okaukuejo rain station to calculate the average monthly rainfall.

3.2.4. Statistical analysis

I used the step-selection function (SSF) to analyze the direction elephants chose to move in response to landscape variables. The SSF is a resource selection function (RSF) that incorporates individual movement characteristics (Forester et al. 2009) and local landscape context. SSF defines the domain of availability of a resource, in terms of the resources available to an animal in its immediate surroundings at each point in time (Forester et al. 2009). For each actual step I created *k*=20 case control steps (Forester et al. 2009), selected at random using data from step-size and turn-angle distribution of all sampled individuals, that have been generated for different temporal scales (see next subsection) and at both an individual and population (i.e. movement data aggregated across individuals) levels. The actual step and each of the 20 case control steps selections essentially identified a particular 231x231 m^2 pixel, from which I extracted the underlying landscape variables that I compared to the values in the selected pixel using conditional logistic regression. (Note: it is possible that some pixels may have been selected twice by each is treated as an independent set of data). The coefficients on landscape variables were calculated by estimating a logistic regression model, which maximizes the conditional likelihood of choosing each step. The log odds comparing the probability of the animal to choose the actual step versus its probability of choosing one of the 20 case control steps is calculated as a function of all the landscape variables underlying these steps and a random effect of the individual and data stratum. The distance walked (step size) and the absolute relative turning angle were also included as covariates in the regression model (Forester et al. 2009). Diurnal and seasonal effects were also included, as described below. I used the clogit command from the survival package in R to calculate this model (Therneau and Lumley 2013).

I compared the magnitude and the direction (sign) of the coefficients to understand the relative importance of each landscape variable in determining elephant movement decisions. I performed the analysis for each of the 15 individuals separately using their own particular data to generate the movement distributions. I than averaged the coefficients of the 15 sets of results in order to assess individual variability. I then compared the analysis to using the aggregated population data to generate the movement distributions, obtained only one combined result set.

I further included sex and age class (adult versus sub-adult) as a covariate in the model to examine the effect of individual traits on the elephants' response to landscape variables. To understand the influence of time of day, I included a 24-hour period sine and cosine function to capture dial cyclicity in one of models. I examined the effect of season on the resource selection by including the month as a cofactor in the model.

3.2.5. Temporal scale variation

I examined the effect of temporal scale on the resulting resource selection by varying the GPS fix rate, the frequency at which the consecutive locations are sampled. I used increasing time intervals between consecutive GPS location to analyze the movement data with the SSF. As I increased the time increments between movement locations (specifically: 1 hr, 2 hr, 3 hr, 6 hr, 12 hr, 1 d (=24 hr), 2 d, …, 29 d, 30 d, with one day intervals) the modeled behavior changes from a movement selection model (SSF) to a habitat selection model (RSF), thereby bridging hourly scales of movement with month distribution patterns.

3.2.6. Influence of landscape variables on speed of movement

Drawing upon an hypothesis that the speed of movement (translocation rate) of an individual in a habitat is inversely related to the perceived quality of that habitat, to the individual concerned (Owen-Smith et al. 2010, de Knegt et al. 2007), I fitted the log of the movement speed as a functions of the landscape variables using a generalized linear model (GLM) function. I then compared the coefficients from GLM to the coefficients derived from the step selection function as a test of this hypothesis.

3.3. Results

My results show that the direction and speed of elephant movement are influenced by the landscape in the immediate surroundings of the elephant at each time step. Elephants in Etosha move quite slowly with high directional persistence. The average step length (the linear displacement from origin position) in one hour is 554 m, corresponding to a speed of 0.55 km/hr (Fig. 2A). Elephants travel, on average, 5.8 km/day (24 hr) and 15.5 km/week, with a maximum weekly travel distance of

128 km/week. The maximum speed, recorded for one hour intervals, is 19.1 km/hr, although only a very small percentage (0.02%) of the movement steps is larger than 5 km/hr. The average speed fluctuates throughout the year: speed is slower (0.3 km/hr) in the hot dry season (August – October) and fastest (0.7 km/hr) in the wet season (February – April). Females move significantly faster than males ($p < 0.001$), specifically in late dry season and the beginning of the wet season (October – January) (Fig. 3). The average turning angle is distributed around zero (-0.0084 radians) (Fig. 2B).

I use the information of step lengths and turning angles in a step selection function (SSF) to obtained detailed information about the elephants' resource preference. My methodology reveals the relative importance of each landscape parameter in determining the movement of elephants (Fig. 4). Anthropogenic landscape features in Etosha influence elephant movement greatly; elephants tend to move closer to water, roads, and to the fence (within 10 km from it) (Fig. 4). The preference to walk closer to roads is correlated with the quality of the road; paved and graded roads are stronger attractors to elephants than roads with lower quality, such as track roads or fire breaks. Elephants prefer higher mean NDVI, which indicates choice of higher vegetation productivity and greenness. However, there is slight avoidance of FPAR, another vegetation index that is associated with vegetation biomass. Elephants prefer higher grass biomass but lower tree density and lower tree biomass.

Individual variation in movement preference

While there is variability in how individual elephants responded to the landscape, as demonstrated by the variation in the resulting SSF coefficients values, these variations do not significantly differ from the overall population coefficients, nor do they change the conclusion about resource selection (Fig. 4). On the other hand, considering individual traits of sex and age in the analysis affects the resulting relationship between the animal and its environment (Fig. 5). There are differences between the sexes in their directional response to landscape variables, both in magnitude, and for some variables, in the direction (sign) of the response (Fig. 5A). Female elephants preferred areas with higher phenological variability of vegetation productivity, as measured by NDVI variance, while males prefer lower variability. The sexes also differ in their preference of FPAR variance, but it is not significant. Females prefer higher shrub biomass but lower tree density, while males' response is the reverse: they prefer areas with lower shrub biomass and higher tree biomass. While both sexes prefer to be closer to water and roads, the directional preference of males towards these features is stronger. Conversely, females tend to walk closer to the fence, while males turn away from it (Fig. 5A). When comparing the resource preference of adult versus sub-adult females the only significant difference is that adults choose higher FPAR variance, while the sub-adults choose low FPAR variance (Fig. 5B). Sub-adults also have slightly stronger preference for high vegetation productivity and variability, as measured by NDVI mean and variance and prefer to be closer to water, roads, and the fence (Fig. 5B).

Movement speed response to the landscape

The speed of elephants' movement is inversely related to the directional preference to landscape variables (Fig. 6). Elephants walk slower in areas where the landscape characteristics are preferable, as indicated by the SSF directional response; they walk slower in higher NDVI, higher grass biomass, and when walking near water and the park's roads. Conversely, elephants walk faster in areas with landscape variables that they turned away from (with negative coefficients in the SSF), such as high NDVI variance, FPAR mean, tree biomass, tree density, and distance from the fence. Movement is also faster in areas with lower FPAR variance, higher shrub biomass, and closer to the fence (Fig. 6).

Temporal variation in resource selection

My results show that resource selection varies with time. Elephants' preference of each landscape parameter varies throughout time of day and time of the year.

Diurnal temporal variation has a marked effect on the intensity and, in some cases, the direction, of the response to landscape variables (Fig. 7). Preference towards higher mean NDVI is higher during the night (23:00-3:00am) (Fig. 7A). On the other hand, while elephants prefer areas with high FPAR during the night, they prefer areas with lower FPAR in daytime (10:00 am- 18:00). Preference of higher grass biomass peaks around early morning (9:00 am) and evening times (19:00) (Fig. 7F).While high tree biomass is avoided most of the day, this avoidance is most pronounced during dark hours (Fig. 7C). Elephants prefer to be closest to water in the morning (around 9:00 am) and late afternoon (around 17:00), but walk away from water at night (Fig. 7D). Similarly, elephants walk closer to roads during the day, but avoid roads during the night (Fig. 7E).

Similarly to the diurnal variations, there is a pronounced seasonal variation in the movement response to landscape variables (Fig. 8). Elephants prefer high NDVI all year round, but this preference is strongest during the dry-cold season (June – August). The response to NDVI temporal variance is inversely correlated to the response to NDVI mean over the year (β = -1.002, R^2 = 0.73, p < 0.001). The most prominent avoidance of NDVI variability is seen during the dry-cold season (June – August). Conversely, there is a preference towards higher NDVI variability in the rainy months (December – March) (Fig. 8A). Elephants' directional responses to FPAR mean and variability are also somewhat opposite to each other (Fig. 8B). Elephants prefer higher FPAR mean during the dry months and avoid high FPAR the rest of the year. They prefer higher FPAR variance most of the year, besides September – November (Fig. 8B). The strongest preference of high grass biomass in the hot – dry months (August – October), and the preference for higher shrub biomass is most prominent in May and in October. High tree biomass is avoided during most of the year; this avoidance is strongest in May and in September (Fig. 8C).

While elephants prefer to be closer to water year-round, the preference to be closer to water is inversely correlated with average monthly rainfall and is strongest during the hot- dry months (Fig. 8D). There is a lag between decline in monthly rainfall and a subsequent reaction of movement closer to water sources in the following months (Fig. 8D). Similarly, while elephants prefer to be closer to roads all year round, this preference is strongest in the dry months (August and October) (Fig. 8E). There is a positive relationship between elephants' preference of roads and the number of tourists entering Etosha each month (Fig. 8E). Finally, elephants walk closer to the fence in the dry months (July – October) but seem to avoid it in the rainy months (February – April).

Importance of scale in resource selection

Resulting coefficients of the step selection function for each landscape parameter fluctuate with increasing time intervals between consecutive steps (Fig. 9). In some cases, the response to landscape variables converges towards a specific value with increasing time intervals, for example the coefficients on distance to water, roads and the fence. In other cases, the response to landscape parameter fluctuates with increasing time intervals between locations and the magnitude of fluctuation increases with larger time interval (Fig. 9).

3.4. Discussion

While there is a wide body of knowledge about the habitat selection, it is not well understood how landscape variables affect individual movement decisions.My methodology reveals the relative importance of each landscape variable in determining the movement of elephants over known landscapes. My results further highlight the importance of temporal variation in determining the relationship between an animal and its environment, and emphasize the importance of considering temporal variation and temporal scale in the analysis of movement data. I demonstrate that the step selection function (SSF) can provide rich insight into how space (the landscape), time (hours to years) and individual animal traits (sex, age) interact to produce an observed movement path. I show the relative importance of difference landscape variables in elephants' movement decisions. Furthermore, by supplementing the SSF analysis with temporal variation I gain further insight on the behavioral mechanism underlying the relationship between the animals and its environment.

I show that examining different movement variables: the direction and the speed of the movement can yield complementary insights into the behavioral mechanism behind resource selection. I show that elephants move slower in a preferred habitat, as demonstrated by the results of the SSF. This supports the hypothesis that the speed of movement is inversely related to the quality of habitat as perceived by the animal. When exploring resource selection, one might ask whether revisitation of same sites or longer residence at a site produce the preference for a particular habitat type (Anderson et al. 2008). Using the speed of movement addresses this question; slower movement through a habitat results in a longer stay at a particular landscape. The inverse relationship I show between the results of higher coefficient on SSF and higher speed, demonstrate that for elephants both mechanisms operate simultaneously. Further investigate is needed to determine whether elephants in this system revisit favorite feeding they have previously identified.

Importantly, I found that anthropogenic landscape features: waterholes, roads and the fence have the strongest influence on elephant movement. Indeed, location of artificial water sources is a common method used in protected areas to manipulate ungulate location, either in order to attract animals for tourists' observation or to prevent human- wildlife conflict around reserve borders (OwenSmith 1996). Elephants' strong preference to be closer to water is expected in an arid environment of Etosha, where surface water is scarce. Elephants depend on water and it has been recorded that elephant drink daily in Etosha (de Beer and van Aarde 2008). Somewhat less expected is the elephants' preference to walk closer to roads. Since elephants prefer differentially higher quality roads, the preference to walk closer on roads probably indicates that elephants use roads as an easily walkable surface to reduce effort and energy spent on movement. Moreover, artificial waterholes are located along the roads, making road the fastest direct route between watering points. Most of the roads in Etosha are gravel roads or fire breaks and therefore do not impose high disturbance. Although highways are known to have negative effect on elephant population (Barnes et al. 1991) roads in protected areas are often used by ungulates due to easier movement along a cleared path, accumulation of greener vegetation in ditches along the roads, or use of traffic as protection from predators (Berger 2007).

Mean NDVI also had strong influence on elephants' movement direction. NDVI is a measure of vegetation productivity and green biomass (Tucker et al. 1985, Pettorelli et al. 2005). As megaherbivores elephants consume 50-200 kg each day and, therefore, require areas with large amounts of forage (Sukumar 2003) the observed preference of areas with relatively high NDVI is expected. In contrast, elephants avoid areas with higher FPAR means. FPAR measures the photosynthetic capacity of vegetation, which continues, to some degree, in dry vegetation as well (Butterfield and Malmstrom 2009, Tsalyuk et al. In reviewb). Therefore, FPAR measures both green and dry vegetation biomass, while NDVI is related only to the green part of the biomass. The negative response to mean FPAR might indicate that elephants differentially choose greener vegetation and not only areas with higher biomass.

My results show that elephants prefer higher NDVI variability in the wet season, but lower NDVI variability in the dry months. In the dry season it is more important to optimize the use of known resources, while in the wet season exploration may result in finding locations that can be used for feeding the dry season as well. Indeed, the preference for NDVI variance is inversely correlated to preference of NDVI mean. Elephants seek the higher variability in the wet month, when their preference of high productivity is less pronounced (Fig. 7). This result is consistent with previous research that shows that in the wet season elephant choose landscape with higher seasonal variability of greenness to maximize chances to locate greener patches (Loarie et al. 2009a). The response to temporal variation in vegetation productivity, as measured by NDVI variance, indicated that the animal explores variable conditions in order to find the best available foraging grounds. Moreover, preference of higher productivity variability can indicate the capacity of the animal to remember the landscape conditions over time, since a significant response to temporal signal indicated the animal had some knowledge of the landscape conditions beyond its current state. The fact that females prefer higher NDVI variance than males suggests that female groups have higher shared social memory (McComb et al. 2001). Better knowledge of the landscape may allow more exploratory behavior.

Interestingly, I found that elephants prefer high grass biomass, but lower tree biomass and density. This may indicate that elephants in Etosha rely more on grazing and prefer open areas, which are easier to move through. Indeed, elephants' diet in Kruger National Park is consistent of 50% grass (Codron et al. 2006). Females, in particular, prefer lower tree density but higher shrub cover, which indicated that they choose areas with more open vegetation. Preference of low tree cover may be associated with predator avoidance by females with calves (Valeix et al. 2009).

The strong effect of the relative turning angle on the results indicates that previous movement direction has a strong effect on future direction. This is also demonstrated by an average turning angle close to zero, and shows that elephants have strong directional persistence. This result is compatible with the previous research showing elephants continue to move in a consistent direction (Wittemyer et al. 2007) and indicates movement towards a destination that the animal remembers, such as a water source or a feeding patch.

My results demonstrate the importance of considering individual traits when analyzing movement response to landscapes. I show that response to landscape variables can significantly change with the sex or the age of the individual animal (Boettiger et al. 2011), even though the overall variance of the population's SSF coefficients was relatively low. These differences between the sexes in their movement behavior may be explained by the other three components of the movement ecology framework: variations in individual state, such as nutritional needs, size, lactation or gestation; variation in memory of the landscape and navigation skills; or variations in the movement capacity of individuals in different life stages. Which of these factors contributes to individual response to landscape variables should be subject to future research. Based on the differences in the response to key variables such as vegetation density and biomass, I emphasize the need to be taking individual traits if age and sex into account when determining resource selection or population habitat preference from telemetry data.

I further demonstrate the importance of temporal variability in movement response to landscape variables. Therefore when examining resource selection one should ask not only where an animal goes, but also when does it go to a particular landscape. The combination of hourly analysis with detailed movement and landscape information provides insight into the behavioral ecology of the elephants. It is not only possible to infer what habitat the animals prefer, but get an idea about what the animal is doing, when and why. For example, while it is known that elephants prefer to be close to water, I found this preference is strongest around 9:00 in the morning and 17:00 in the afternoon (Fig. 7), which are indeed the hours elephants go to drink in Etosha, as we know from field observations. Similarly, the lower preference of grass biomass but higher NDVI during 1-2 am might indicate that elephants are testing in woody areas during these hours.

