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Research on Texas savannas: fractional woody cover mapping, potential woody cover modelling, and woody plant encroachment analysis

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by

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Dedication

To my motherland of the People's Republic of China.

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With the end of this dissertation, I am finishing up my six-year PhD life. It was a magical journey of exploring uncharted territory in geography. It was a wonderful journey of experiencing different custom, culture, and tradition in a new country. It was a tortuous journey of self-challenging in a new life stage.

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Research on Texas savannas: fractional woody cover mapping, potential woody cover modelling, and woody plant encroachment analysis

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Tested in Texas savannas of a wide rainfall gradient, this dissertation endeavors to (1) map fractional woody cover at Landsat scale, for close and continuous woody plant encroachment monitoring, (2) model the pattern of potential woody cover over the present rainfall gradient, for implication of the end-point of woody plant encroachment, (3) analyze the rate and effect factors of woody plant encroachment under the regional context, for pertinent savanna management strategy.

Web-Enabled Landsat Data (WELD) was used to calibrate the Salford Systems' Classification and Regression Trees (CART) against training data of fractional woody cover derived from 1m resolution digital orthophotos. The CART model output was verified against an independent test data. This study provides a way to accurately monitor woody plant encroachment across savanna ecosystems at a fine spatial scale, and sets up a protocol for landscape components mapping at sub-pixel level in other ecosystems.

The pattern of potential woody cover was modelled over the wide rainfall gradient at Landsat scale (30m) and MODIS scale (500m) respectively. While a positive linear relationship between potential woody cover and mean annual precipitation (MAP) was revealed at Landsat scale, a prominent three-segment relationship was observed at MODIS scale. This discrepancy corroborates the scale dependency of the primary determinants of savanna woody plant density. According to the three-segment pattern at MODIS scale, Texas savannas are divided into arid savanna (MAP < 600mm), semi-arid savanna (600mm < MAP < 735mm), and mesic savanna (MAP > 735mm).

Analysis of the encroachment of Ashe juniper at its early life stage (initial ~20 years) at local (hectare) scale suggests that water availability has a significant positive effect on the encroachment rate in semi-arid savanna, but not in mesic savanna. In addition, a quadratic relationship was revealed between the encroachment rate and woody plant density in mesic savanna. That is, the encroachment rate increases with woody plant density by a threshold density, then starts decreasing with woody plant density. These results demonstrate that regional context such as rainfall and biological traits of woody species are critical to understand the trend of woody plant encroachment.

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Chapter 1: Introduction

Research motivation

Importance of savanna ecosystems

Savannas ecosystems are characterized by the coexistence of woody and herbaceous vegetation, as well as distinct dry season (Scholes & Archer, 1997). They exist across a wide range of conditions in terms of precipitation, soil nutrient content, fire regime and herbivory level, covering 33 million km^2 (approximately 20%) of the earth's terrestrial surface (Ramankutty & Foley, 1999). Mainly found in tropics and subtropics, savannas are home to a large proportion of human population, livestock and wildlife of the world. Moreover, savanna ecosystems play an important role in global land-atmosphere energy balance, biodiversity, as well as in carbon, nutrient, and water cycles (Scholes, 1993; Lal, 2004; Solbrig et al., 2013). The balance between woody and herbaceous vegetation in savanna ecosystems is critical to their structure and function (Sankaran et al., 2005; Mazía et al., 2016).

Problems facing savanna ecosystems

Woody plant encroachment – the directional increase of woody plants in biomass, density, and cover at the expense of herbaceous vegetation in grassland and savanna communities – has been observed in many parts of the world, such as Southern United States (Hobbs & Mooney, 1986; Archer, 1995; Creamer et al., 2013), South America

(Cabral et al., 2003; Anadón et al., 2014), Australia (Fensham et al., 2005), and Africa (Van Vegten, 1984; Mitchard et al., 2011; Coetsee et al., 2013). In most cases, the encroachment was found to adversely affect the ecological and economic function of the savanna ecosystems (Blaser et al., 2014). For instance, soil moisture and nutrient content, microclimate conditions, herbaceous vegetation productivity, and species diversity are all vulnerable to the encroachment process (Pressland, 1973; Stuart-Hill & Tainton, 1989; Alofs & Fowler, 2013). Both the scientific community and stakeholders such as residents, ranchers, and governments / NGOs are concerned about this phenomenon, especially in consideration of future changing climate and land use that are anticipated to worsen the scenario (Sala et al., 2000; House et al., 2003; Stocker, 2014). Accurate monitoring of woody plant encroachment and thorough understanding of the underlying mechanism of this phenomenon is in need for savanna management and restoration.

Existing research on savanna ecosystems

Different types of models have been put forward to conceptualize the dynamics of savanna ecosystems, including the traditional succession models and state-and-transition models (Fowler & Simmons, 2009). The state-and-transition models are more widely used and assume two or more alternate reversible stable states such as savanna, woodland and grassland communities (Laycock, 1991; Allen-Diaz & Bartolome, 1998). In contrast, succession models are focused on transient dynamics and suppose that savanna ecosystems experience an ordered series of states chronologically without direct human manipulation.

Numerous factors were found to affect savanna structure and function (Scholes, 1993). However, climate (e.g. precipitation), soil type (e.g. texture, nutrient content), fire regime and herbivory level are recognized as ‘key determinants’ (Walker, 1987; Skarpe, 1991), while all the other factors are related to these four key determinants and work through them (Frost et al., 1986; House et al., 2003; Sankaran et al., 2008). Tree-grass balance change in savanna ecosystems such as woody plant encroachment is regarded as response to the changes in those key determinants (Roberts, 1987; Stevens et al., 2017).

Precipitation is widely believed to be the fundamental factor of savanna distribution and function, determining the potential woody cover (maximum realizable woody cover) at any given place (Scholes & Walker, 1993; Sankaran et al., 2005). Given that the dry season length influences savanna dynamics a lot, the temporal variation of precipitation can also have strong implication for sustainable management and/or ecological restoration (Holmgren & Scheffer, 2001; Sankaran & Anderson, 2009).

Soil texture is important for savanna structure and function in that it can affect plant available water and nutrient retention (Frost et al., 1986; Scholes & Archer; 1997). Co-varying with texture, soil nutrient availability can influence vegetation quantity and quality, and consequently influence the levels of herbivory the savannas can support. Since the two contrasting life forms of woody and herbaceous vegetation have different preferences toward nutrients, different levels of nutrients may affect the competitive abilities between them. For example, areas with high levels of nitrogen availability would favor grasses over woody plants (Davis et al., 2000; Kraaij & Ward; 2006).

Fire usually occurs in the dry season and can eliminate any plant biomass under appropriate conditions. Due to the vulnerability of both tree seedlings and saplings to fires of even low frequency or low intensity, fires usually result in reduced woody cover. However, for a given system, the historical fire regime together with the fire tolerance of woody plants and their resprouting abilities constrain the elimination effect of fires (Heisler et al., 2004; Briggs et al., 2002). Fires can also change the level of nutrients such as nitrogen, carbon, sulfur, and even phosphorus and potassium to some degree through volatilization (Frost & Robertson, 1987).

Herbivory can remove above ground plant biomass like fires. But compared to the role of “generalist herbivore” of fires in savannas (Bond & Keeley, 2005), herbivory can be more selective. Different herbivores have different preferences over plant functional types. Moreover, each individual may select different plant species and different plant tissues (Augustine & McNaughton, 1998). As for the timing of herbivory, it differs among native ungulates and domestic livestock. The intensity of ungulates herbivory synchronizes with plant growth rate and nutrient concentration, while domestic livestock show less variability in time and space for plant consumption (McNaughton, 1990). Besides elimination, herbivory can affect soil fertility through their effects on nutrient cycling and decomposition (McNaughton, 1988; McNaughton et al., 1997).