Monthly variation in the response to landscape variables illustrates the ecological importance of each resource to the elephants. For example, the preference to be closer to water when rainfall is lower demonstrates the higher dependency on anthropogenic water sources when seasonal surface water dries up (Fig. 8). Similarly, preference for higher grass biomass is higher in the dry months. This is consistent with previous research that showed that the proportion of browse and grass in elephants' diet changes with season (Codron et al. 2006, Sukumar 2003). Another interesting result is the seasonal variation in the proximity of elephants to roads, which seems to coincide with the number of tourists cars in the park. This might be explained by the fact that as the dry season progresses road conditions are improved and the fire breaks are graded. Therefore, road conditions promote both tourism Etosha, peaking around August, and the ease of movement on roads for elephants.

Finally, an important conclusion of this research is that temporal scale of analysis can significantly affect results and a distinction needs to be made between SSFs at close to immediate scales, sub-diurnal scales, diurnal scales, and scales at which the distinction between SSFs and RSFs disappears. Previous research has shown that reduced sampling rate can reduce error in analysis of movement path and of habitat selection predictions (Heard et al. 2008). In this research, while for some variables, such as distance to water and to roads, reducing sampling rate (increasing intervals between consecutive steps) resulted in convergence of the coefficient to a particular value, for other variables, increasing the interval size increased the noise in the resulting coefficients. Therefore, it is important to choose temporal scale of analysis that match the spatial resolution of the underlying landscape information and correspond to behavior relevant to answering the research question at hand (Fleming et al. 2014, Johnson et al. 2002).

Management implications

Temporal analysis of resource selection has important implications for managing resources for elephants. Elephants exert considerable impact on savanna vegetation by overgrazing/ browsing, breaking trees, bark stripping, and destroying potentially endangered plant species. In southern Africa elephants are culled in attempt to mitigate their impact on vegetation degradation. However, my detailed examination of elephants' resource use shows that they use resources differentially and that their resource selection changes throughout the year and therefore might not impose lasting damage. For example, I show that elephants in Etosha might avoid high tree density. Therefore, elephants might not be the primary cause for tree mortality in Etosha, contrary to previous assumption that elephants are responsible for tree mortality around waterholes (de Beer et al. 2006). Furthermore, my results show that while elephants prefer to be closer to water, concentration around waterholes changes during day and in different seasons. Because there is at least some rotation in elephant use of the area around artificial waterhole, severe vegetation degradation around waterhole might be due to other ungulates. This suggests that detailed temporal examination of resource use by elephants should be made separately for each location before making decisions on controlling elephants' populations.

My results have additional implication for human - wildlife conflict around the reserve borders. In the northern part of Etosha most of the conflict around the fences occurs in the wet season, when the crops ripen in the agricultural fields north of the reserve and elephants cross the fence to raid the green lush crops. The elephants in my sample, however, were collared around the Okaukuejo area, in the central part of the park. These elephants mostly walk near the south border of the park. The preference to walk near the fence is primarily in the dry season, and might be explained therefore explained by use of the road along the fence and not by attempts to cross it. Hence, my methodology of analyzing detailed movement patterns and temporal variation can be used to better understand and manage elephants' behavior.

Conclusions

In this chapter I show that African elephants respond to landscape variables both in the direction and the speed of their movement. I show that anthropogenic land features such as artificial water sources, roads and fences have overwhelmingly strong influence of elephants' use of the landscape. My methodology of using both Step Selection Functions and speed of movement through habitats provides a wealth of information on the behavioral response of elephants to their environment. Further, I show that this response alternates with individual traits, such as sex and age, as well as with time—from daily to seasonal scales. Inclusion of temporal variation in the analysis provides valuable insight into the behavioral mechanism of how animals choose resources and what is the ecological role of these resources to the animal. Lastly, I show the effect of temporal scale of analysis on conclusions about resource selection. I emphasize the need for including temporal variation in analysis of movement and resource selection. Using detailed information on the landscape and considering time can provide guidance on how to better protect African elephants and conserve their habitat.

3.5. Acknowledgements

I thank the Namibian Ministry of Environment and Tourism (MET) for permission to conduct field work and for providing facility resources for this work. I am grateful to the staff at the Etosha Ecological Institute (EEI) for scientific and technical assistance and for providing record information on GIS data for Etosha, rain gauges records, and information on tourist visitation to the reserve. I am particularly grateful to Shayne Kòtting, Wilferd Versfeld, Marthin Kasaona, Birgit Kòtting, Ndapanda Kanime, and Erastus Ithana. I thank Etosha’s wardens and rangers, and the staff of Namibia Wildlife Resorts (NWR) in Etosha. The Geospatial Innovation Facility at the University of California, Berkeley provided state of the art facilities and geospatial support. I thank professor Justin Brashares and Maggi Kelly for their fruitful ideas and helpful comments on the manuscript. This research was funded by the Science and Engineering fellowship from the Center for Emerging and Neglected diseases (CEND), by the Andrew and Mary Thomson Rocca dissertation research fellowship, and by the NIH Grant GM083863 and a USFWS Grant to WMG. Sponsors did not have a role in planning, executing or writing this research.

3.6. Figures

Figure 1. Map of study area, Etosha National Park, and its location in Namibia. Vegetation classification is based on Sannier et al. 1996

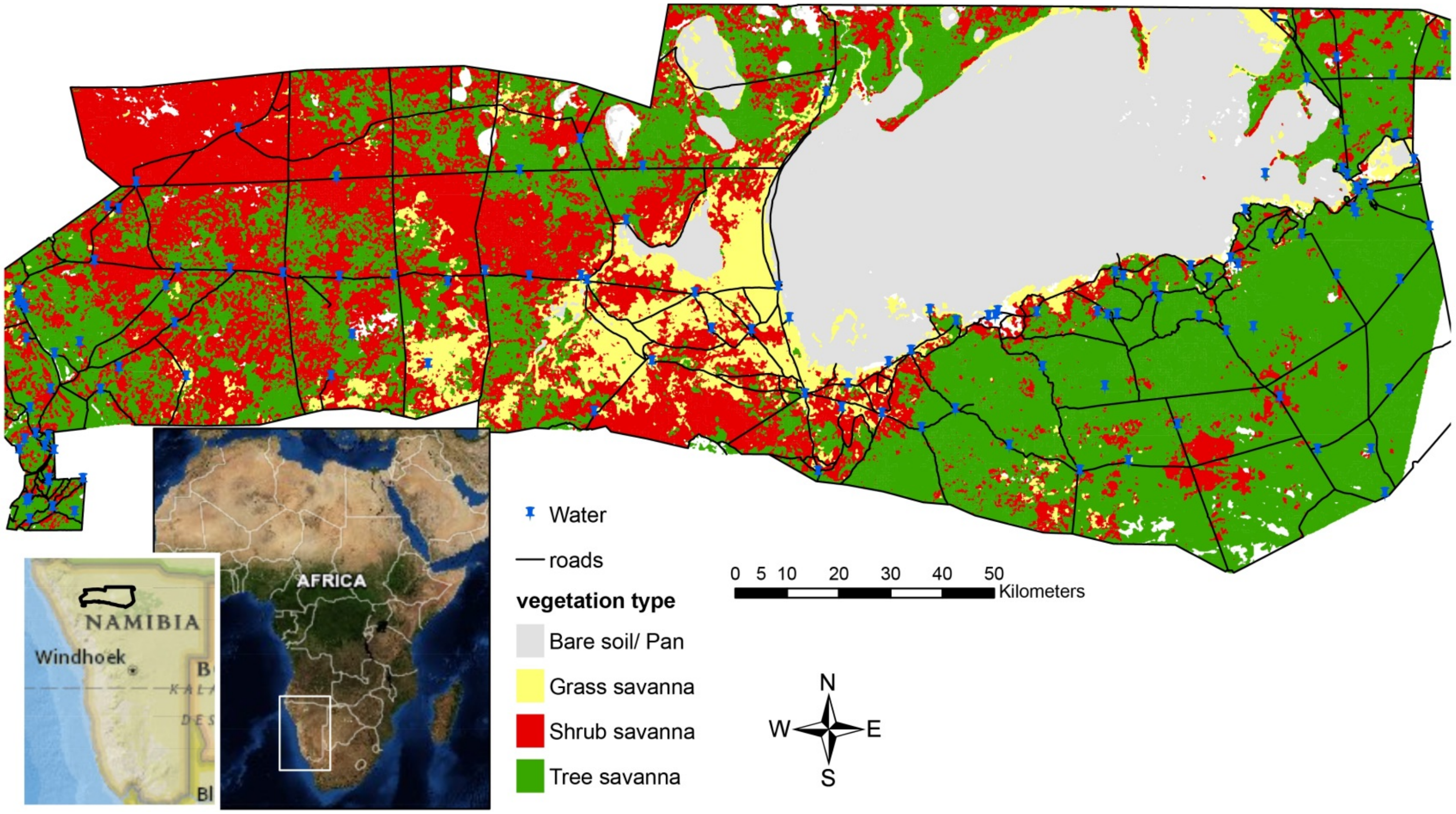


Figure 2. Distribution of elephants' movement parameters for one hour sampling interval. **A.** Step size (kilometers) every one hour and **B.** Turning angle (radians)

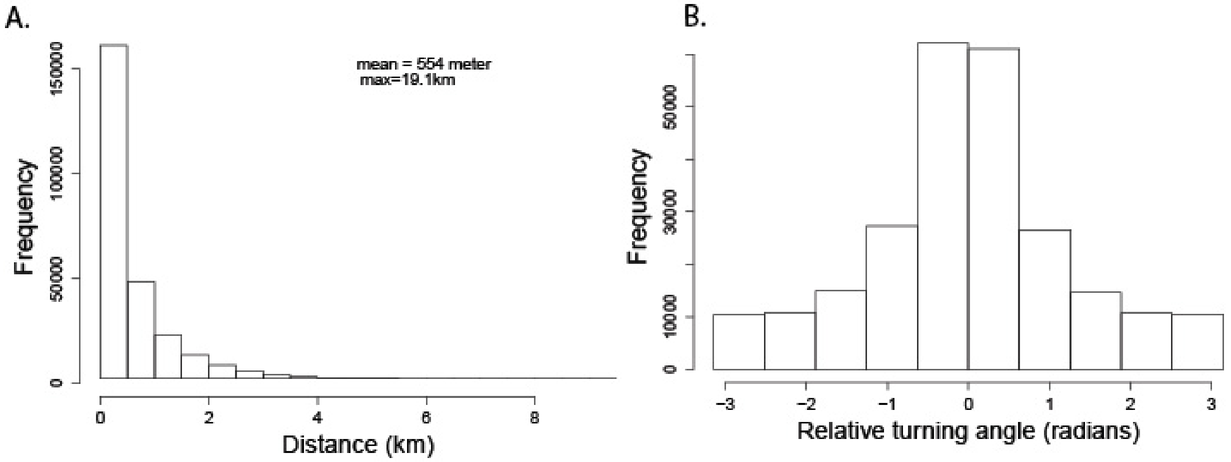


Figure 3. Average movement speed (km/hr) ± standard error in each month, for males (circles) and females (triangles), based on distances moved every one hour. Asterisks on top denote Tukey Honest Significant Difference between males and females: ( ) $P < 1$; (•) $P < 0.1$; (*) $P < 0.05$; (**) $P < 0.01$; (***) $P < 0.001$.

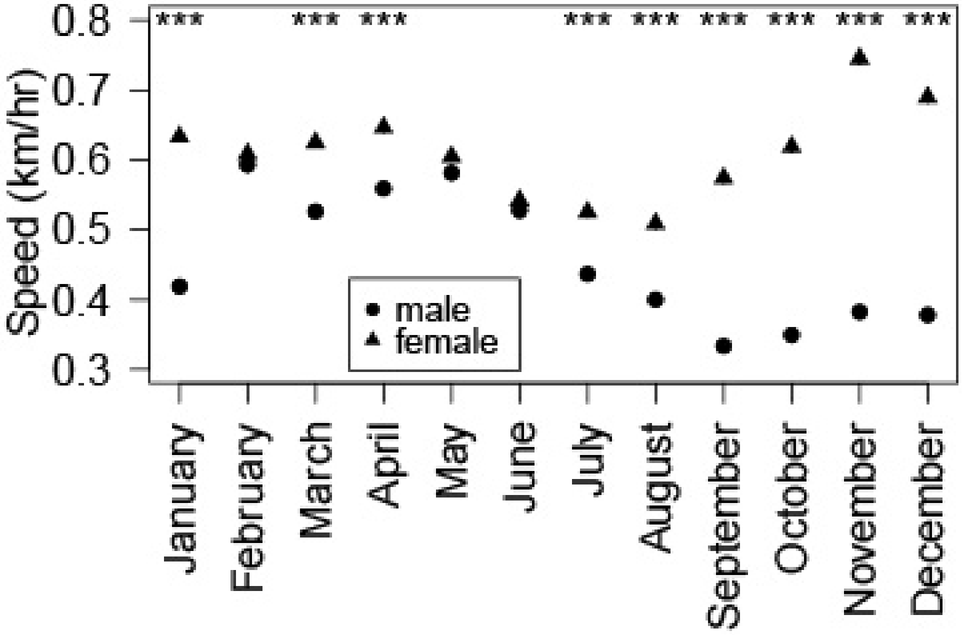


Figure 4. Coefficients ± standard error on landscape variables calculated using conditional logistic regression from step selection function (SSF). Standard error around coefficients is marked both for an analysis performed on the whole population (dotted line) or standard error analysis performed on each individual separately and then averaging the coefficients (dot-dashed line). Asterisks above columns denote significance value of the coefficients: ( ) $P < 1$; (•) $P < 0.1$; (*) $P < 0.05$; (**) $P < 0.01$; (***) $P < 0.001$.

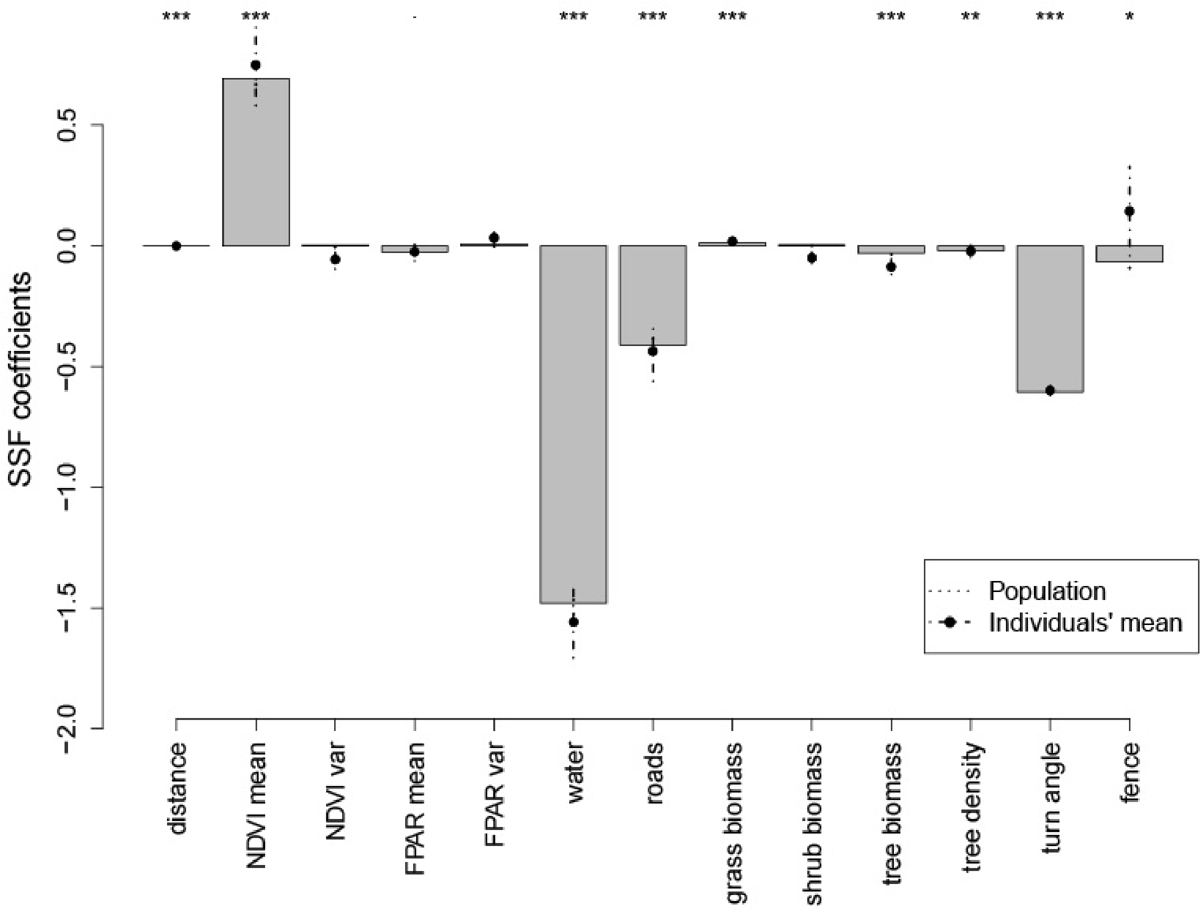


Figure 5. Coefficients ± standard error on landscape variables calculated using conditional logistic regression from step selection function (SSF). **A.** Males versus females. **B.** Adults versus young adults. All variables were scaled to have mean of zero and standard deviation of one. Asterisks above columns denote significance value of the coefficients: ( ) $P < 1$; (•) $P < 0.1$; (*) $P < 0.05$; (**) $P < 0.01$; (***) $P < 0.001$.

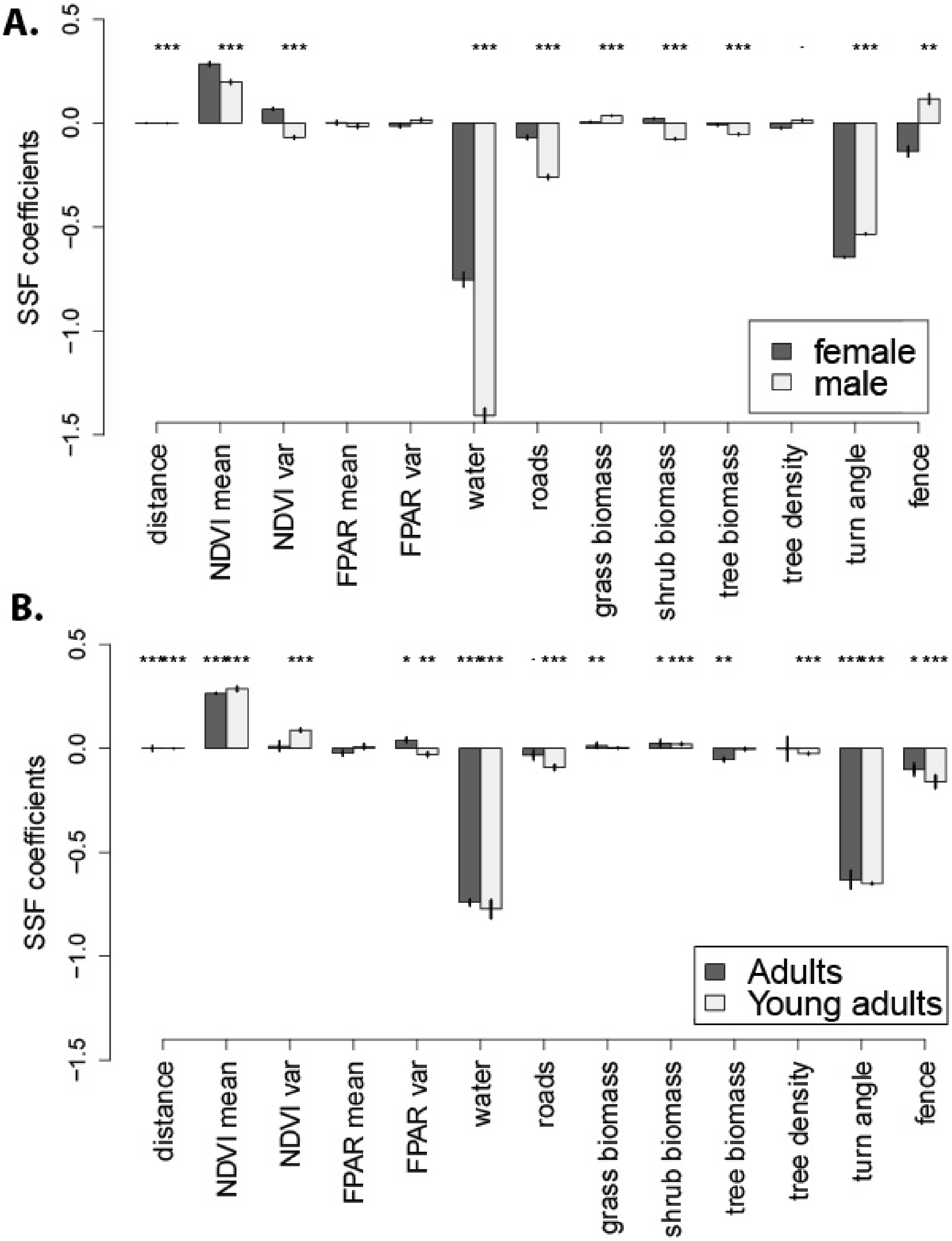


Figure 6. Coefficients of generalized linear model for log of movement speed versus landscape variables. Asterisk above columns denote significance value of the coefficients: ( ) $P < 1$; (•) $P < 0.1$; (*) $P < 0.05$; (**) $P < 0.01$; (***) $P < 0.001$.

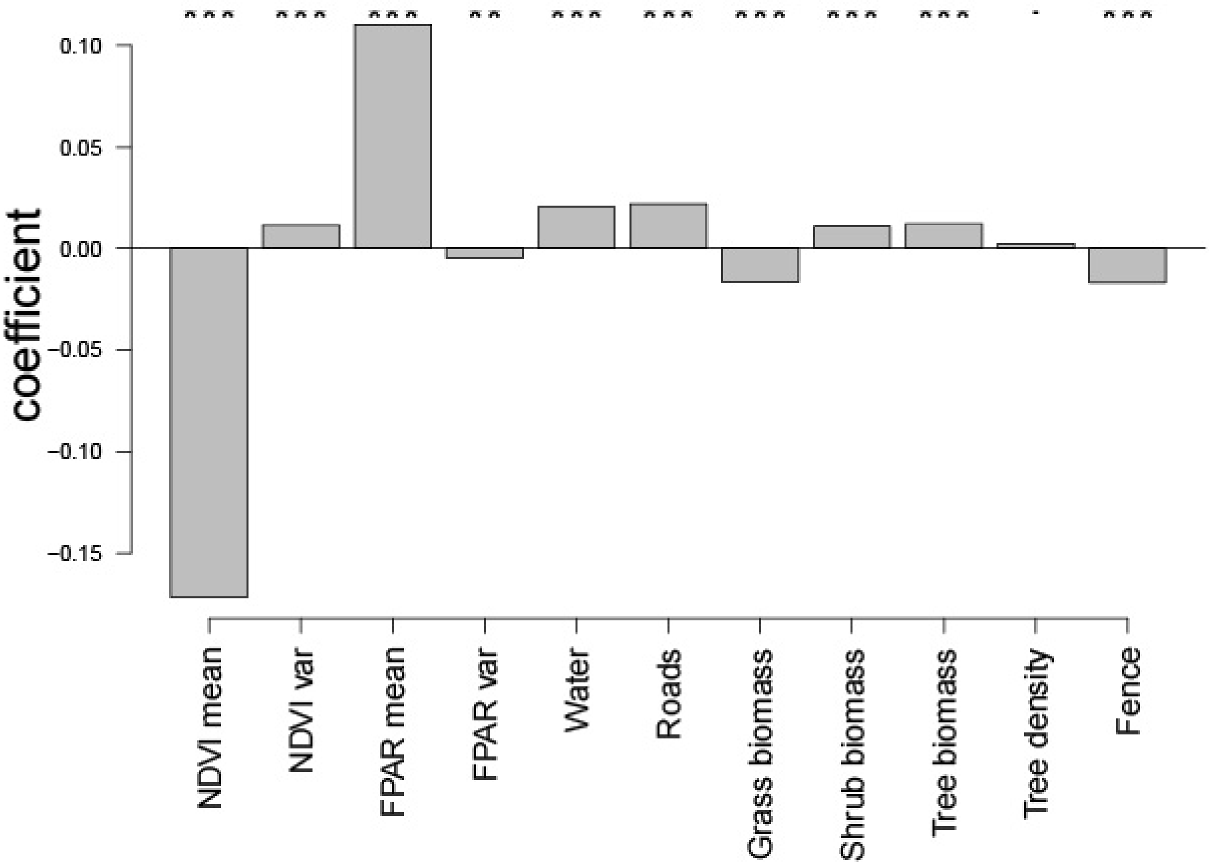


Figure 7. Diurnal variation in the coefficients on step selection function (SSF) for: **A.** Mean NDVI, **B.** Mean FPAR, **C.** Tree biomass, **D.** Distance to water, **E.** Distance to roads, **F.** Distance to fence.

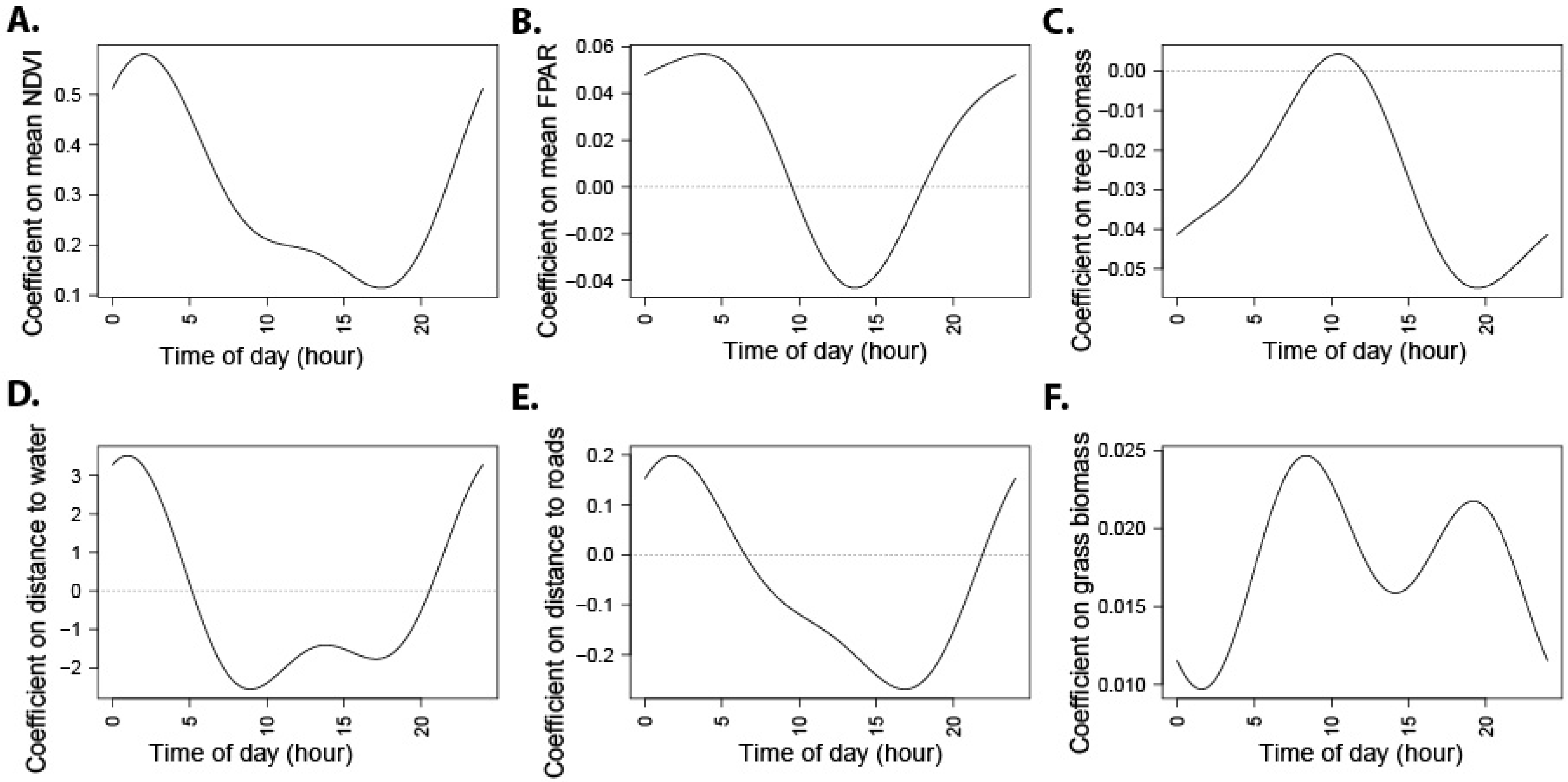


Figure 8. Monthly variation of coefficients on step selection function (SSF) for: **A.** Mean and variance of NDVI, **B.** Mean and variance of FPAR, **C.** Biomass of trees, shrubs and grasses, **D.** Distance to water. Dot-dashed line denotes mean monthly rainfall, **E.** Distance to roads. Dot-dashed line denotes mean number of tourist cars entering the reserve, **F.** Distance to the reserve fence.

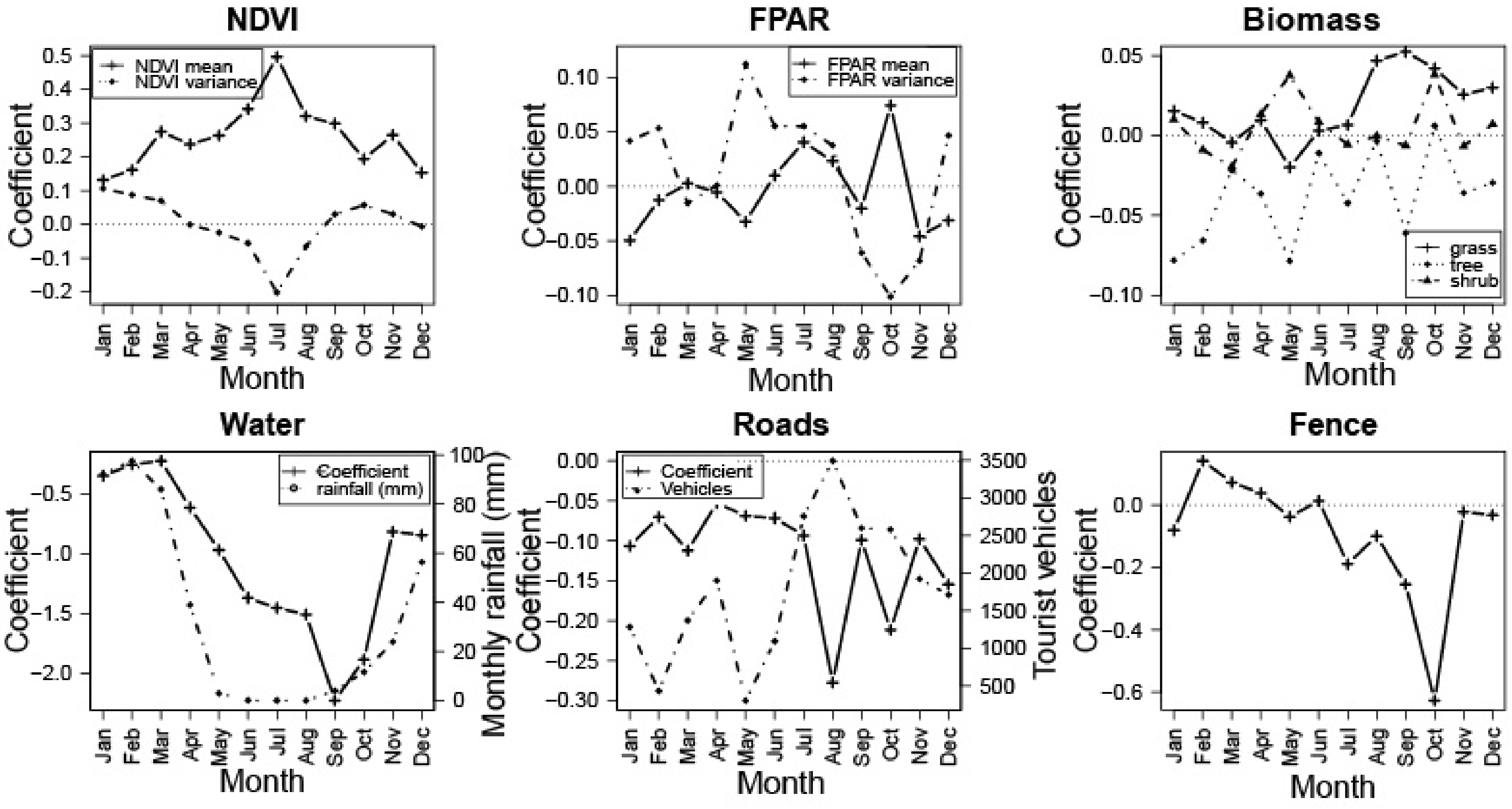
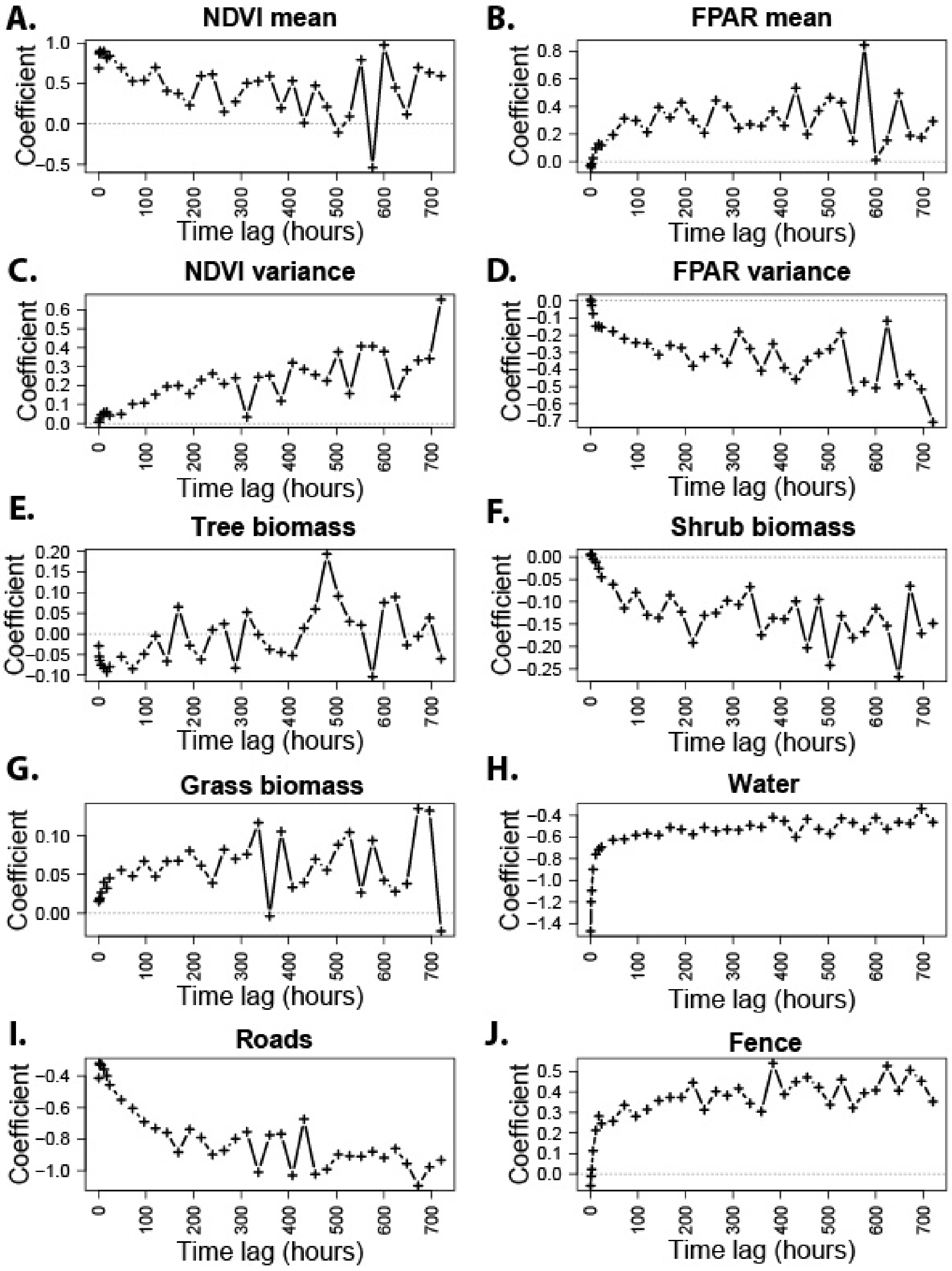