While not mutually exclusive, fire and herbivory interact with each other a lot (Hobbs et al., 1991; Hobbs, 1996). Reduction of fuel load by herbivory would lead to the change of fire frequency, intensity and extent (Frost & Robertson, 1987; McNaughton, 1992; Hobbs, 1996). On the other side, the fires can affect the supporting capability of savannas for different-sized herbivores through their effects on the available amount and quality of forage (Wilsey, 1996). The combination of fire and herbivory can have a huge impact on the evolution of savannas. For example, the current status of African savannas is considered largely the result of historical effects of fire and herbivory on morphological and physiological characteristics of savanna plants (Stebbins, 1981; Coughenour, 1985; Bond & van Wilgen, 1996).

In terms of the coexistence of woody and herbaceous components as well as their relative proportion in savanna ecosystems, a variety of theories have been proposed to understand it, including competition for water and nutrients (Walter, 1971; Walker et al., 1981, 1982), disturbances by fire and herbivory (Scholes & Archer, 1997; Jeltsch et al., 2000; van Langevelde et al., 2003), and demographic bottlenecks to tree recruitment (Higgins et al., 2000; Jeltsch et al., 2000). However, both supporting and negating evidence exists for each alternative mechanism and none of them is generalizable across all types of savannas (Sankaran et al., 2005; Meyer et al., 2009; Kulmatiski & Beard, 2013; Zeeman et al., 2014; Su et al., 2015).

Specifically, these theories conflict with each other on the relative importance of different factors (House et al., 2003; Sankaran et al., 2004). For instance, the competition-based approaches are centered on tree-grass competitive balance in soil moisture and nutrient and ignore the effect of life stages. The demographic bottleneck models focus on tree recruitment and growth, taking into account disturbances, climatic variability, and life stages (Sankaran et al., 2004). These discrepancies are largely due to that the existing theories usually arise from small-scale and site-specific studies that focus on certain environmental factors and processes, which are important under a given condition but may not occur across all sites, gradients, or expanses (House et al., 2003).

Later, Wiegand et al. (2006) and Meyer et al. (2009) tried to unify these existing theories and proposed to understand the coexistence and relative abundance of woody and herbaceous components with patch dynamics perspective, which was initially applied to other plant communities (Watt, 1947). Under this perspective, savannas are consisted of a spatial mosaic of patches that experience the same cyclical succession between grassy and woody dominance, driven by environmental factors such as fire and overlapping rainfall. However, both positive and negative evidence were found for the patch dynamics perspective (Meyer et al., 2009).

However, none of these existing theories is capable of explaining woody plant encroachment across all types of savannas. With regard to the wide range of geographic occurrence and diversity of bioclimatic conditions of savanna ecosystems, one possible explanation for the particularization of and conflict among the existing theories is that the role of different factors and processes in the structure and function of savanna ecosystems varies across different types of savannas (e.g., arid, semi-arid, and mesic) (Sankaran et al., 2005). Given so, a comprehensive study over broad environmental gradients is necessary for an improved understanding of the dynamics of savanna ecosystems.

Texas savannas

Texas savannas are located on the ecological region of Edwards Plateau in central Texas (Figure 1.1), featured by a wide rainfall gradient of west-east direction (Figure 1.2). They experienced high spatial and temporal heterogeneity in resource availability and disturbance regimes, and several decades of previous encroachment (Wilcox & Huang, 2010; Alofs & Fowler, 2013). As such they provide a 'natural laboratory' for a comprehensive study of woody plant encroachment, which will complement the Southern Hemisphere-heavy literature (Meyer et al., 2009; Yessoufou et al., 2013; Zeeman et al., 2014). The study area in Figure 1.1 is displayed with Landsat GeoCover Mosaics of 2000, under band combination of 7, 4 and 2 for a natural-like rendition.

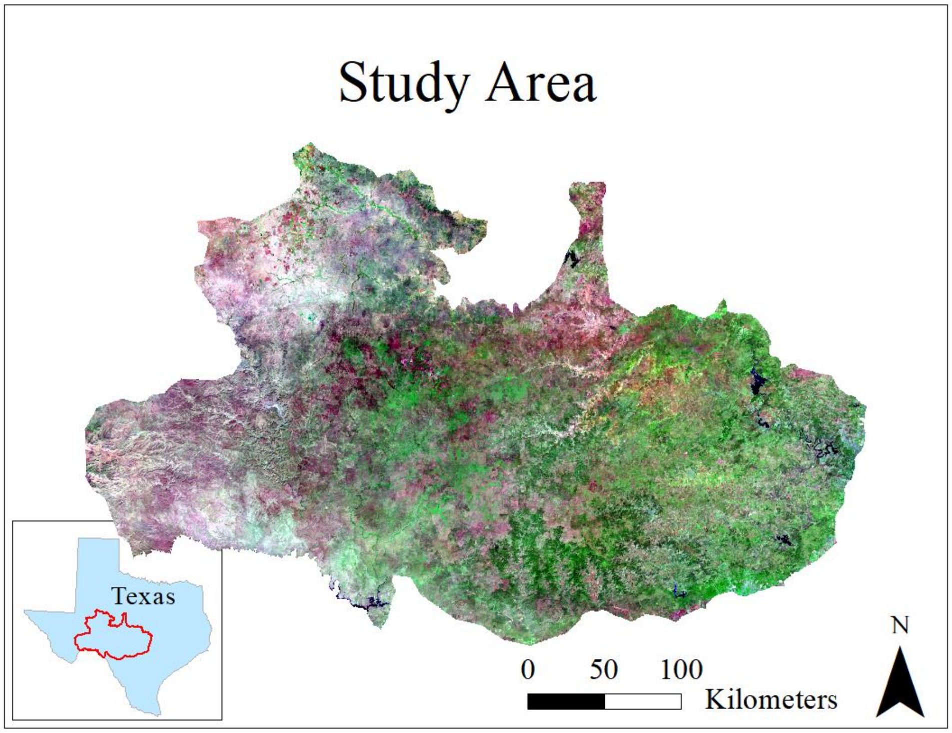


Figure 1.1: The study area of Texas savannas in central Texas.

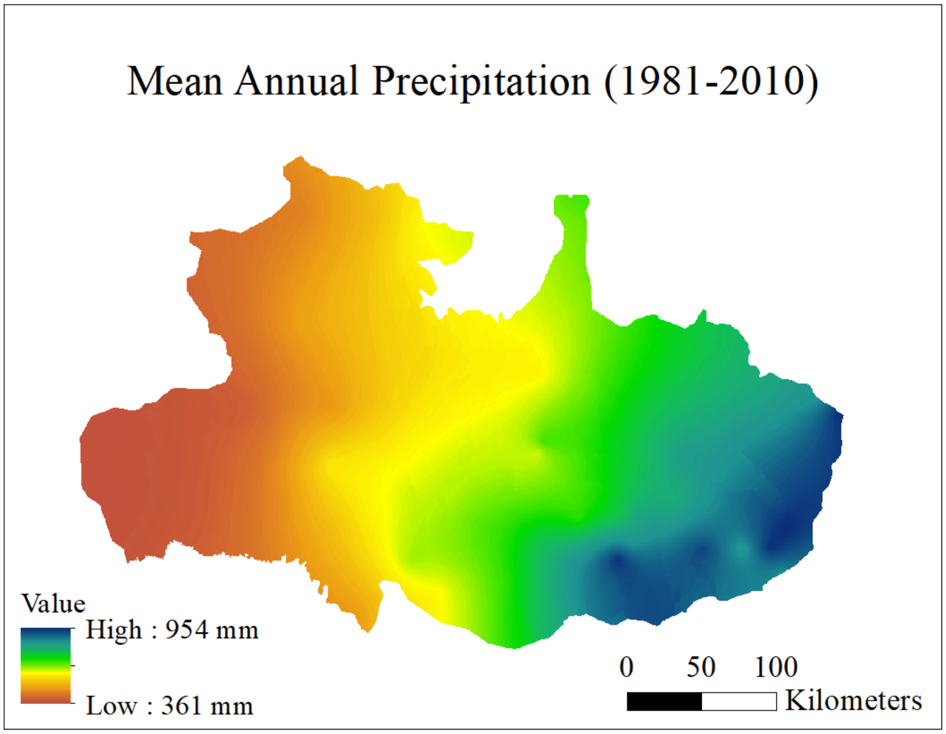


Figure 1.2: The rainfall gradient in Texas savannas.