Figure 9. Variation in coefficients on step selection function (SSF) over increasing time intervals between consecutive movement steps for: **A.** NDVI mean, **B.** NDVI variance, **C.** FPAR mean, **D.** FPAR variance, **E.** Tree biomass, **F.** Shrub biomass, **G.** Grass biomass, **H.** Distance to water, **I.** Distance to roads, **J.** Distance to fence.



Chapter 4. Monitoring the impact of grazing on rangeland conservation easements using MODIS vegetation indices

Abstract

Monitoring the effects of grazing on rangelands is crucial for ensuring rangeland ecosystem functioning and maintaining its conservation values. Residual dry matter (RDM), the dry grass biomass left on the ground at the end of the grazing season, is a commonly used proxy for rangeland conditions in a Mediterranean climate. Moderate levels of RDM are correlated with soil stability, forage production, wildlife habitat, and diversity of native plants. Therefore, RDM is widely monitored on rangeland conservation properties. Current ground-based methods for RDM monitoring are expensive, labor intensive, and provide information in the fall, after the effects of grazing have already occurred. In this chapter I present a cost effective, rapid and robust methodology to monitor and predict RDM using Moderate Resolution Imaging Spectroradiometer (MODIS) satellite data. I performed a time series analysis of three MODIS-based vegetation indices (VI) measured over the period 2000 – 2012: Normalized Difference Vegetation Index (NDVI), Leaf Area Index (LAI) and Fraction of Photosynthetically Active Radiation (FPAR). I examined the correlation between the VIs and fall RDM at The Nature Conservancy's Simon Newman Ranch in central California. I found strong and significant correlations between maximum VIs in late spring and RDM in the fall. Among the VIs, LAI annual values had the most significant correlations with fall RDM. MODIS based multivariate models predicted up to 63% of fall RDM. Importantly, maximum and sum VIs values were significantly higher in management units with RDM levels in compliance with RDM conservation easement terms, versus those out of compliance. Based on those results I propose a management model which uses time series analysis of MODIS VIs to predict forage quantities, manage stocking rates, and monitor rangeland easement compliance. This model can be used to improve monitoring of rangeland conservation by providing information on range conditions throughout the year.

4.1. Introduction

Rangelands provide important ecosystem services, such as water filtration, biodiversity, pollination, and wildlife habitat (Ferranto et al. 2011), and serve as a substantial carbon sequestration pool, accounting for 20% of the world's soil carbon (Follett and Reed 2010). In addition, they are often grazed by cattle and are a large component of the meat and dairy production (Follett and Reed 2010) in Western USA, as well as other regions. While overgrazing of rangelands has led to land degradation and in some cases desertification (Dregne 2002), moderate grazing that ensures regeneration processes and biodiversity protection can serve as an economically viable land use that helps to preserve rangelands from land transformation (Watkinson and Ormerod 2001, McIntyre et al. 2003). Indeed, many conservation organizations maintain sustainable livestock grazing on their conservation easement and fee-owned properties (Reiner 1999, Hacker et al. 2010). Therefore, monitoring the effects of grazing on rangeland conditions is essential for long-term management and stewardship. To decrease the extensive time, labor and economic resources demanded by rangeland monitoring, many proxies for rangeland condition have been developed. One of the most widely applied proxies is residual dry matter (RDM), the dry grass material left on the ground in the fall, at the end of the grazing season (Bartolome et al. 2007). Currently, RDM levels are used as a key conservation easement compliance requirement (Reiner 1999).

Extensive literature shows the relationship between RDM levels and several aspects of rangeland productivity. For example, intermediate RDM encourages grass regeneration and supports higher forage production in the next growing season (Bartolome et al. 2007, Allen-Diaz and Jackson 2000). RDM quantities are also correlated with soil stability, nutrient cycling, water infiltration, and grass community health (Bartolome et al. 2007, Bartolome 2002). Moreover, RDM is related to numerous biodiversity values, including native species diversity, marsh vegetation cover, wildlife and endangered bird habitat, butterfly diversity, and native forb diversity (Richmond et al. 2012, Allen-Diaz and Jackson 2005, Allen-Diaz et al. 2004, Diaz et al. 1998, Jackson and Allen-Diaz 2001, Cingolani et al. 2005).

In California, RDM is monitored annually across hundreds of thousands of acres of conservation properties, at considerable cost. Currently, all estimates of RDM are ground-based and are performed in the fall, at the end of the grazing season (Wildland Solutions 2008). RDM is monitored by clipping grass at sample points across the landscape or by double sampling, which is using calibrated visual estimation or a photo point system (Wildland Solutions 2008, Harris et al. 2002). While the visual estimation methods are faster than destructive sampling, RDM monitoring is still time consuming and costly, especially when performed over large landscapes. Moreover, the typical ground-based method suffers from several potential drawbacks. First, insufficient sampling across large spatial scales can yield overly coarse estimates, with relatively wide error intervals. Second, since RDM estimates are observer dependent and somewhat subjective, it is challenging to compare results across observers, as they change with respect to properties and years (Harris et al. 2002). Finally, the effectiveness of RDM monitoring is limited since the results can be implemented only in the year following collection of data (Harris et al. 2002).

In contrast to observer collected monitoring approaches, remote sensing provides information to support a synoptic and temporal view of the landscape. In recent decades there has been advancement in using remote sensing for monitoring rangeland ecosystems. Remote sensing is applied to forecast forage yields, measure primary productivity and vegetation cover, and quantify the effects of restoration practices on forage productivity (Malmstrom et al. 2009, Washington-Allen et al. 2006, Todd et al. 1998). For example, aerial photographs and the Normalized Difference Vegetation Index (NDVI) have been used to monitor the effect of implementing best management grazing practices on prairie cordgrass establishment (Kamp et al. 2013). MODIS-based Enhanced Vegetation Index (EVI), Leaf Area Index (LAI), and land surface temperature have been used to assess rangeland vegetation cover, net primary productivity and fire occurrence in Cerrado Pastures, Brazil (Ferreira et al. 2013), while NDVI has been used to estimate stocking rates across large areas (Hunt and Miyake 2006) or to model the ecosystem performance in sagebrush habitat (Wylie et al. 2012). Washington-Allen et al. (2006) have used Landsat time series to monitor degradation on rangelands, including measuring productivity, composition, soil erosion, and soil quality. More recently, Li et al. (2012) have demonstrated a model based on MODIS EVI and NDVI that is used to measure Net Primary Production and forage production in pastures with different grazing regimes in California. In spite of these advancements, remote sensing tools are not widely applied in rangeland management (Karl et al. 2012, Butterfield and Malmstrom 2006), despite landowner interest, nor is remote sensing commonly used for monitoring RDM.

When RDM is measured in the fall, grasses are typically non-green or senescent (Wildland Solutions 2008). Low chlorophyll content of senescent vegetation reduces the red-to-near infrared (NIR) spectral contrast, which reduces the ability to distinguish vegetation from the background soil (Huete 1988, Butterfield and Malmstrom 2009). This presents a challenge in using remote sensing to directly measure dry grass biomass (Roberts et al. 1993, Huete 1988). While the literature on the application of remote sensing for estimating dry vegetation biomass is substantial, the following examples are particularly relevant to this chapter. Hand-held devices (Wang et al. 2013), hyperspectral sensors (Arsenault and Bonn 2005) and Landsat and ASTER satellites (Serbin et al. 2013, Serbin et al. 2009) have all been used to measure dry vegetation remotely. For example, Harris et al. (2003) used hyperspectral Airborne Visible/Infrared Imaging Spectrometer (AVIRIS) to detect photosynthetic vegetation (PV), non-photosynthetic vegetation (NPV) and bare soil cover on a gradient of grazing pressures, while the Soil-Adjusted Total Vegetation Index (SATVI) has been used to measure both green and dry vegetation cover and biomass (Marsett et al. 2006). In a more recent case, ground data was combined with MODIS and Landsat satellite data to produce estimates of total and non-green or senescent vegetation cover (Hagen et al. 2012). Many recent developments in the application of remote sensing for assessing non-green vegetation focus on the measurement of crop residue on agricultural land (Arsenault and Bonn 2005, Zhao et al. 2012, Zheng et al. 2012). For example, the Normalized Difference Tillage Index (NDTI), the Shortwave Infrared Difference Residue Index (SINDRI), and the Cellulose Absorption Index (CAI) have been used to measure dry crop residue cover and to classify the effects of different tillage practices (Watts et al. 2011, Paul and de Paul 2012). These methods often require extensive field work, are expensive and they need specialized training and pre-processing steps, which makes them impractical for extensive management application.

In contrast to the above-mentioned methods, I present in this chapter a rapid, cost effective and near-real-time system to monitor annual rangeland forage production and to estimate RDM, using freely available Terra-MODIS satellite imagery. My overall objective was to examine the relationship between MODIS-derived vegetation indices and RDM in a variety of spatial and temporal resolutions and habitat types, in order to determine if there is a reliable protocol that can help rangeland managers monitor RDM with freely available remote sensing data. My specific objectives were to: 1) determine which of three MODIS-driven vegetation indices (VI), Normalized Difference Vegetation Index (NDVI), Leaf Area Index (LAI) and Fraction of Photosynthetically Active Radiation (FPAR), best predicts RDM; 2) identify which covariates improve RDM prediction; 3) assess whether vegetation indices can be used across habitats to identify management units in and out of RDM easement compliance; and based on the results of the three steps above, 4) identify a model that uses MODIS data for improved RDM monitoring and management. This management model is a three-step approach that uses remotely sensed vegetation indices in three modes during the grazing year: *prediction* in early spring, *management* for the whole year, and *monitoring* RDM in the fall. To my knowledge, this is the first time remote sensing has been used in a direct easement compliance context to measure RDM.

4.2. Methods

4.2.1. Study site

Simon Newman Ranch is a 133 km^2 property located in Stanislaus and Merced Counties, California, USA (37º20′N, 121º10′W). It was selected as the study site because it is managed to achieve land conservation alongside a sustainable grazing regime (Guenther 2005). The property has been owned by The Nature Conservancy (TNC) since 1998. TNC annually monitors the compliance of its land management activities against conservation easement terms developed for conservation objectives. The prevalent vegetation types are annual grassland, chaparral, oak woodland and riparian vegetation. The property is divided by fences into fifty-six pastures, or, management units (Guenther 2005).

4.2.2. Data acquisition

Residual Dry Matter (RDM) Data. RDM has been monitored annually at Simon Newman Ranch since 2000 (Guenther 2005). Data has been collected in early October of each year, at the end of the grazing season, using photographed reference monitoring sites, as described in Guenther (2008). Zones with similar RDM value were delineated visually around each reference site, and varied in size between 0.1 – 8 km^2 (Guenther 2012).

RDM Classification. TNC's conservation easement terms require quantitative fall RDM goals for each management unit. At the Simon Newman Ranch, management units dominated by grassland or riparian vegetation have a RDM goal of 750-1 000 pounds per acre[1] (840-1 120 Kg · Ha^{-1}), while management units dominated by Oak woodland or chaparral vegetation have RDM goal of 1 000 – 1 500 pounds per acre (Guenther 2012). Although RDM is a continuous value, RDM in Simon Newman is measured and reported as a categorical value (Table 1).

Geographic Information System (GIS) data. GIS layers for the Simon Newman Ranch included the property boundary, boundaries of the management units, locations of the reference points, and the vegetation type at each management unit. GIS data was available in Universal Transverse Mercator (UTM 1983) projection. For analysis, I re-projected GIS layers to the sinusoidal projection of MODIS satellite data.

Terra-MODIS satellite data acquisition. MODIS remote sensing data has many advantages for efficient conservation management use. MODIS data is freely available through NASA's Reverb system (EODIS 2013). Further, MODIS satellite imagery is pre-processed, geo-

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[1] Pound · acre^{-1} is the common units used by rangeland managers, hence I will use this unit here

referenced and atmospherically corrected (Solano et al. 2010). In this chapter I used three Terra-MODIS indices: NDVI, LAI, and FPAR. The VIs product algorithms are confirmed with extensive modeling and ground based data (Solano et al. 2010, LP DAAC 2000-2012). The MODIS sensor has daily earth coverage; daily data is averaged over 16 or 8 days for NDVI or LAI/FPAR products, respectively. The 250 x 250 m (0.065 km^2) spatial resolution of MODIS-NDVI and 1 km resolution of MODIS-LAI and -FPAR is adequate for measurement of aboveground biomass on each management unit, as the ground-based RDM is estimated for zones with an average size of 1.9 km^2 (Guenther 2012). Since one MODIS scene covers most of California, it can be used to analyze multiple conservation properties. I acquired MODIS LAI and FPAR for 2002-2012 (LP DAAC 2000-2012, LP DAAC 2002-2012), and NDVI data for 2000-2012 (Table 2).

NDVI is defined as $\mathrm{NDVI} = \frac{\rho_{NIR} - \rho_{red}}{\rho_{NIR} + \rho_{red}}$, where ρ_{red} and ρ_{NIR} are the reflectance measured by the satellite sensor in the red (centered at 645 nm) and near infrared (858 nm) wavelength, respectively (Tucker et al. 1981). The relationship between NDVI and green aboveground biomass has been well established (Gamon et al. 1995, Tucker 1979). While I have predicted that NDVI would capture grass productivity well, I examined two additional VIs that I thought might improve quantification of dry biomass in the fall. MODIS-based LAI and FPAR use information on the canopy spectral properties and structural attributes hence might be better predictors of dry vegetation biomass (Knyazikhin et al. 1999). Research has demonstrated that both of these VIs have superior correlation than NDVI with senesced grass height and biomass (Butterfield and Malmstrom 2009). LAI is an important structural property of a plant canopy measuring the number of equivalent layers of leaves vegetation displays relative to a unit ground area (Knyazikhin et al. 1999, LP DAAC 2002-2012). FPAR is a unitless fraction, measuring the proportion of radiation that the canopy absorbs, out of the total available radiation in the photosynthetically active wavelengths of the spectrum 400 - 700 nm.

I compared which of the three VIs most accurately predicts RDM levels and RDM easement compliance. I removed null VI values and resampled FPAR and LAI data to 250 m pixel size, to match the resolution of NDVI data.

Climate data. Detailed climate data for California was obtained from the PRISM (Parameter-elevation Regressions on Independent Slopes Model) database (PRISM Climate Group 2000 - 2012). I used monthly rainfall data for 2000-2010, at a resolution of 0.0416 decimal degrees (PRISM Climate Group 2000 - 2012).

GIS Spatial Statistics. I extracted values of three MODIS VIs for the whole Simon Newman Ranch and for each of the fifty-six management units, using the Zonal Statistics ++ Auto function in Hawth's tools extension in ArcGIS 9.3 (Beyer 2004). I extracted PRISM rainfall data for the property, using the same methodology.

4.2.3. Statistical analysis

I performed all statistical analysis using R 2.15.2 software (R Development Core Team 2007).

Time series analysis of vegetation indices and RDM. In order to characterize the vegetation productivity patterns over time and its response to rainfall at the Simon Newman Ranch, I constructed a time series for each VI. In California's Mediterranean climate, the growing season starts with the onset of rains in the fall of the previous calendar year and concludes with senescence in the current calendar year (Allen-Diaz and Jackson 2005). Therefore, I consider one “growth year” to start from mid-October of the previous year until mid-October of the present year: for example, data for 2011 was calculated from 16 October 2010 to 15 October 2011. This approach synchronizes with the timing of RDM data collection in October. All statistical analyses for each of the three VIs were performed separately for the whole property, as well as for each management unit on the property. RDM values for the whole property were calculated as an area-weighted average of RDM values for all the management units.

For each growth year, I calculated the following summary statistics values for each VI: annual average, annual median, annual minimum, date of minimum occurrence, annual maximum, and date of maximum occurrence. Additionally, I calculated the annual sum of the VI values in a growth year, defined as $\sum_{i=1}^{n} \mathrm{VI}_i$, where i is each date the VI is calculated by MODIS (n is 23 or 46, for NDVI and for LAI/FPAR, respectively). I calculated the length of the growing season, which I define as the number of days where the VI levels exceeded 50% of the difference between the minimum and the maximum VI value for that year. To calculate this value, I counted the number of contiguous dates where VI values exceeded the 50% and multiplied it by the sampling interval of the VI in days (16 or 8, for NDVI or LAI/FPAR, respectively).

Linear and multivariate regression. I performed regression between RDM and each VI at two spatial scales: the whole property and each management unit. Since one of the goals of this research is to examine which MODIS-based VI is the most useful as a management tool for RDM prediction, for all the statistical analyses below, I created a separate model for each of the three VIs: NDVI, LAI, and FPAR.

Since my method is developed for management implementation, I focused on keeping the methods as simple as possible. I started with the simplest statistical model - a model with only one prediction variable, since this requires minimal data acquisition. Thus, to identify the VI and summary statistics that best predicts for RDM, I performed a univariate linear regression between RDM as the predicted variable and each of the summary statistics values for each VI: that is for NDVI, LAI, or FPAR.

Next, to create a model for predicting RDM in the fall, I performed multivariate regression. At the spatial scale of individual management units, a univariate model did not provide adequate predictive power. I included as covariates all the individual MODIS-measured VI values (23 or 46 parameters, for NDVI or LAI/FPAR, respectively) and their summary statistics (additional nine parameters). The year and vegetation type were included in the model as categorical variables. In order to optimize this model, to reduce the number of covariates used in the model, and to identify the most important parameters for RDM prediction, I performed automated backward stepwise model selection procedure, which uses the Akaike Information Criterion (AIC) values as the model selection criterion (Murtaugh 2009).

Analysis of Variance (ANOVA). To assess how well VI summary statistics measure RDM easement compliance, I performed ANOVA, comparing VI values for management units in or out of compliance. The compliance threshold for each management unit was determined based on its vegetation type, where RDM ≥ 750 pounds/acre is required for management units with grassland or riparian vegetation, and RDM ≥ 1 000 pounds/acre is required for management units with Oak woodland or chaparral vegetation. I performed the analysis for NDVI, LAI, and FPAR, separately, and used the VI annual maximum, sum, and average values, as predictors of compliance. To verify how well MODIS data predicted RDM in different habitats, I repeated the ANOVA with compliance and habitat type as interaction factors. I performed factorial ANOVA and then compared the means of each pair combination, using Tukey Honest Significant Differences (HSD) to correct for multiple comparisons (Yandell 1997).

4.2.4. Case Study: Monitoring one-year of RDM

After testing the process, I developed a standardized workflow in order to demonstrate a proof-of-concept monitoring framework that can be used by rangeland managers. This workflow proceeds from imagery acquisition through multivariate analysis using LAI, and is focused on the entire property, as well as individual management units. LAI values for the Simon Newman ranch and the individual management units were acquired and analyzed to derive a baseline value for areas with RDM easement compliance, specific for each habitat type. These baseline values were used in a three-step model during the grazing year: first, during early spring, predicting productivity of that year; second, while making management decisions about stocking rates in the property; and third, while monitoring RDM in the fall.

4.3. Results

Relationship between time series of vegetation indices and RDM

Time series of NDVI data over eleven years shows a distinct annual vegetation growth cycle that is highly repetitive throughout the decade (Fig. 1), with one peak of green vegetation growth per year, which occurs around the same time every year. Maximum greenness occurs around March 6th in areas with riparian and grassland vegetation, and around March 22nd in oak woodland and chaparral areas. Minimum vegetation greenness appears at the end of September. The time series analysis shows a close relationship between the amount of green vegetation and the amount of rainfall. For example, in 2007 precipitation was about half the average annual value for the decade. The NDVI values of that year were the lowest of the decade. Average annual precipitation is highly correlated with average annual NDVI ($R^2 = 0.69$, $P = 0.001$). Similarly, the timing of vegetation growth follows rainfall closely, with a lag of about two weeks between the timing of rainfall and the resulting growth (Fig. 1). For example, a very low NDVI value for December 2005 can be likely ascribed to the late rainfall that year, which began January 2006. Likewise, there is a significant correlation between the maximum monthly rainfall and the maximum NDVI values each year ($R^2 = 0.57$, $P = 0.007$). There is also a moderate correlation between RDM and the total annual rainfall ($R^2 = 0.39$; $P < 0.01$). While NDVI is influenced by the timing of the rainfall, there was no significant correlation between the timing of the first and last rains of the year and the RDM values.

Time series of LAI and FPAR showed similar patterns to NDVI, with one growing cycle each year (Figs. 2A-2B). However, LAI and FPAR increased more slowly than NDVI and decreased slightly faster. The FPAR temporal pattern had the highest inter-annual variability among the three vegetation indices (Fig. 2B).

There were significant correlations between RDM and the annual maximum, average, and sum levels of LAI and FPAR, and between RDM and maximum NDVI (Figs. 3A-3C). Importantly, for all three VIs, the annual maximum value was the most significant predictor of RDM in the fall. LAI had the strongest correlation with RDM, explaining a large portion of the variability in fall RDM. Maximum annual values of LAI explained as much as 68% of RDM variability (Fig. 3B).

Prediction of RDM with multivariate regression

The multivariate model containing all the covariates for NDVI predicted RDM with $R^2 = 0.6$,

$P < 0.001$; for LAI $R^2 = 0.56$, $P < 0.001$; and for FPAR $R^2 = 0.57$, $P < 0.001$. Using stepwise model selection with AIC criteria, all of the selected RDM prediction models contained the vegetation type and the year as significant covariates (Table 3). The selected NDVI-based model (AIC=7914.24) contained NDVI values for four months, the annual NDVI standard deviation, the minimum and the maximum annual values, and the length of the growing season (Table 3). This final NDVI model predicted 63% of the variability in fall RDM ($R^2 = 0.63$, $P < 0.0001$). The selected LAI model (AIC=6832.96) predicted RDM with $R^2 = 0.57$, $P < 0.0001$, contained LAI values from eight months, the annual LAI standard deviation, the minimum annual value, and the length of the growing season. The FPAR selected model (AIC=6820.3) included values from six different months, the annual median, sum, and standard deviation values (Table 3). It predicted fall RDM with $R^2 = 0.58$, $P < 0.001$.

RDM compliance monitoring

Management units in compliance with RDM conservation easement terms had significantly higher annual maximum, sum, and average VIs than those out of compliance ($P < 0.01$) (Figs. 4A-4C). Maximum LAI had the most pronounced and significant difference between management units in and out of compliance (Fig. 4B).

When comparing RDM management units in and out of compliance separately in each habitat type (i.e. Chaparral, grassland, oak woodland and riparian habitat), the overall resulting ANOVA was significantly different for units in and out of compliance within each habitat type, for all three VIs (NDVI sum and mean: $P = 0.055$; LAI and FPAR: $P < 0.001$). However, when comparing each pair of habitat type separately, using Tukey's Honest Significant Difference method, there was a significant difference only in the values of LAI and FPAR for the grassland and oak woodland habitat types (Figs. 5A-5C).

Three step management model and application at Simon Newman ranch

My results suggest the feasibility of a RDM monitoring framework that is based on MODIS NDVI, LAI, and/or FPAR satellite data. In this section I present such a framework and demonstrate an operational monitoring process using MODIS-LAI data acquired for the Simon Newman Ranch. I acquired LAI data for the entire ranch and for the individual management units and analyzed them according to the methods above. I calculated baseline LAI values that coincide with RDM compliance for the whole property and for each habitat type. Based on my analysis of the MODIS-LAI time courses and data on RDM compliance from 2002-2012, I determined that years when the overall property RDM was in compliance had annual maximum LAI values of 2.2. Management units in compliance with RDM terms should have maximum LAI values of 1.7, 2.8, 2.1 and 2.3 for chaparral, grassland, oak woodland and riparian habitat, respectively. These baseline values were used in a three step methodology during the grazing year: *prediction* in early spring, *management* for the whole year, and *monitoring* RDM in the fall.

Step 1: Prediction. During early spring (mid-March), property- and management unit-based LAI values are extracted for the current year. These values are compared to the MODIS-LAI time course (e.g. 2002-2012), focusing on how current year LAI values compare to years when the property (or specific management units) are in vs. Out of compliance with RDM easement terms. For example, at Simon Newman Ranch, in March 2007 the property-wide LAI average was 1.02, which was below the value for years in RDM compliance of 2.2 (Fig. 6). Based on this March LAI value, I would predict that property-wide fall RDM level would be lower than a minimum value of 850 lbs/acre required for easement compliance, and that is indeed what I saw; the property-wide RDM average in 2007 was 843 lbs/acre (Fig. 6). In contrast, in March 2004 the property-wide LAI was 2.4, which was above the threshold for easement compliance. Based on this March LAI value, I would predict that fall RDM levels would be within easement compliance terms, and that is indeed what I saw; the property-wide RDM average in 2004 was 993 lbs/acre (Fig. 6). I suggest that land managers should closely evaluate areas with LAI below the established spring LAI value for easement compliance.

Step 2: Management. Evaluating forage conditions and potential easement compliance in March allows land managers and conservation practitioners to adjust grazing practices to meet both the needs of the cattle operation and the terms of the conservation easement. By proactively comparing March LAI values to established baseline values for compliance, managers can identify potential problem areas, and consider adjustments to their stocking rates and grazing rotations early in the season. For example, cattle may be rotated out of management units where potential problems exist and into units where additional forage may be available. In extreme conditions, like extended drought, managers can determine early in the season, before the largest economic impacts may occur, that cattle need to be moved off of an easement property where forage conditions are low and threats to conservation values are greatest, and on to a property where more forage exists. Figure 7A shows a map of RDM values for each management unit at the Simon Newman Ranch in fall 2008. Indeed, areas with higher RDM also had higher spring LAI values (Fig. 7B) and, in the some cases, higher LAI values in the fall (Fig. 7C).

Step 3: Monitoring. By the end of September, LAI data for the rest of the growth year should be extracted and plotted, as demonstrated in Figure 6. The sum and the average of LAI values for the year are calculated and compared to the established compliance values for each area. By this time in the growth year, managers can use LAI time course and all three statistics (annual maximum, sum, and average) to help identify management units which are likely to be out of compliance (Fig. 5). This will inform more targeted ground monitoring. For example, at the Simon Newman Ranch, management units with RDM compliance should have annual LAI sum ≥ 33, and LAI average ≥ 0.72. In 2004, 31 out of the 56 management units were in compliance.

4.4. Discussion

Understanding rangeland dynamics from remote sensing. A time series analysis of the three MODIS vegetation indices I considered, NDVI, LAI, and FPAR, showed a strongly repetitive pattern across a California rangeland (Figs. 1 and 2): in this Mediterranean climate, the growth cycle of annual grass-dominated rangelands has one clear peak during March and reaches minimum value during the summer months when vegetation is senescent (Jackson 1985, Mooney and Dunn 1970). The maximum value of each of the three VIs occurs at the same time every year, around mid-March, at my study site (Figs. 1 and 2). This suggests that data can be extracted for an assessment of ranch conditions at the same time of spring every year, without the need to wait until the end of the season. I expect a similar phenological pattern across California's rangeland ecosystems, which are mostly dominated by annual grass species. For other areas, the exact timing of maximum NDVI, LAI, or FPAR would need to be assessed. The strong correlation I found between NDVI and the quantity and timing of rainfall is consistent with previous research across rangeland ecosystems (Garcia et al. 2010, Mao et al. 2012).

Spring maximum values of all three VIs had the strongest correlation with fall RDM in my study area (Fig. 3). This finding has important management implications, especially across lands with conservation easements where RDM is typically monitored in the fall at the end of the grazing season, when the impacts of grazing, whether positive or negative, have already occurred (Harris et al. 2002). These results suggest that land managers and conservation practitioners can use MODIS-based estimates of maximum productivity, as measured by maximum NDVI, LAI, or FPAR, to make within season decisions about grazing practices, including those related to stocking rate and grazing timing that help ensure easement compliance, protect conservation values, and maximize the productivity and profitability of the grazing operation. I also found a significant difference between the annual maximum, sum, and average values of NDVI, LAI and FPAR within management units that were in versus out of compliance with The Nature Conservancy's RDM easement terms; these findings were consistent when evaluated property-wide (Fig. 4) and within individual habitat types (Fig. 5). This demonstrates the robustness of my approach for the prediction of RDM easement compliance across the grazing season and within a variety of rangeland ecosystems.

LAI and FPAR were more strongly correlated to RDM and were better predictors of RDM across my study site than NDVI. There are few possible explanations for this result. First, while NDVI is a measure of vegetation greenness, LAI and FPAR measure structural and functional properties of vegetation, which are more relevant for measuring senesced vegetation (Myneni et al. 2002, Knyazikhin et al. 1999). LAI and FPAR have been shown to have a strong relationship with grassland biomass, both green and senescent, in variety of ecosystems (Asner et al. 1998), including California rangelands (Malmstrom et al. 2009, Butterfield and Malmstrom 2009). LAI describes the canopy structure of the number of equivalent layers of leaves relative to a unit ground area (Knyazikhin et al. 1999), which may explain its superiority at predicting RDM in the fall, since RDM is the cumulative outcome of year round grass availability. FPAR measures the photosynthetic capacity of vegetation. This capacity continues, to some degree, in dry vegetation as well (Butterfield and Malmstrom 2009). Second, MODIS-based LAI and FPAR data has a higher temporal resolution (every eight days) than NDVI (every 16 days), which allows it to capture potential finer vegetation dynamics, hence might be more sensitive to changes in biomass. Finally, the model that MODIS uses to calculate LAI and FPAR includes NDVI as well as canopy reflectance data, sun-view geometry, a cover radiance transfer model specific for each land cover type, and extensive ground validation (Knyazikhin et al. 1999). These additional data sets may improve the correlation between LAI and FPAR and the ground-based measure of RDM.