The underlying formations of the Edwards Plateau in central Texas are mainly hard early Cretaceous limestone and relatively flat (Schmid, 1969). The flat plateaus in the eastern part are now separated by slopes of different degrees caused by deep erosion. Due the origin of limestone, soil in this region is generally shallow (less than 10 inches) and rich in clay content, which is not suitable for farming (Fuhlendorf et al., 1996; Fowler & Simmons, 2009). Prior to European contact, most region of the plateau was probably a kind of open landscape, mainly consisting of thickets of live oak and shinoak, as well as honey mesquite (Thurow et al., 1986). Valleys, slopes and shallow soils were dominated by a large variety of grasses such as little bluestem, sideoats grama and cane bluestem. A diverse mixture of woody shrubs including Texas mulberry, plum and littleleaf leadtree was also popular across this area (Taylor, 2008). Plant grows fast from late spring till early summer and later the growth would be limited by hot dry weather. Early fall moisture would then initiate a secondary plant growth (Brown & Archer, 1989).

The climate of the Edwards Plateau ranges from mesothermal to subhumid and semiarid (Toomey et al., 1993). Mean annual precipitation varies a lot across the plateau, ranging from more than 95 cm on the eastern margin to about 36 cm in the west. There are usually two rainfall peaks. While the general one associated with frontal activity happens between middle April and middle June, the second peak associated with the Mexico Gulf storms occurs between August and October. However, this area has larger potential evapotranspiration than precipitation for every month, resulting in drought in the plateau (Rodríguez-Iturbe al., 1999).

This area was maintained as grassland before the European settlement in the mid-1800s, mainly by grazing (bison and antelope) and frequent fires (natural and man-made) (Taylor & Smeins, 1994). From the middle 1800s to late 1800s, a lot of German emigrants and American people moved from Europe or humid farming areas to the semiarid plateau and settled there. Along with the settlement was the introduction of large population of domestic livestock (e.g. cows, sheep, goats, and horses), as well as ranching industry (Fowler & Simmons, 2009). Sometimes people prescribed fire for fuel load. However, after a lot of negative experiences with fire for ranching industry, people started suppressing fires rather than prescribe fire. Different suppression techniques were implemented such as ‘fire guard’ and ‘beef drag’ (Haley, 1929). Later, Texans even legislated for fire suppression. The first law in 1848 stated that making fire in public prairies between July 1 and February 15 was illegal. A second law for fire suppression was passed by the Texas legislature in 1884, according to which people would receive a felony if they set fire to grass (Haley, 1929). Wildfires were further reduced to a minimum by field management, roads building, overgrazing and so on.

Along with livestock introduction, fire suppression exhibited huge ecological impact on the plateau. It provided opportunity for survival and establishment of woody plants and initiated the transition from grassland to savanna during the past 150 years (González, 2010). Due to the selective eating habits of livestock and wildlife, the plateau was left with poor quality woody and herbaceous vegetation. The expansion of Ashe juniper and honey mesquite accounted much of the woody plant encroachment and greatly reduced species diversity in this area (Archer et al., 1995; Van Auken, 2009).

Nowadays, most part of the Edwards Plateau is occupied by live oak (Quercus virginiana)-Ashe juniper (Juniperus asheii) savannas, interspersed by perennial and mixed C3/C4 grasslands (Archer, 1989; Taylor, 2008; Alofs & Fowler, 2010). LIDAR measurements suggest that 48% of the plateau was covered by woody plants by 2006 (Litvak et al., 2011).

Research objective

The **first objective** of this dissertation research is to map the fractional woody cover of Texas savannas at Landsat scale (30m) to assess the coverage and distribution of woody plants, as a first step toward woody plant encroachment modelling. Compared to the traditional discrete classification, continuous fields (fractional coverage) of landscape components are more accurate and have greater potential in land cover change study (Hansen & DeFries, 2003). Moreover, many land cover change and human cultivation occur at small spatial scale, calling for fine spatial scale fractional woody cover product (Townshend and Justice, 1988).

The **second objective** of this research is to model the pattern of potential woody cover (*maximum realizable woody cover that a given site can support*) over the present rainfall gradient in Texas savannas, at Landsat and MODIS scales respectively. Potential woody cover has strong implication on the dynamics of savanna ecosystems and particularly on the end-point of woody plant encroachment. If potential woody cover is well below canopy closure, the encroachment will be a bounded process. Otherwise, savannas could switch to a wooded state as a result of the encroachment, and disturbances such as fire and herbivory would be necessary to maintain the coexistence of woody and herbaceous vegetation (Sankaran et al., 2005). In addition, the multi-scale analysis of potential woody cover would shed light on the scale dependency of the primary determinants of woody plant density in savanna ecosystems (Gillson, 2004).

The **third objective** of this research is to quantitatively analyze the rate and effect factors of woody plant encroachment over broad environmental gradients. It took Ashe juniper in Texas savannas as a case study. While fire, herbivory, and soil type were found to have very minimal effect on Ashe juniper encroachment under the regional context (Roques et al., 2001; Fowler & Simmons 2009; Lyons et al., 2009), the role of mean annual precipitation (MAP) and woody plant density was explored. This study was conducted at local (hectare) scale and over decadal time frame, appropriate for understanding woody plant encroachment (Roques et al. 2001). Conclusion from this woody species-specific and observation scale-specific study will provide more pertinent strategy on Texas savannas management.

Dissertation structure

This dissertation research endeavors to set up protocols to closely monitor woody plant encroachment at a fine spatial scale in savanna ecosystems and understand the underlying mechanism of this phenomenon. It was tested in Texas savannas of a wide rainfall gradient. This dissertation is organized into six chapters. Chapter 1 describes the motivation and research objectives. Chapters 2 to 5 are in the form of research articles, either published or under review by peer-reviewed scientific journals. Among them, chapter 2 presents a protocol for woody cover mapping at sub-pixel level in savanna ecosystems, by remote sensing imagery of medium to coarse spatial resolution. Chapter 3 and chapter 4 are focused on the pattern of potential woody cover over rainfall gradient. While chapter 3 models the pattern of potential woody cover with MODIS tree cover product (MOD44B, 250m), chapter 4 performs the same analysis at Landsat scale (30m) and MODIS scale (500m) with 1m resolution digital orthophotos. Chapter 5 analyzes the encroachment rate of Ashe juniper at its early life stage (initial ~20 years) at local (hectare) scale, as well as the role of mean annual precipitation and woody plant density in the encroachment process. Chapter 6 summarizes the contribution of this dissertation research to the scientific literature and outlines future research direction.

Chapter 2: Fractional woody cover mapping of Texas savannas at Landsat scale

Abstract

Woody cover - the vertical projection of trees, shrubs and bushes - plays an important role in the structure and function of savanna ecosystems, and is in need of increased research and application. Problems facing savanna ecosystems such as woody plant encroachment and resultant reduced species diversity further underscore the relevance of regional and even larger scale woody cover mapping. This need is particularly illustrated in Texas savannas, where substantial increase of woody plants has been observed during the past several decades. The objective of this study is to map the fractional woody cover of Texas savannas at Landsat TM / ETM scale (30m) as a first step toward improved woody plant encroachment modelling and monitoring. Compared to traditional discrete classification scheme, continuous fields of landscape components are more accurate and robust. The annual product of Web-Enabled Landsat Data (WELD) of 2012 was used as predictor for fractional woody cover mapping. Specifically, top of atmosphere (TOA) reflectance and thermal band and their derivatives were utilized. Training data over the whole range of fractional woody cover at Landsat scale was derived from thirty 1m resolution Digital Orthophoto Quarter Quads (DOQQs) of 2012, randomly distributed across the study area. Salford Systems' CART (Classification and Regression Trees) was applied and created nine regression trees. Each regression tree was grown out of a random 60% portion of the training data, with replacement for each other. For each pixel, the median value out of the nine regression trees was taken as the final fractional woody cover. The robust results proved by accuracy assessment suggest continued exploration into this approach can contribute to best practices of landscape components mapping in savanna and other ecosystems.