I examined a range of univariate and multivariate models to determine whether I could accurately predict RDM levels using remote sensing data. I found that these models were highly significant and could measure 55-68% of the RDM variability in the fall (Table 3). LAI provided the best RDM prediction in the univariate models (68%), while NDVI provided the best RDM prediction in the multivariate models (63%) (Table 3). All of the selected multivariate models included fall and spring VI values. The year factor had an important role in the model, which may indicate the central effect annual climate variability has on RDM outcomes. The vegetation type also appeared as an important factor in each selected model, emphasizing the importance of habitat type in the relationship between the VI and RDM.

Interestingly, I found excellent RDM compliance prediction ability in oak woodland areas. A possible explanation is that the tree cover in these regions is relatively sparse (Guenther 2012). Moreover, the difference between RDM compliant and non-compliant areas is more significant when measured by LAI or FPAR. The algorithm calculating these indices takes vegetation type into consideration, and normalizes the relative influence of tree canopy cover (Myneni et al. 2002). Finally, the correlation between VIs and RDM in woody vegetation may be explained by an indirect effect. Tree canopy enhances grass productivity by concentrating nutrients and providing shade (Belsky 1994). Higher tree greenness may predict greater grass biomass. This hypothesis needs to be further examined using field data and finer resolution satellite imagery.

Future improvements to my analysis may include more refined field RDM measurements. Since I used RDM data that was acquired for management purposes, using photo points, this data was relatively coarse both in spatial and class resolution. Incorporating detailed topographic data and cattle stocking rates into the analysis should improve the RDM prediction. In the future, if finer spectral and spatial resolution satellite data is made available to the public in a preprocessed form, it may improve RDM prediction ability (Irons et al. 2012).

4.5. Management implications

A Rangeland Monitoring Framework. My rangeland monitoring and adaptive management approach using MODIS-LAI has three steps: “Predict, Manage and Monitor”. My model uses time series analysis to establish a multiyear LAI baseline of annual maximum, average, and sum values, for a property with good RDM conditions. In early spring, ***prediction*** uses LAI data, extracted for a site, compared to the baseline LAI values and assesses relative forage availability. Next, ***adaptive management*** entails choosing stocking rates according to forage availability that assures moderate grazing pressure. Finally, RDM ***monitoring*** during October is improved by using LAI sum and average values to identify management units with low RDM, and targeting potential problem areas for monitoring. I suggest this method as an augmentation, rather than a replacement of typical ground-based monitoring. While remote sensing cannot replace the direct contact of land managers with the land, it can enhance monitoring efforts by directing them to the most needed areas.

To help ensure that my methodology can be more easily implemented by land managers and conservation practitioners, I developed a methodology that is cost-effective, simple, and easily scalable. I used MODIS satellite remote sensing data, which is free, available for long time periods (which can allow for retrospective analyses as well as current and future ones), pre-processed, and easily manipulated using open-source software (e.g. GDAL, R). The low cost and technical simplicity of my methodology makes it especially viable for use across large rangeland properties. I demonstrated that MODIS data can be used to predict RDM levels and RDM easement compliance at a variety of spatial and temporal scales.

Conclusions

Monitoring the effects of grazing on rangelands is essential to ensure proper ecological functioning of the ecosystem and to protect biodiversity on conservation easement properties. Field-based monitoring of vast rangeland easement areas demands considerable time and resources, making such monitoring difficult with increasingly limited funds available for conservation. In this chapter, I developed a method that uses multi-temporal MODIS data that is cost effective and efficient at monitoring RDM on rangeland conservation easements. To my knowledge this is the first time that remote sensing has been applied to monitor RDM in the context of rangeland easement compliance.

4.6. Acknowledgements

I thank The Geospatial Innovation Facility (GIF) at the University of California (UC) Berkeley for providing state of the art computers, software and technical support for the geospatial analysis. Brian Galey developed the data transformation procedures in GDAL. I thank Keith Guenther and The Nature Conservancy for providing the residual dry matter data for The Nature Conservancy's Simon Newman Ranch. The MODIS vegetation index products were obtained through the online Data Pool at the NASA Land Processes Distributed Active Archive Center (LP DAAC), USGS/Earth Resources Observation and Science (EROS) Center, Sioux Falls, South Dakota (https://lpdaac.usgs.gov/data_access). The Nature Conservancy provided data and financial support for this project. I thank Professor Maureen Lahiff, UC Berkeley, for assistance with the statistical analysis and Professor James Bartolome, for helpful advice and ideas, and two anonymous reviewers whose helpful comments have improved this manuscript.

4.7. Tables

Table 1. Residual dry matter (RDM) classifications for Simon Newman ranch

RDM categories for 2000-2007		**RDM categories used after 2008**		
Category	**RDM class (pounds per acre)**	**Class**	**RDM value for grassland/ riparian vegetation (pounds per acre)**	**RDM value for Oak woodland/ Chaparral vegetation (pounds per acre)**
	---	Very low	<100	<100
1	300	Low	<300	<500
2	500	Below	350-750	500-100
3	700	Meets	750-1000	1000-1500
4	1000	Exceeds	1000-1500	15000-2000
5	1500	High	1500-3000	2000- 4000
6	3000 (added 2007)	Very high	>3000	>4000

Table 2. Moderate Resolution Imaging Spectroradiometer (MODIS) vegetation indices used in this research and the parameters of each index.

Vegetation index shortcut	Vegetation index name	MODIS product name	Temporal resolution	Spatial resolution	Boolean dates used	Data Range	Scale factor
NDVI	Normalized Difference Vegetation index	MOD13Q1	16-days	250 meters	049.2000 – 275.2010	–2000, 10000 Fill value: –3000	0.0001
FPAR	Fraction of Photosynthetically Active Radiation	MCD15A2	8- days	1 kilometer	185.2002 – 321.2010	0–100 Null values: 249–255	0.01
LAI	Leaf Area Index	MCD15A2	8-days	1 kilometer	185.2002 – 321.2010	0-100 Null values: 249–255	0.1

Table 3. Best model selected by stepwise regression for fall residual dry matter (RDM) prediction.

Best model : Normalized Difference Vegetation Index (NDVI)			
Parameter	**Coefficient Estimate**	**Standard error**	**Pr(>|t|)**
Intercept	-3891.67	831.84	0.00
vegetation type	-501.38	139.60	0.00
year factor	5739.86	606.48	0.00
NDVI value at January 17	-3149.73	780.88	0.00
NDVI value at June 10	-13994.97	3734.04	0.00
NDVI value at June 26	9302.11	4241.49	0.03
NDVI value at August 29	13381.28	2835.08	0.00
NDVI value at September 30	-4122.78	1219.15	0.00
Standard deviation	15364.13	2092.71	0.00
Minimum value	-2767.46	1552.50	0.08
Maximum value	5.45	2.41	0.02
Length of growth period (days)	-2.30	1.41	0.10

Best model : Leaf Area Index (LAI)			
Parameter	**Coefficient Estimate**	**Standard error**	**Pr(>|t|)**
Intercept	338.37	364.94	0.35
vegetation type	356.30	172.26	0.04
year factor	2911.67	348.16	0.00
LAI value at October 16	-1047.06	467.49	0.03
LAI value at December 03	-994.46	645.57	0.12
LAI value at December 19	667.17	442.18	0.13
LAI value at January 17	-353.34	167.43	0.04
LAI value at February 2	-307.54	134.49	0.02
LAI value at February 18	-181.83	87.59	0.04
LAI value at March 22	155.88	85.38	0.07
LAI value at April 7	-185.50	107.13	0.08
LAI value at May 25	-1341.44	695.17	0.05
LAI value at June 10	1817.68	909.46	0.05
LAI value at June 26	-1490.39	821.95	0.07
Standard deviation	1504.09	535.99	0.01
Minimum value	1840.68	742.82	0.01
Length of growth period (days)	1.91	1.28	0.14

Best model : Fraction of Photosynthetically Active Radiation (FPAR)

Parameter	**Coefficient Estimate**	**Standard error**	**Pr(>|t|)**
Intercept	675.02	517.54	0.19
vegetation type	-420.52	161.63	0.01
year factor	2314.46	685.56	0.00
FPAR value January 1	1280.30	648.38	0.05
FPAR value February 2	-1675.04	736.72	0.02
FPAR value March 6	2334.69	1081.21	0.03
FPAR value March 22	1332.20	769.08	0.08
FPAR value June 10	3177.46	2213.58	0.15
FPAR value August 29	7892.30	2429.07	0.00
FPAR value September 14	-2161.03	1482.60	0.15
FPAR value September 30	-4068.46	2341.71	0.08
Median	4842.42	1624.05	0.00
Sum	-412.26	99.20	0.00
Standard deviation	12600.19	3508.63	0.00

4.8. Figure

Figure 1. Normalized Difference Vegetation Index (NDVI) and rainfall time series for the Simon Newman Ranch from 2000-2010. Each NDVI data point is a 16-day average, extracted for the entire property. Bars represent monthly rainfall (in millimeters) for the ranch.

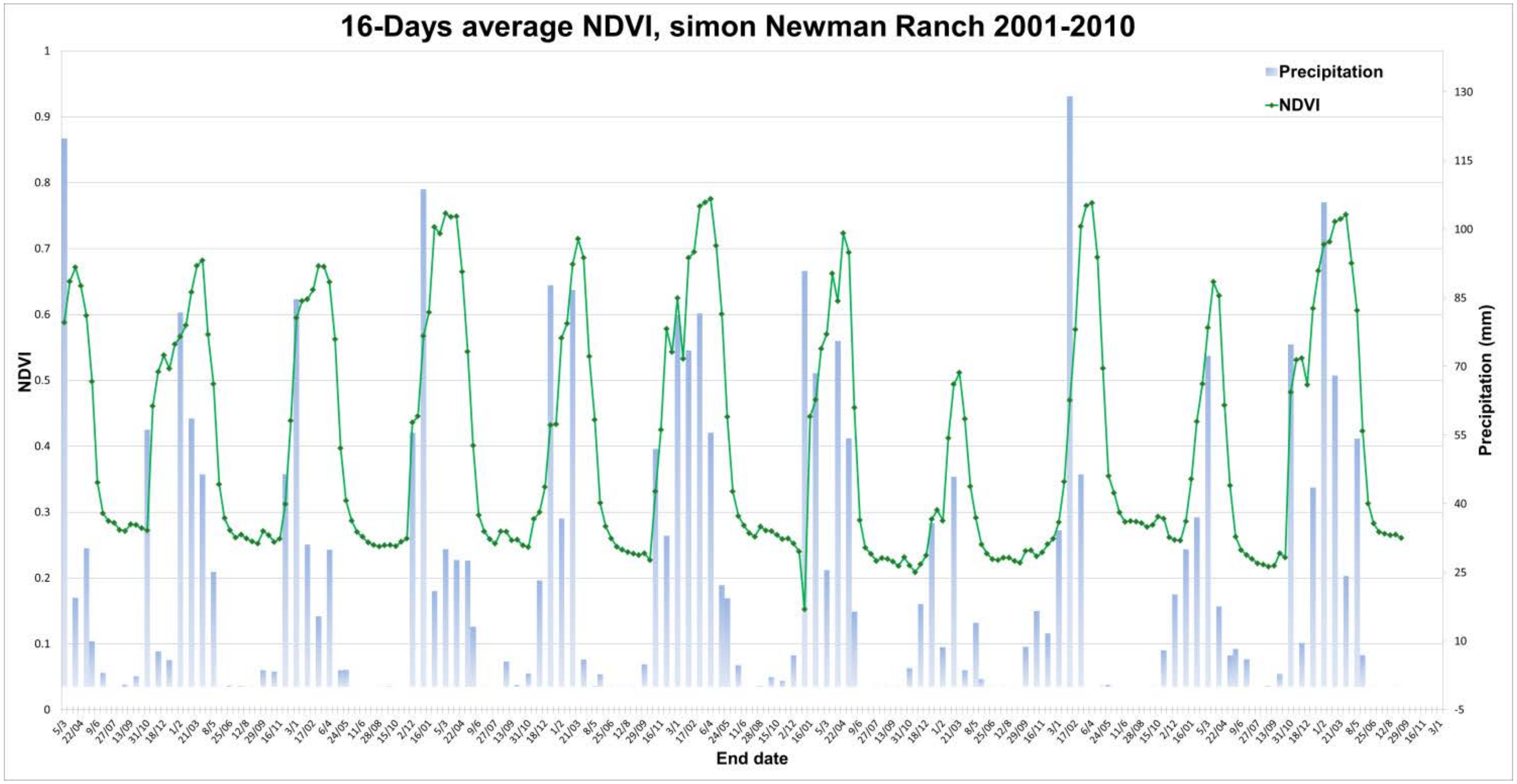


Figure 2. Time series profile of vegetation index values for the Simon Newman Ranch. Each line represents one year from 2002 – 2010. **A.** Leaf Area Index (LAI). **B.** Fraction of Photosynthetically Active Radiation (FPAR).

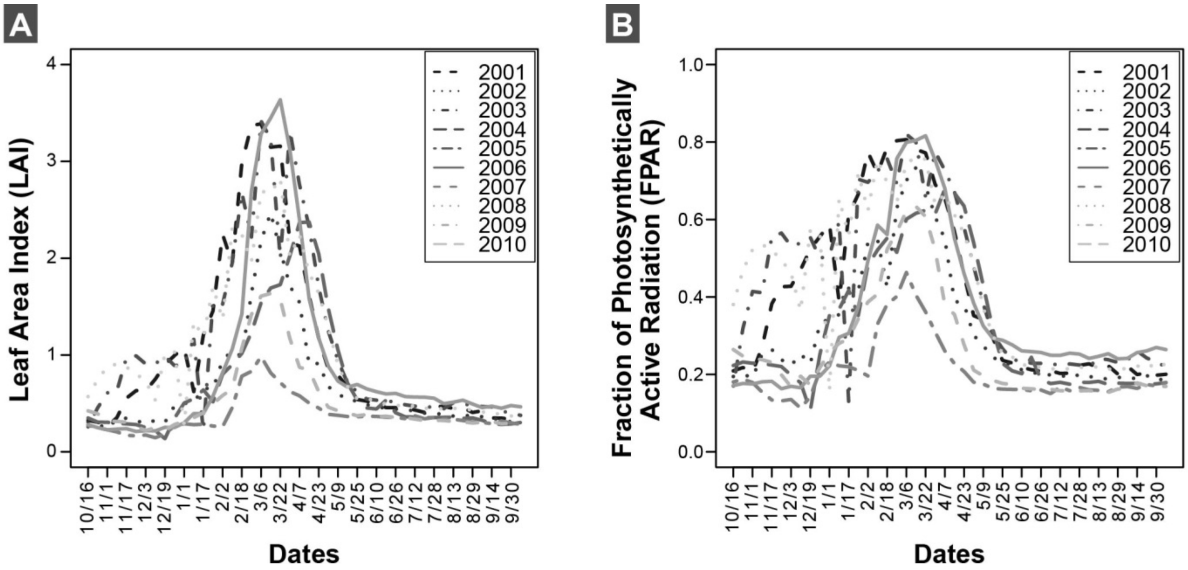


Figure 3. Correlations between property-based residual dry matter (RDM) (pounds/acre) levels and the annual maximum, sum and average of MODIS-based data for Simon Newman Ranch. **A.** Normalized Difference Vegetation Index (NDVI). **B**. Leaf Area Index (LAI). **C.** Fraction of Photosynthetically Active Radiation (FPAR).