Key words: fractional woody cover, Texas, savanna, WELD, CART, Landsat TM

Introduction

Woody plant cover – the area covered by trees, shrubs and bushes - plays an important role in terrestrial ecosystem services such as energy and water exchanges, carbon and nutrient cycles, and primary production (DeFries et al., 1997). Particularly in savanna ecosystems, woody plant cover has a profound effect on the ecosystems' structure and function, like livestock production and species diversity (Sankaran et al., 2005; Hill & Hanan, 2010). Large scale woody plant cover assessment is in need of research and application (Sankaran et al., 2008; Hanan et al., 2014; Yang et al., 2016), such as monitoring and modelling of woody plant encroachment observed worldwide in savanna ecosystems (Archer et al., 1995; Bucini & Hanan, 2007; Alofs & Fowler, 2013).

The increasing availability of remote sensing data provides an opportunity to map woody plant cover over large areas. Traditionally, land cover mapping was based on discrete classification scheme that assigns each pixel a specific land cover type. As an alternative, continuous fields of landscape components estimate fractional coverage of landscape components in each pixel (DeFries et al., 1995). The improvement of this methodology lies in more accurate depiction of the heterogeneity of complex landscapes.

Moreover, successive fractional mapping of landscape components enables detection and measurement of minimal land cover change at sub-pixel level (Hansen et al., 2003), critical for savanna landscapes that are mixed by woody plant, herbaceous vegetation, and bare ground.

With regard to fractional woody cover mapping, there have been many efforts at regional and global scales (DeFries et al., 2000; Hansen et al., 2002, 2011; Brandt et al., 2016). MODIS and Landsat vegetation continuous fields (MODIS VCF and Landsat VCF) of tree cover have been available globally and benefited related research and application communities (DiMiceli et al., 2011; Sexton et al., 2013). However, the reliability of these products may be contested when derivation of training data draws from discrete land cover classification system (e.g., woodland, grassland) (DeFries et al., 2000). Moreover -- and problematic in areas with shorter woody plants -- their training data only account for woody plants above 5m height (Hansen et al., 2002; Sexton et al., 2013), further weakening their efficiency in savanna areas where many short woody plants exist. These limitations have also been reported in other similar studies (DeFries et al., 2000; Hansen et al., 2011) and noted as potentially limiting practicability for savanna ecosystems where short woody vegetation is the most typical morphology.

Issues facing savanna ecosystems such as woody plant encroachment and reduced species diversity underscore the relevance of regional or even larger scale woody plant mapping for savanna ecosystems (Ratajczak et al., 2012; Alofs and Fowler, 2013). However, efforts targeted savanna ecosystems have been rarely seen. Urbazaev et al.

(2015) mapped fractional woody cover of semi-arid savannas in southern Africa utilizing L-band SAR data. Brandt et al. (2016) estimated fractional woody cover of the drylands of Sahel area in Africa at 1 km scale based on vegetation phenology. This research aims to create a continuous field of woody plant cover at a much finer spatial resolution (30m) across different types of savannas (arid, semi-arid, and mesic savannas), utilizing optical remote sensing data. To overcome the aforementioned weaknesses of the existing products, training data was derived from 1m resolution Digital Orthophoto Quarter Quads (DOQQs), which are detailed enough to distinguish woody plants of various heights.

High spatial resolution imagery such as those capable of recognizing individual woody plants is favorable for woody cover mapping (Rasmussen et al., 2011). But the small extent, low temporal frequency, and vulnerability to cloud contamination limit their potential application in regional or even larger scale woody cover mapping. Instead, moderate- to coarse-spatial resolution data featured by high coverage and temporal frequency would be more appropriate for large scale woody cover mapping. While the higher coverage reduces the data volume at a regional or global scale, the high temporal frequency is able to offset the effect of cloud contamination (Hansen et al., 2005).

Currently, most continuous tree cover products have been generated at MODIS or even coarser spatial resolution such as AVHRR (DeFries et al., 2000; Schwarz and Zimmermann et al., 2005; Heiskanen and Kivinen, 2008; DiMiceli et al., 2011). However, many land cover changes including human cultivation and woody plant encroachment occur and are only observable at a much smaller spatial scale than that of

MODIS, calling for finer scale products for land cover change studies (Townshend and Justice, 1988). The availability of the spatially mosaicked and temporally composited Web-Enabled Landsat Data (WELD) provides a channel for fractional woody cover mapping over a large area at a fine resolution of 30m (Roy et al., 2010).

Background

Inputs and modelling methods are the two key components in remote sensing fractional woody cover mapping. Inputs used include single-date images (Schwarz et al., 2004; Schwarz & Zimmermann, 2005), composited data such as monthly maximum near-infrared values (DeFries et al., 1997; Hansen et al., 2003; Brandt et al., 2016), and annual multi-temporal metrics or indices (e.g. mean annual NDVI) derived from time series remote sensing data, especially from moderate- to coarse-spatial resolution data (Hansen et al., 2002, 2005, 2011). These inputs are advantageous in different aspects. While multiple single-date images are sensitive to the seasonality of vegetation, the composited data is able to retain phenological information with reduced data volume and minimal cloud contamination (Hansen et al., 2005). Annual multi-temporal metrics such as annual maxima, means, minima and amplitudes of spectral information are able to depict the characteristic points of phenological cycles of vegetation, and less susceptible to seasonal cycles and atmospheric contamination (Hansen et al., 2002).

With respect to modelling methods, various statistical procedures are popular in the literature. Schwarz & Zimmermann (2005) and Heiskanen & Kivinen (2008) applied generalized linear models (GLM) - an extension of the ordinary linear regression - in fractional tree cover mapping at MODIS scale. DeFries et al. (2000) built a linear mixture model to estimate fractional coverage of woody vegetation, herbaceous vegetation and bare ground at a global scale with AVHRR data. While Hansen et al. (2005) utilized regression tree at MODIS scale, Hansen et al. (2002, 2003) fitted a linear regression model to each terminal node of the regression tree for an improved estimation of global fractional tree cover. Hansen et al. (2011) grew multiple regression trees out of random portions of training data with replacement for each other, and then took the median value of the regression trees as the fractional coverage of trees, non-tree vegetation, and bare ground for the conterminous United States. Brandt et al (2016) calibrated a multi-linear regression model between training data of fractional woody cover and three selected metrics for fractional woody cover estimation in the Sahel of Africa.

It is evident from the above studies that the choice of inputs and modelling methods is related to the spatial range and characteristics of study area. Texas savannas have a complex distribution of different woody species of asynchronous phenological cycles across the present rainfall gradient (Fowler & Simmons, 2009; Alofs & Fowler, 2010). Thus, remote sensing data that are able to depict the characteristic points of vegetation phenology cycles were preferred for this area. The annual product of the aforementioned Web-Enabled Landsat Data (WELD) is such a candidate, as it captures the annual maximum NDVI (Roy, 2010).

On the other hand, given the large variation of physiognomic characteristics, composition, and structure of vegetation related to the rainfall gradient across Texas savannas (González, 2010), a regression tree approach was considered more appropriate for this environment, since it is more capable of handling complex relationships between response and predictor variables (Breiman et al., 1984). Specifically, Salford Systems' Classification and Regression Trees (CART) based on the algorithm by Breiman et al. (1984) was applied in this study. CART's advantages over others decision tree techniques make it more and more popular in remote sensing community (Laliberte et al., 2007; Hanan et al., 2014). Firstly, this algorithm is non-parametric and does not assume any underlying distribution of the predictors. Secondly, the binary partitioning it adopts divides the data into child nodes at a slower rate than multi-way splits, being able to detect more data structures. Thirdly, the identification of "splitting" variables was the result of exhaustive searches of all possibilities. Fourthly, CART is capable of handling missing variables.

Study area

This study was tested in a central Texas savanna system, specifically on the Edwards Plateau ecological region (Figure 1.1). The plateau is characterized by both juniper-oak savanna and mesquite-acacia savanna with mid- to short herbaceous vegetation (Küchler 1964). It is in a roughly oblong shape, adjacent with dry plains on its western border and moist prairies and woods on the east. It has thick and mostly flat bedrock, mainly consisting of hard early Cretaceous limestone. As a result, soils are generally shallow (less than 10 inches) but rich in clay content (Schmid, 1969). A strong rainfall gradient is present, with mean annual precipitation (MAP) increasing from 361 mm to 954 mm in the west-east direction (Figure 1.2).

Methodology

Data

The Web-Enabled Landsat Data (WELD) product was utilized as predictor in this study. Based on the radiometrically and geometrically corrected USGS Level 1T Landsat data, the NASA project Web-Enabled Landsat Data (WELD) created 30m spatially mosaicked, and monthly, seasonally, and annually composited data (Lee et al., 2004; Roy et al., 2010). Pixels with maximum NDVI were selected out of the time series (Holben, 1986; Roy, 2010). The 14 layers in WELD data include top of atmosphere (TOA) reflectance, brightness temperature, NDVI, band saturation status and cloud state information. Being insusceptible to Sun-Earth distance, solar geometry, and exoatmospheric solar irradiance, the WELD product is comparable spatially and temporally, which makes it suitable for large scale research and application (Chander et al., 2009; Krehbiel et al., 2015). Here, the annual product of WELD of 2012 was chosen, having been derived from Level 1T Landsat ETM+ data acquired in 2012. It is displayed in true-color and false-color composites in Figure 2.1 and Figure 2.2 respectively.

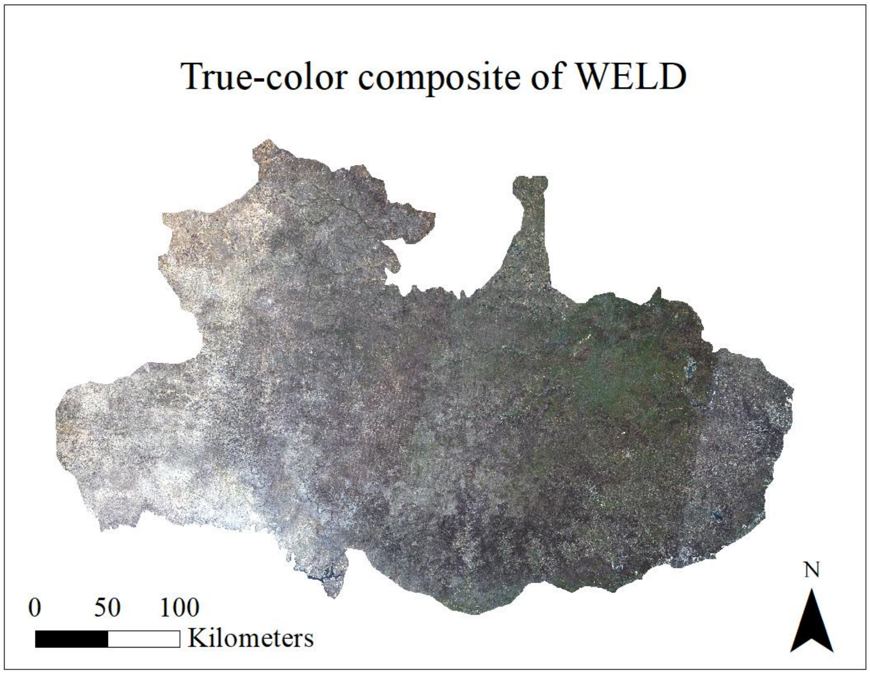


Figure 2.1: Display of WELD product in true-color composite.

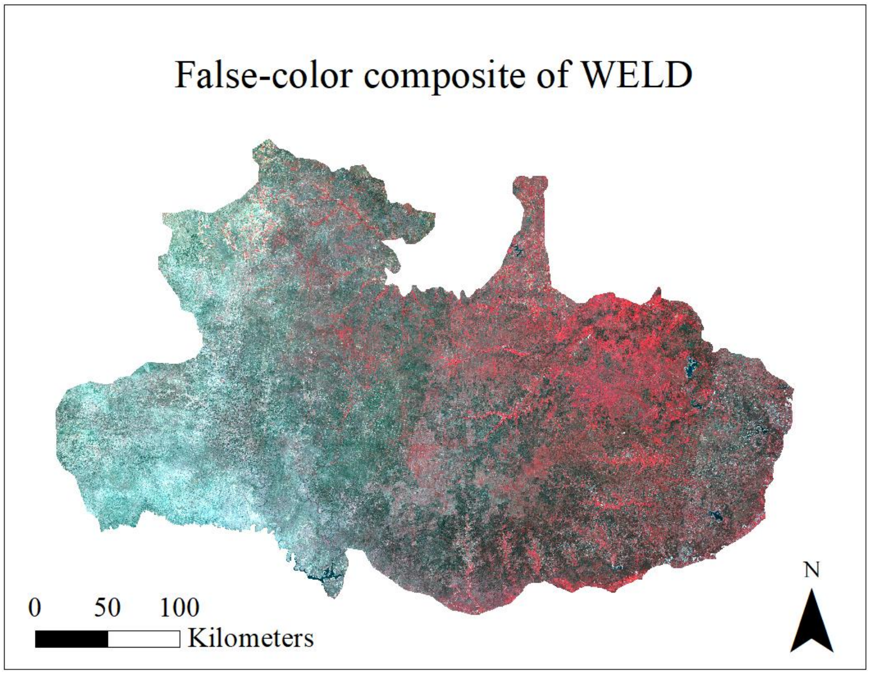


Figure 2.2: Display of WELD product in false-color composite.

Training data of fractional woody cover was derived from 1m resolution Digital Orthophoto Quarter Quads (DOQQs) of 2012, provided by Texas Natural Resources Information System. Each DOQQ covers an area of 6.7km×7.7km. The multi-spectral information of the DOQQs (red, green, blue, and near infrared) as well as the imaging time of growing season greatly facilitated the distinguishing of woody plants of various heights from the background. Unsupervised pixel-based classification was applied and each DOQQ was classified into 30 thematic classes. Each class was then attributed as either woody plant or all else through visual inspection.

Fractional woody cover modelling

As indicated by the large rainfall gradient, Texas savannas span arid, semi-arid, and mesic environments. Fieldwork and ancillary data (maps and geolocated photographs) suggest that these savannas vary greatly in physiognomic characteristics as well as in composition and structure over the present rainfall gradient. In response to the principle that training data in land cover mapping should be representative of the study area and land cover classes (Hansen et al., 2011), a total of 30 random DOQQs were selected across the study area (Figure 2.3). Within each DOQQ, 100 random Landsat pixels of the WELD data were sampled for a whole range of fractional woody cover. Landsat pixels crossing the boundary of the DOQQs were excluded and a total of 2979 Landsat pixels were retrieved. The fractional woody cover of each Landsat pixel was derived from the classified binary map of the DOQQs. While a random 90% portion

(2679) of 2979 Landsat pixels was used for model calibration, the remaining 10% (300 pixels) were reserved for model validation.