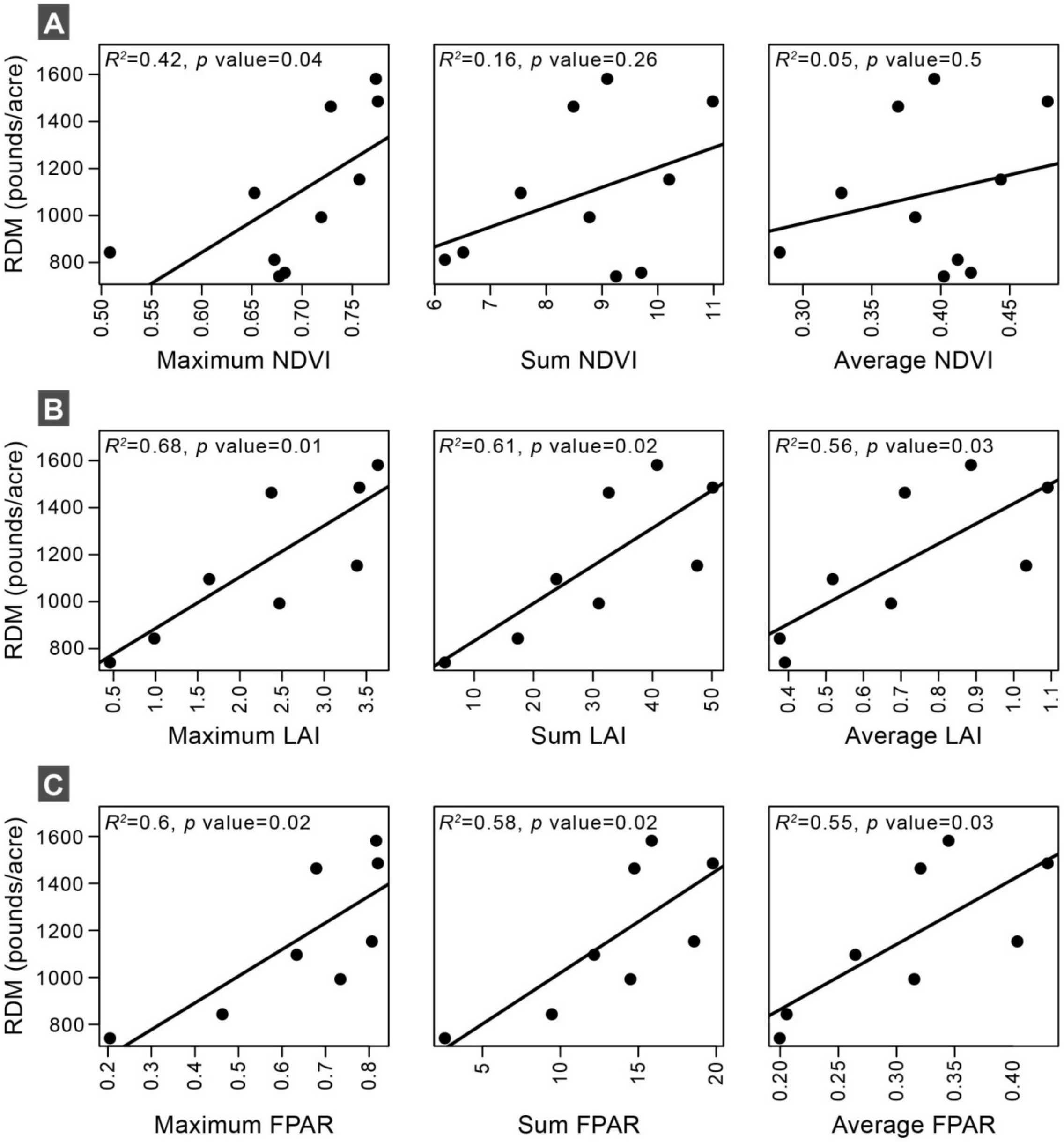


Figure 4. Analysis of variance (ANOVA) of annual maximum, sum and average of each vegetation index (VI), in management units in compliance with RDM easement terms (symbolized with a "1") compared to management units out of RDM compliance (symbolized with a "0"). **A.** Normalized Difference Vegetation Index (NDVI). **B.** Leaf Area Index (LAI). **C.** Fraction of Photosynthetically Active Radiation (FPAR). Asterix above columns denote ANOVA statistical significance: ( ) $P < 1$; (•) $P < 0.1$; (*) $P < 0.05$; (**) $P < 0.01$; (***) $P < 0.001$.

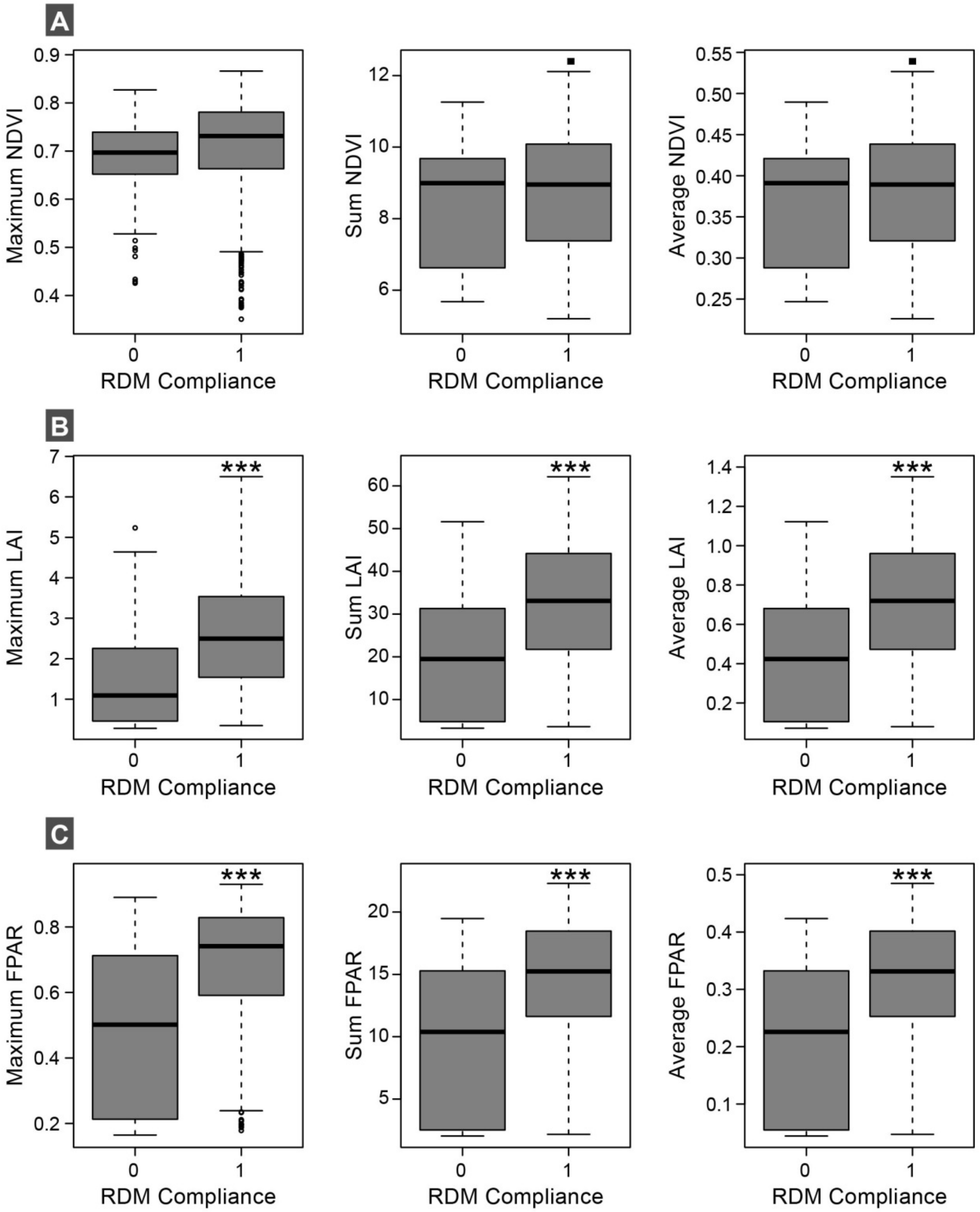


Figure 5. Difference in the mean of each VI in management units in RDM compliance compared to management units out of compliance, depending on habitat type, for the values of annual maximum, sum and average of : **A**. Normalized Difference Vegetation Index (NDVI),
B. Leaf Area Index (LAI) and **C.** Fraction of Photosynthetically Active Radiation (FPAR). Asterix above columns denote Tukey Honest Significant Differences: ( ) $P < 1$; (•) $P < 0.1$; (*) $P < 0.05$; (**) $P < 0.01$; (***) $P < 0.001$.

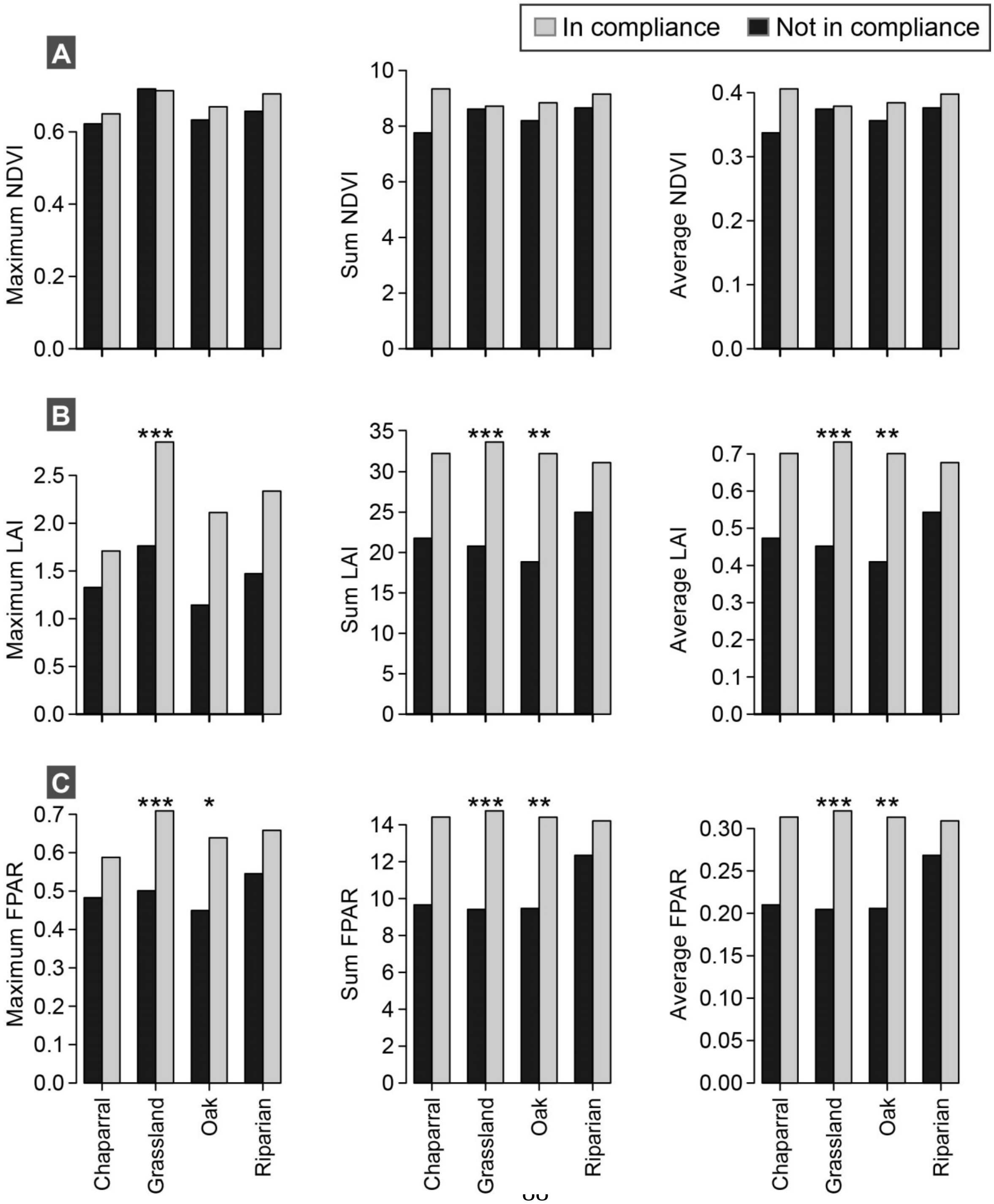


Figure 6. Comparing Leaf Area Index (LAI) time series for Simon Newman Ranch property-wide average in years with low (2007), medium (2004), and high (2008) RDM outcomes in the fall. Horizontal line marks LAI = 2.2, the threshold property-wide maximum LAI value for RDM in compliance.

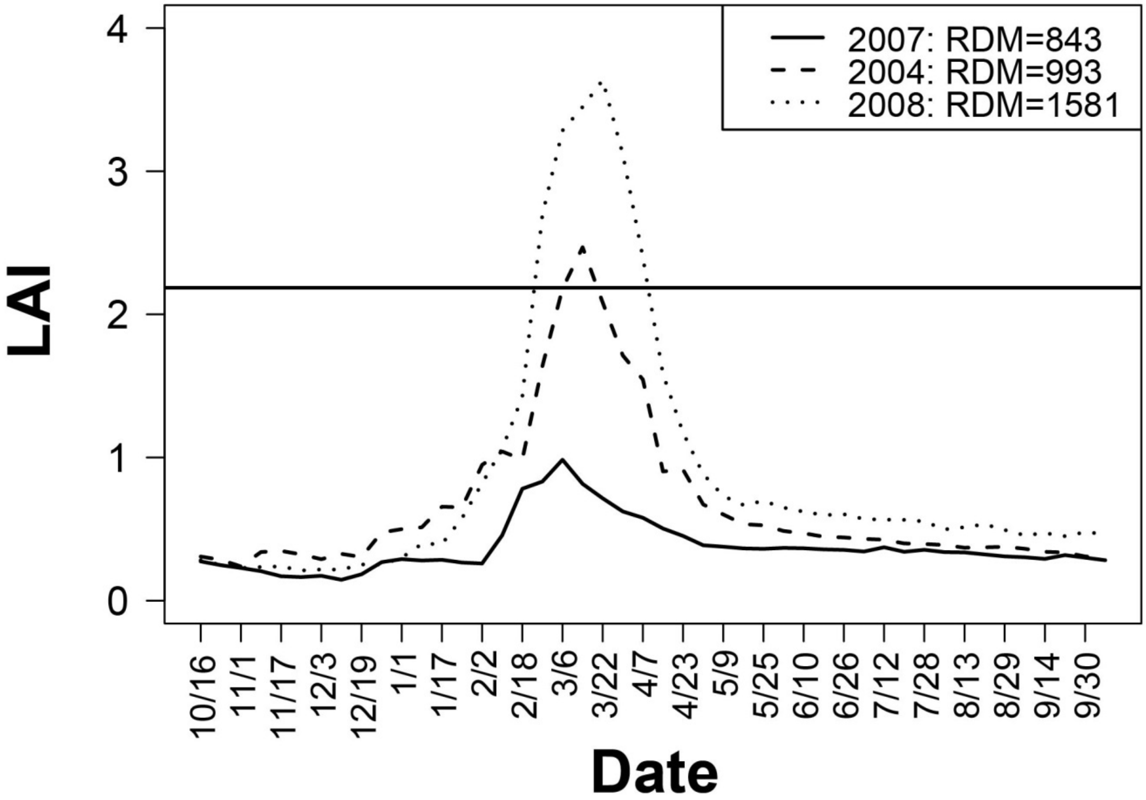
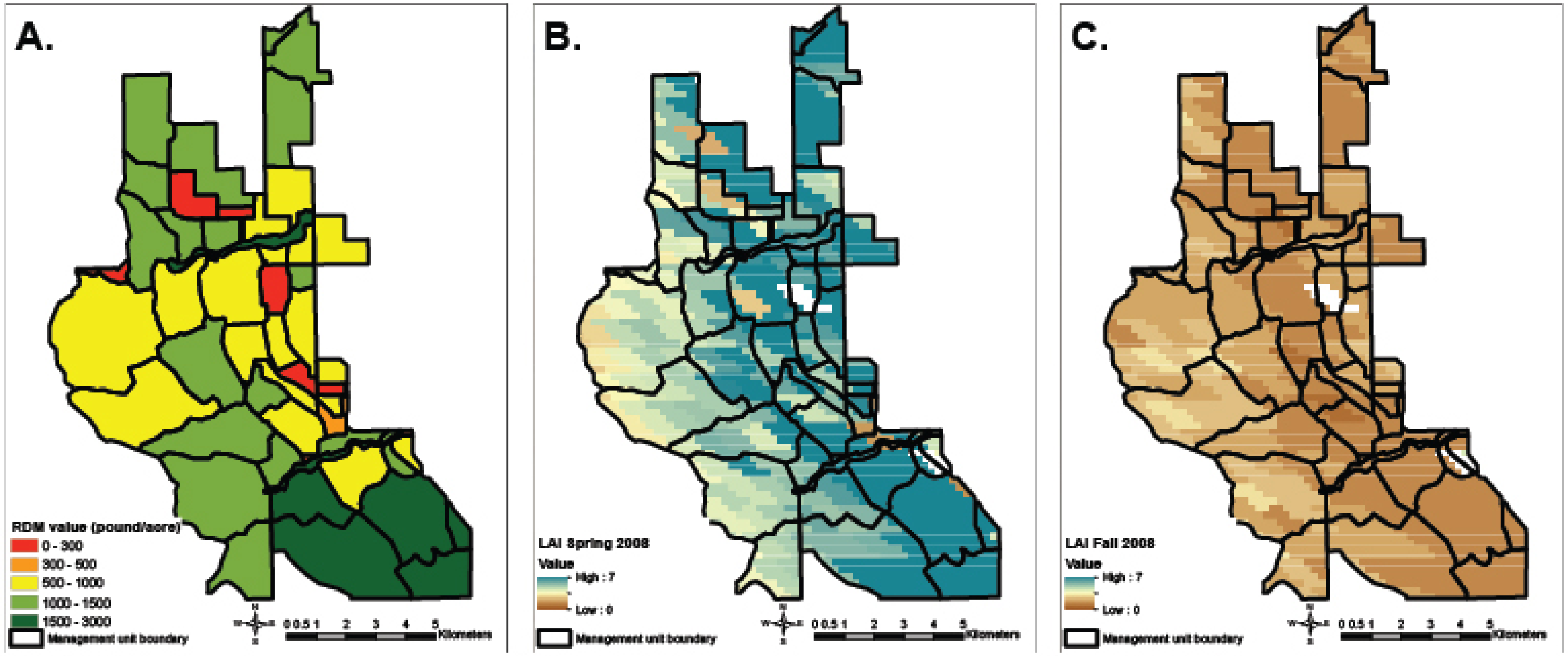