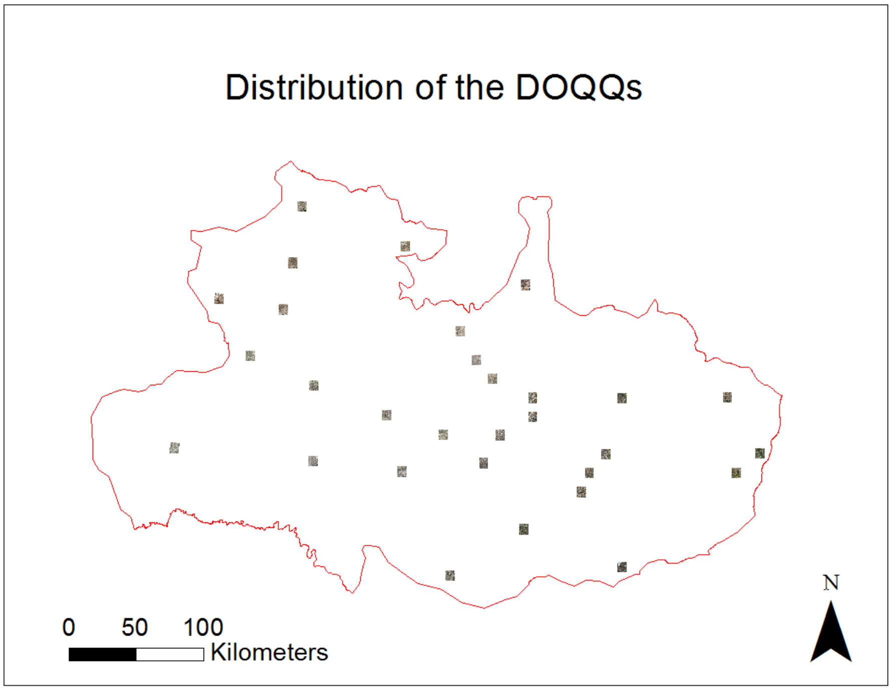


Figure 2.3: Distribution of the random DOQQs across Texas savannas.

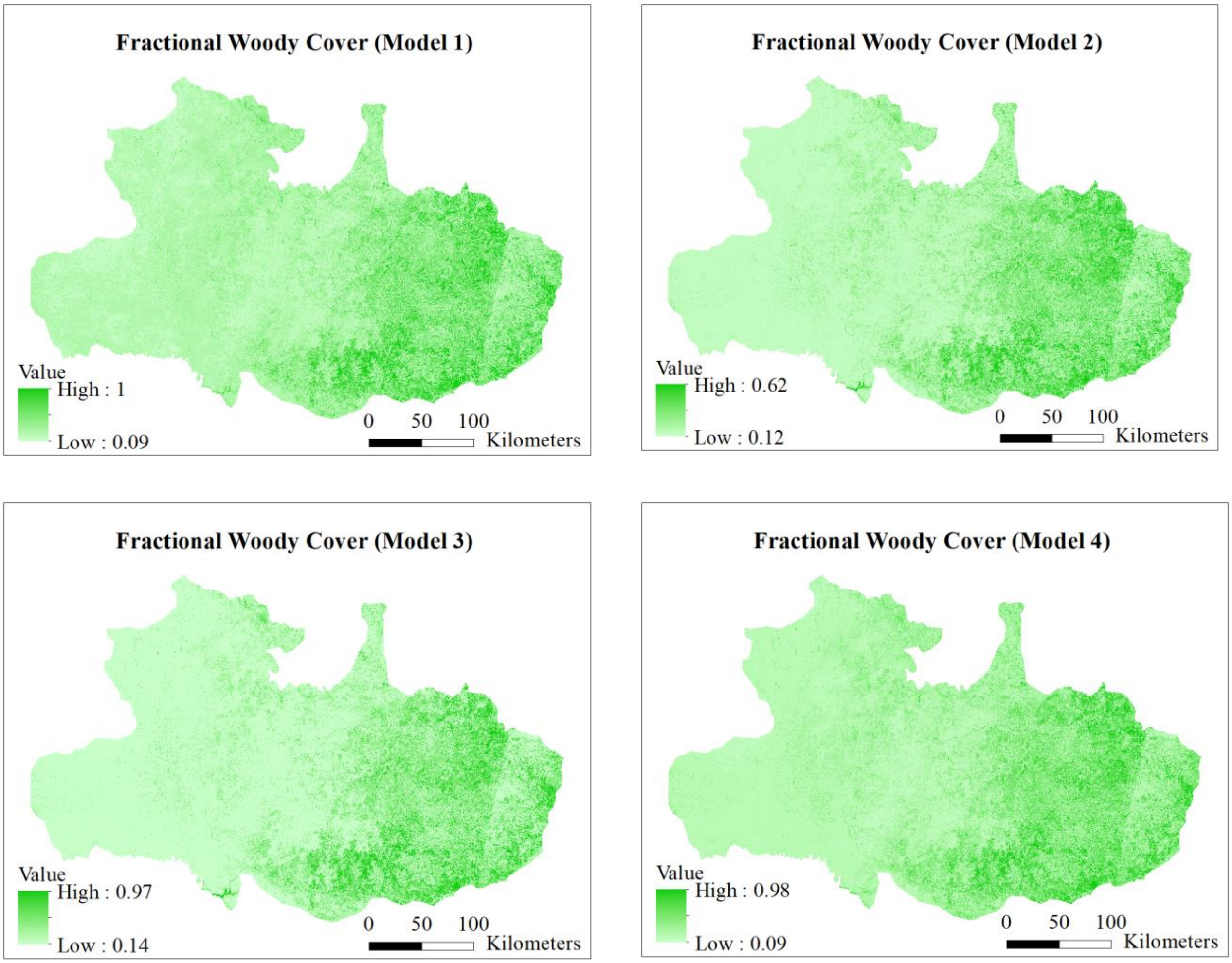
The Web-Enabled Landsat Data (WELD) was used to calibrate the Salford Systems' Classification and Regression Trees (CART) against training data of fractional woody cover derived from 1m resolution digital orthophotos. On the basis of prior studies, the TOA reflectance bands 3, 4, 5 and 7, low-gain thermal band and NDVI layer were utilized (Hansen et al., 2008, 2011). The shorter wavelength bands 1 and 2 were excluded out of the analysis due to their high susceptibility to atmospheric effects (Ouaidrari and Vermote, 1999).

The mean annual precipitation (MAP) was also incorporated and tested as a predictor in CART modelling. However, the result shows that MAP does not have any significant contribution to the output model as supposed. This is probably because that though water availability is necessary for the establishment and survival of woody plants in savanna ecosystems, it does not guarantee the presence of woody plants in a given site, which are susceptible to external disturbances such as land use and human cultivation. Given so, MAP was excluded to avoid data redundancy. The availability and choice of predictors are summarized in Table 2.1.

Table 2.1: The choice of predictor bands (layers)

Bands (Layers)	Choice
Band 1 - Blue	No
Band 2 - Green	No
Band 3 - Red	Yes
Band 4 - Near Infrared	Yes
Band 5 - Shortwave Infrared 1	Yes
Band 6 - Thermal (low-gain)	Yes
Band 7 - Shortwave Infrared 2	Yes
NDVI	Yes
Mean annual precipitation	No

To reduce random error, nine regression tree models were created. Each regression tree was grown out of a random portion of 60% (1607 pixels) of the full training dataset (2679 pixels), with replacement of those pixels back into the full training dataset for the random sampling for next regression tree. The nine regression trees unanimously suggest that band 3 (red) and band 5 (shortwave infrared) of the WELD product are most important in fractional woody cover estimation. Each regression tree model was then applied to the WELD data, yielding a Landsat-scale fractional woody cover map of Texas savannas. The maps of fractional woody cover by individual CART models are displayed in Figure 2.4 and Figure 2.5.



Fractional Woody Cover (Model 1)

Fractional Woody Cover (Model 2)

Fractional Woody Cover (Model 3)

Fractional Woody Cover (Model 4)

Figure 2.4: The maps of fractional woody cover by CART models 1-4.

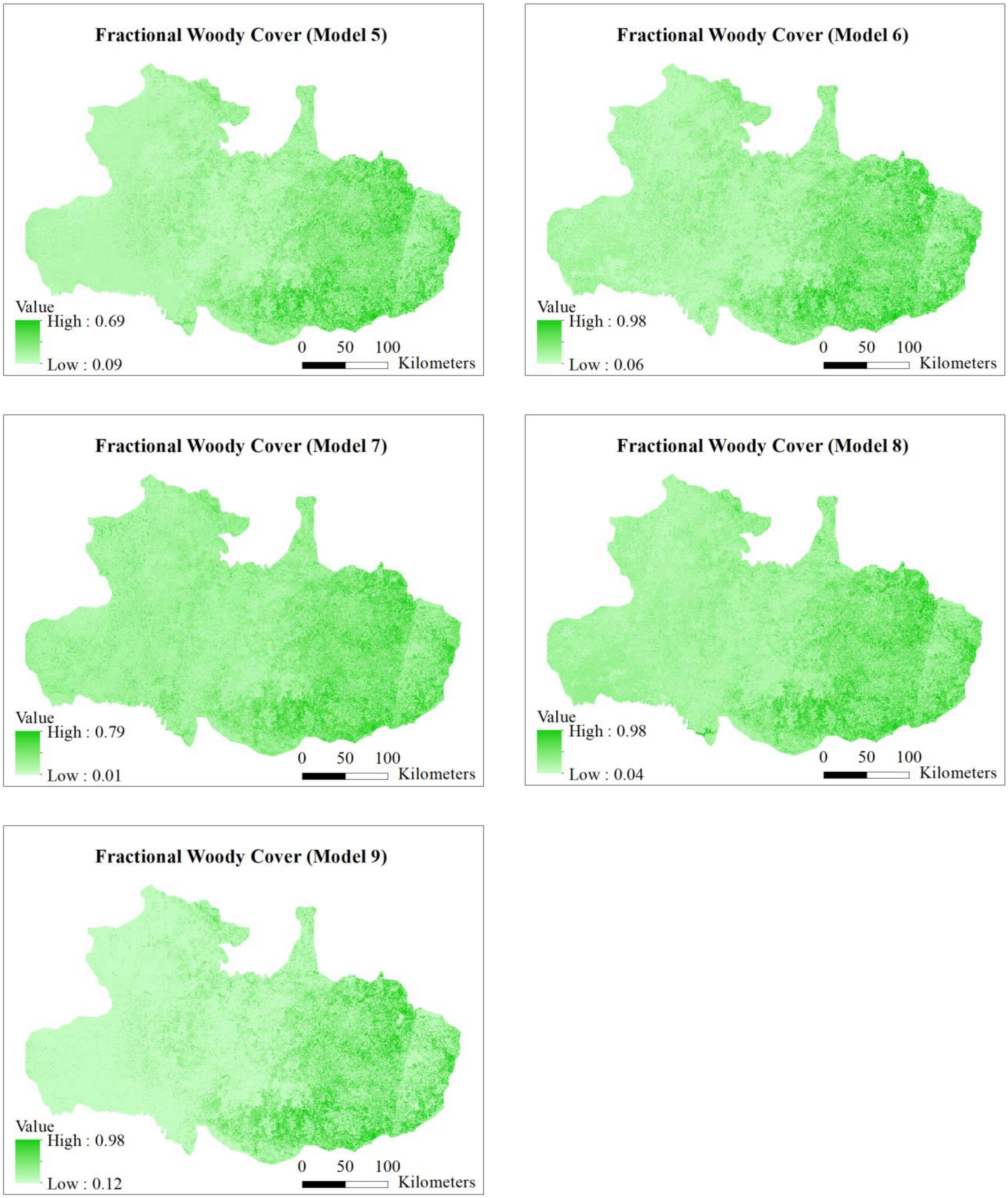


Figure 2.5: The maps of fractional woody cover by CART models 5-9.

On the whole, all these fractional woody cover maps by different CART models exhibit a similar pattern of woody plant distribution across the study area, as that reflected by the false-color composite (NIR/Red/Green) of the WELD data in Figure 2.2. When zoomed in, however, nuanced differences appear among these individual maps in the range and pattern of fractional woody cover. Given so, the median value of the nine maps was taken for each pixel as the final fractional woody cover, which is supposed to be more reliable (Figure 2.6) (Hansen et al., 2003).

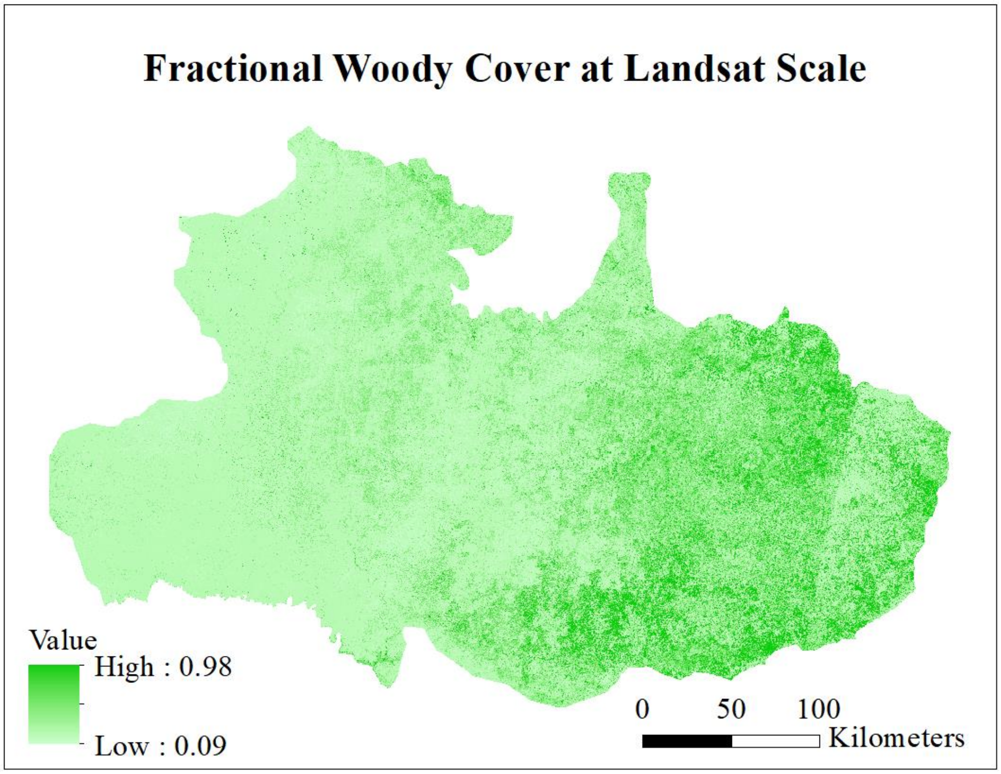


Figure 2.6: The final result of fractional woody cover of Texas savannas.

In Figure 2.6, the color ramp of light green to dark green illustrates the range of fractional woody cover from 0.09 to 0.98. Compared to the rainfall gradient in Figure 1.2, this map shows a high spatial coherency, particularly an increasing trend of fractional woody cover with MAP. It agrees with the pattern of potential woody cover limited by water availability in Texas savannas (Yang et al., 2016).

Accuracy assessment

The reserved measured fractional woody cover for 300 Landsat pixels was used to assess accuracy of the fractional woody cover map displayed in Figure 2.6 in the manner reported in the literature for continuous field products (Hansen et al., 2003; Montesano et al., 2009; Brandt et al., 2016). The scatterplot of the measured vs. modelled (estimated) fractional woody cover is shown in Figure 2.7. The black line is a visual aid to illustrate over- and under-estimation generally (without respect to the regression line).