Figure 7. Results from the three step management model from Simon Newman Ranch. **A.** RDM values in each management unit of Simon Newman Ranch for fall 2008. **B.** Leaf Area Index (LAI) during March 2008. **C,** LAI during October 2008



Chapter 5. Discussion and conclusions

Conservation of the Earth's biodiversity is an immense challenge. Species extinction rates are mounting to compare with paleontological mass extinctions on a scale that the Planet has rarely seen before (Barnosky et al. 2011). At the same time, political and economic pressures for development around the world and massive changes in land use and climate are ever increasing. The conservation community is often left without adequate resources to face such incredible challenges. Therefore, for research results and methodologies to be applicable for biodiversity conservation it is important to use information that is accessible, easy to use, and freely available.

In this dissertation, I demonstrated the efficacy of geospatial tools such as geographic information systems (GIS) and remote sensing for characterizing, measuring and conserving rangeland ecosystems and the wildlife that depend on them. I focused on conducting research that could be applicable for conservation managers by using freely available data and developing tools than can be used broadly. Moreover, I conducted research on a broad spatial scale, spanning two continents. My research fits into the proposed framework of rangeland ecology I present in the beginning. This framework connects between four main components: landscape, climate, herbivores and human activity. First, I use geospatial tools to characterize the savanna landscape. Next, I use this information to understand how landscape information affects the movement of a large mammalian herbivore, the African elephant. Finally, I use geospatial tools to measure the effect of herbivory on rangeland productivity.

Key findings

The first chapter outlined the importance of rangelands and the threats these ecosystems face. I then reviewed the main challenges of measuring change process on rangelands and some of the remote sensing - based approaches that have been used to address these challenges. In the second chapter, I showed that time series analysis of MODIS vegetation indices can produce excellent results in predicting detailed field measurement of vegetation. Using three innovative approaches I improved the prediction of woody and herbaceous vegetation on the landscape, providing good measurements of vegetation cover, density, and biomass over large spatial extent. To that end, I first developed field methodology that combines visual estimation of vegetation cover and vegetation type together with accurate field measurements. This efficient and relatively rapid field methodology allowed me to gather a plethora of information over the extensive area of Etosha National Park. Second, by integrating time series of remote sensing data over six years and consolidating this information with partial least square regression, I achieved accurate models of vegetation measurements. Third, by using four different MODIS-based vegetation indices, each of which is based on different spectral information and algorithm, I was able to measure different vegetation forms – grasses, shrubs, and trees, and therefore provide valuable information for monitoring and conservation of Etosha's savanna vegetation. An exciting result from this chapter was the ability to transfer the use of the models through space, to other parts of the reserve, and through time, to other seasons and years. This emphasizes the validity of the predictive models I developed and enables the use of these models in other locations.

In the third chapter, I used the detailed vegetation maps I have created in chapter 2 for Etosha National Park to understand resource selection of African elephants. I showed how landscape parameters affect both the speed and the direction of elephants' movement. An interesting finding from this analysis was that elephants prefer to move into areas with higher grass and shrub biomass, but lower tree biomass. Moreover, elephants prefer to be closer to water sources and to roads. Furthermore, I showed that elephants' resource selection on the landscape is influenced by sex and age. Importantly, temporal variation significantly influences movement in response to the landscape: elephants choose different resources at different times of the day, which illustrates the behavior mechanism of their resource selection. Moreover, response to resources varied in different times of the year, results that highlights the ecological importance of these resources to the elephants. This chapter provides valuable information on how to manage resources in a manner that will promote the conservation of these magnificent animals.

In the fourth chapter, I used MODIS satellite data to monitor the effects of grazing on rangeland conservation easements in California. I used time series data of three vegetation indices to measure Residual Dry Matter (RDM). RDM levels are used by The Nature Conservancy and other land managers as a conservation easement compliance measure. I developed a rapid, easy to use, efficient and robust methodology to predict RDM in the fall using spring maximum and annual sum of vegetation index values. MODIS-based Leaf Area Index (LAI) is the best measure of dry grass biomass. Most importantly, I demonstrated that MODIS data can be efficiently used by range managers and conservationists to estimate RDM easement compliance.

Lessons learned: from science to conservation across scales

Common conclusions have emerged from all parts of my dissertation, regardless if the research focused on vegetation or wildlife, a national park in Namibia or a multiuse conservation easement in California. These can be summarized around four main themes: First, throughout the dissertation I emphasized the real-world biodiversity conservation application. Second, I demonstrated the utility of freely available satellite imagery and open source software for ecological research, monitoring and management. Third, in all parts of this work I developed spatial quantitative approaches to address ecological question. Fourth, I demonstrated the crucial importance of spatial and temporal scaled in determining research results.

Keeping an eye on the immense challenge of biodiversity protection, I intended for each of my research chapters to have a real-world conservation application. My methodologies for measuring rangeland vegetation and for quantifying the effects of grazing on productivity, can promote rangeland monitoring worldwide. The fast pace changes in rangeland ecosystems emphasize the need to monitor and understand the processes leading to these changes. Identifying locations at risk of degradation can promote restoration, replanting, or temporary fencing out grazers from sensitive areas.

My conclusions about the spatial and temporal use of resources by elephants can help protect these animals and their habitat. For example, I found that there are natural temporal cycle in waterhole use. This implies that elephant may be not the main cause for degradation around waterholes in Etosha. The relatively low use of areas with high tree density may indicate that the quality or species of trees in the park are not the ones elephants prefer, pushing them to rely more on grasses in their diet. The integration of detailed landscape information, the direction and speed of movement, and temporal variation in this research was useful to the understanding of wildlife resource selection and can be used as a valuable tool for wildlife conservation.

A second theme in this dissertation is the use of freely available satellites imagery and open source software to address ecological and conservation questions. I used vegetation indices from

MODIS, a platform that provides daily satellite data for the whole world. MODIS data it is freely available and easily accessed worldwide. A plethora of ecological knowledge that is invaluable for protecting natural systems can be extracted from MODIS data. Most of the analyses in this dissertation were performed using the open source software R (R Development Core Team 2007). R is incredibly powerful statistical analysis software with a rapidly growing users' community worldwide. Finally, the movement information used in this research will be shared through Movebank, a free online depository for animal tracking information (Wikelski and Kays 2011). Sharing movement data with the worldwide community promotes valuable insights into the ecology, distribution and resources utilizing of species across continents. Such online data sharing can serve as an important tool to promote the conservation of migrating and wide roaming species (Jeltsch et al. 2013).

The importance of using freely available tools in my work is twofold: first, it promotes the reproduction of my research methodologies across the world, allowing it to be implemented in U.S. or in developing countries in Africa, alike. Furthermore, the large community of users of freely available information allows this research to be part of a rapidly developing field of knowledge. Second, the use of free software and remote sensing data may promote the application of this research by conservation managers who have limited resources.

A third common theme in this work is the use of quantitative spatial ecology techniques. The use of such tools allowed me to integrate large amount of information from different sources: field data, GPS location, and satellite imagery to gain ecological insights. I used a combination of multivariate statistics techniques, including partial least square regression, logistical regression, generalized linear models, and stepwise model selection, together with spatial modeling techniques, such as variograms, kriging, and voronoi diagrams, to answer question on spatial distribution of plants and animals.

Finally, scale is a key element of landscape ecology (Turner 2001). Scale of analysis can significantly change research results and therefore needs to be appropriate for the research question. Remote sensing technologies such as the ones used in this research, satellite imagery and GPS telemetry, allow us to remove ourselves, literally speaking, from the object of observation. I believe that this removal promotes our ability to explore scales that are beyond what is intuitive to us as limited human observers. By looking remotely on the wider picture, it is easier to overcome the bias of our own perceptions and find the scale that is appropriate for the process at hand. I show how integration across temporal scales (from hourly to multiannual) while moving between spatial scales (from small field plots to thousands of square kilometers), can affect the results and the conclusions about the system.

The effect of scale was demonstrated in each of the research chapters. In Chapter 2, I showed how moving across temporal scales, improves the predictions of field vegetation measurements. Integrating information across time allows us to include the temporal variation of vegetation phenology as well as the inter-annual variation, caused by fluctuating climate conditions. Moreover, I showed that the increase in the temporal scale enables measurement of vegetation in increasing spatial scale; not only I successfully measure vegetation over the extensive area (23,000 km^2) of Etosha, but I could transfer the use this methodology from one location to the other. In Chapter 3, I emphasized the importance of matching the temporal scale of movement analysis to the spatial resolution of underlying landscape information. Additionally, it is crucial to adapt the scale of observation to be relevant to the elephants' behavior. Elephants migrate over large distances and can cover huge plains in search of new grounds (Sukumar 2003, Viljoen and Bothma 1990, Thouless 1995). However, I found that the elephants I sampled walk as little as

10m/hr and moved on average only 0.5 km/hr. Importantly, I found that the temporal scale of analysis, defined here as the time intervals between consecutive GPS locations, can have significant impact on the results. In Chapter 4, spatial scale affected also the model results; RDM predictions for the whole Simon Newman property were different than model prediction for individual management units within the ranch. Similarly to the first chapter, transition to a smaller spatial scale demanded integration over larger temporal scales. RDM prediction improved significantly when integrating multivariate temporal satellite data. In summary, my dissertation showed that research across variety of scales not only influences research conclusions but serves as a tool to gain valuable knowledge and further insight about how the system works.

Future research

Few research directions that I intend to address in future research are emerging from the results of this dissertation. First, I would explore what additional insight can be gained about the questions addressed in this research by integrating additional spatial scales of analysis. To further improve the characterization of Etosha vegetation the field information I collected can be correlated with remote sensing at finer resolution, for example, Landsat (30 m), SPOT (10-15 m), and Quickbird (0.6 m). Integrating data from these scales may address the spatial variability in savanna landscape by identifying vegetation patches and communities. Additionally, combining MODIS with imagery in finer resolution could improve the measurement of vegetation temporal variability, in terms of phenological variations and long term changes. Further, I would explore the effect of different spatial scales on elephant movement, as a supplement to my research on the influence of temporal scale on elephants' resources selection. Finer spatial scales can provide more details about the underlying vegetation and identify elephants' feeding patches.

In Chapter 3 I have explored one element of the movement ecology framework (Nathan et al. 2008) to explain elephants' movement: external factors of landscape variable and temporal variation. Incorporation the other components of the framework: internal state of the animal, memory, navigation skills, and movement capacity, may improve the understanding of elephant movement paths. To examine the effect of internal state of the animal, such as hunger and thirst, landscape variables at the previous locations of the animal can be integrated with landscape variables at its future step. For example, time since last drinking can be uses as a proxy for thirst to understand future movement towards water. Likewise, the time past since the elephant was last located in a feeding patch can serve as a proxy for hunger.

The interaction between ungulates and the landscape of Etosha can be examined on a community level by understanding the movement patterns of other prevalent ungulate species in Etosha. Using the step section function, we can compare the resource selection of ungulate species with different feeding ecology: grazers, (e.g. plains zebra (*Equus quagga*), Gemsbok (*Oryx gazella*), and blue wildebeest (*Connochaetes taurinus*)), mixed feeder (e.g. springbok (*Antidorcas marsupialis*)), and browsers (e.g. Greater kudu (*Tragelaphus strepsiceros*) and giraffe (*Giraffa camelopardalis*)). The feeding guild of a species determines the resources the animal is using and therefore affects how its movement patterns are related to the landscape. Moreover, feeding ecology influences dependency on water, and therefore affects the degree to which surface water determines the animal's movement patterns.

The effect of herbivores on natural ecosystems can measured using similar techniques I used in Chapter 4. Better understanding of ungulate movement patterns in Etosha, can be used to analyze how these patters affect vegetation degradation in the short and long terms. Satellite imagery with fine temporal resolution (e.g. MODIS) can be used to examine effect of grazing in the short term. For example, how grass biomass varies as a result of zebra and springbok move through the landscape. Time series of Landsat data can be used to understand effects of grazing in the long term. For example, monitor degradation around waterholes and other centers of ungulates concentrations in Etosha.

My research was a part of a larger research project on the ecology of Anthrax in Etosha (PI Wayne Getz), which is trying to understand the seasonality and the spatial distribution of the disease. Anthrax is caused by the bacterium *Bacillus anthracis* and reoccurs seasonally in Etosha. Anthrax is endemic to Etosha and kills ungulates in the reserve annually, mainly elephants, springbok, and zebra (Turner et al. 2013)ROR. Anthrax occurrences can be better understood using the movement patterns of the main host species. The landscape parameters at the anthrax carcass sites can be related to the landscape variables preferred by the host. Furthermore, the seasonality of the disease outbreaks can be explained by the seasonality of resource selected by the host species.

Finally, I have been interested for long time to understand how movement patterns of individual animals are related to population distribution. Few considerations need to be taken into account when integrating across these scales. While all individuals of a species have generally similar habitat preference, there is variability in resource selection within a population (Hawkes 2009). Moreover, as noted above, shifting the hierarchy of analysis may change the functional shape of the response. Therefore, it is important to examine to what extent individual movement patterns can be extrapolated to predict the distribution of the whole population. Furthermore, both aerial/road census data and telemetry data are used to create distribution models for wildlife. However, the resulting models from these two sources have rarely been compared. We can compare the results of census dataset versus GPS locations data by modeling these two data sets and comparing the resulting preference of landscape variables. Those two datasets can be analyzed using step selection function, resources selection function, and distribution modeling techniques (Mexent, Generalized Additive Models) and comparing resulting resource preference and the ungulate spatial distribution.

Final notes

Throughout this dissertation I aimed to conduct interdisciplinary research, drawing on combination of few fields: landscape ecology, wildlife ecology, movement ecology, and remote sensing science. Likewise, I used a wide variety of research tools, including extensive fields work, remote sensing analysis, spatial research and statistical analysis. The most important factor that assisted me along the way was collaboration with researchers from diverse disciplines. I was lucky to have two highly interdisciplinary advisors – Professor Wayne Getz, who is a mathematical ecologist, disease ecologist and a modeler, and Professor Maggi Kelly, who is a landscape ecologist, geographer and a remote sensing scientist. Each of them provided unique point of views and expertise which allowed me to develop new ideas and learn new analytical approaches. Collaboration with other professors on the Berkeley campus and working together with graduate students in my department further enhanced my work. Additionally, I discovered the importance of collaborating with conservation practitioners. I have gained much insight and knowledge working with researchers at the Etosha Ecological Institute and with the Etosha wardens, who have years of experience in the field. Likewise, working with The Nature Conservancy enhanced my understanding of how conservation practice works. Working with these organizations allowed me to understand some of the real-world needs of conservation work. Thanks to them my research was more applicable, more relevant for problem solving, and more satisfying. Our world faces grave environmental challenges. Interdisciplinary approach and collaboration between academia and conservation practitioners are key for relevant and applicable science.

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