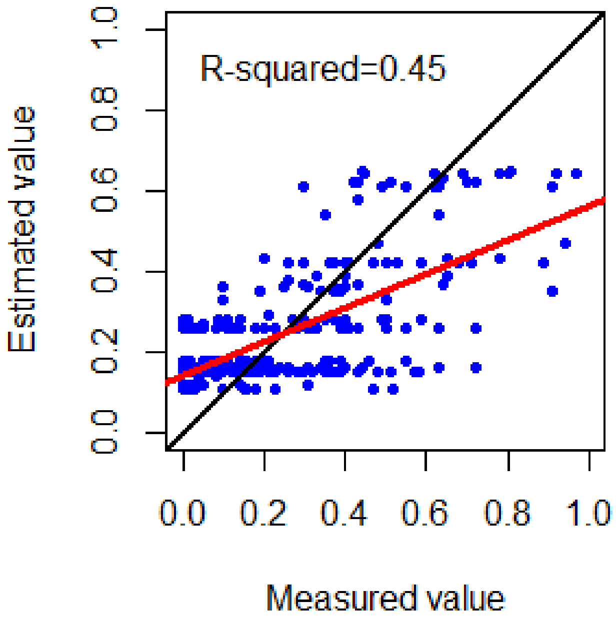


Figure 2.7: The scatterplot and simple linear regression of estimated vs. measured fractional woody cover.

It is evident that the modelled fractional woody cover roughly agrees with the measured value. However, the modelled fractional woody cover has a more limited range. It tends to overestimate in the lower end of fractional woody cover and underestimate in the higher end. As shown in the scatterplot of Figure 2.7, the measured fractional woody cover can be as high as 1, while the estimation barely reaches 0.7. The measured value ranges from 0, whereas the estimated fractional woody cover starts from about 0.1. In addition, points in the scatterplot fall in a limited number of horizontal lines, indicating a limited number of modelled fractional woody cover values.

A simple linear regression was performed between the modelled and measured fractional woody cover. The regression line is overlaid on the scatterplot in red in Figure 2.7. The details of the regression are summarized in Table 2.2.

Table 2.2: Details of the simple linear regression.

Variable	Slope	Intercept	R-Squared	P-value (95% CI)
Value	0.41	0.14	0.45	< 2.2e-16

Discussion

The modelled fractional woody cover map (Figure 2.6) reflects the pattern of woody plant density over the present rainfall gradient, which agrees with reconnaissance fieldwork across the study area from roadside and state park access. The accuracy validation suggests that this result is acceptable at single pixel level, and is supposed to be more reliable when used to predict the fractional woody cover of large area covering groups of pixels. However, in common with other similar products, the respective trend of overestimation and underestimation in sparse and dense woody areas should be cautioned (White et al., 2005; Montesano et al., 2009).

Despite of the overall increasing trend of fractional woody cover over the rainfall gradient, there is a vertical line in the easternmost part of the study area (see Figure 2.6), which affects the coherency a little bit. This line is an inheritance from the WELD product, as shown in Figure 2.1 and Figure 2.2, and is an important reminder regarding data / error propagation. When comparing to the left part of the line, the right side does not strictly follow the increasing tendency of fractional woody cover with mean annual precipitation as supposed. This is because that the right side corresponds to the suburbs of the larger cities of Austin and San Antonio and is subject to human cultivation and development.

Water bodies in the study area mistakenly appear as dense woody area, which is most evident in the sharp point located in the middle bottom of the study area (see Figure 2.6). It is probably due to that water body reflects similarly as woody plants in red and shortwave infrared bands of Landsat ETM+ data, which prove most important in the regression tree analysis. Thus, an addition of a water mask layer is necessary in future research to eliminate this error.

This study represents the pioneer effort of woody cover mapping at sub-pixel level targeted at savanna ecosystems. Its success draws on several aspects. First, the availability and coherency of the WELD product is critical to this study. The radiometric normalization, temporal composition, and spatial mosaic represent a dramatic advance in Landsat data processing, and provide a great channel for large scale landscape components mapping at fine resolution. Second, the advantages of Classification and Regression Trees (CART) ensure reliable prediction models, especially when referring to the nonlinear relationships between response and predictor variables. Further, the adoption of median value of the regression trees strengthens the reliability of the result.

Though useful in this study, the CART can be implicated in the aforementioned trend of overestimation and underestimation, as the mean value of the training pixels present in each terminal node was taken as the prediction. Doing so lowers the value in the high end of fractional woody cover, and raises the estimation at the low end (Hansen et al., 2002). As mentioned before, points in the scatterplot of Figure 2.7 are arrayed in a limited number of horizontal lines. It is a manifestation of the discontinuous character of the modelled fractional woody cover, which does not conform to reality. This discontinuity is due to the limited number of terminal nodes in CART. It further corroborates the discontinuity of remote sensing-derived earth surface properties by CART (Hanan et al., 2014). As a possible solution to the bias of over- and under-estimation and discontinuity, future test of fitting a linear regression to each terminal node may be of interest.

The finding of the manifested importance of red and shortwave infrared bands of Landsat ETM+ data in fractional woody cover mapping may benefit similar studies in future with predictor selection. It will facilitate the automated production of time series fractional woody cover and thus woody plant encroachment monitoring. This finding can also be tested with other sensor systems such as MODIS and AVHRR.

Conclusion

Compared to traditional discrete land cover classification, coverage depiction of landscape components at sub-pixel level is more sensitive to subtle land cover change. This study, in particular, provides a way to closely and continuously monitor woody plant encroachment in savanna ecosystems at Landsat scale (30m) as verified through high resolution (1m) digital orthophotos. It may also contribute to best practices of landscape components mapping over large areas in other ecosystems with these and other sensor systems. Moreover, the success of this study demonstrates the potential and advantage of the WELD product in land cover study. Furthermore, the occurrence of overestimation in sparse woody area and underestimation in dense woody area indicates the direction of critically needed next steps in research, notably in structurally complex regions and systems where a high percentage of the woody vegetation is under 5m in height, notoriously a "great challenge to characterize" (Hansen, 2016).

Chapter 3: Preliminary analysis of the pattern of potential woody cover in Texas savannas utilizing MODIS tree cover product

Note: This chapter is already published and here is the full citation: *Yang, X., K. A. Crews, and B. Yan. 2016. Analysis of the pattern of potential woody cover in Texas savanna.* International Journal of Applied Earth Observation and Geoinformation 52:527–531.

Xuebin Yang conducted this study and wrote this manuscript. Kelley A. Crews supported this study and revised the manuscript. Bowei Yan provided help on statistical modelling.

Abstract

While woody plant encroachment has been observed worldwide in savannas and adversely affected the ecosystem structure and function, a thorough understanding of the nature of this phenomenon is urgently required for savanna management and restoration. Among others, potential woody cover (the maximum realizable woody cover that a given site can support), especially its variation over environment has huge implication on the encroachment management in particular, and on tree-grass interactions in general. This project was designed to explore the pattern of potential woody cover in Texas savanna, an ecosystem with a large rainfall gradient in west–east direction. Substantial random pixels were sampled across the study area from MODIS Vegetation Continuous Fields (VCF) tree cover layer (250m). Since potential woody cover is suggested to be limited by water availability, a nonlinear 99th quantile regression was performed between the observed woody cover and mean annual precipitation (MAP) to model the pattern of potential woody cover. Research result suggests a segmented relationship between potential woody cover and MAP at MODIS scale. Potential biases as well as the practical and theoretical implications were discussed. Through this study, the hypothesis about the primary role of water availability in determining savanna woody cover was further confirmed in a relatively understudied US-located savanna.

Key words: Texas savanna, potential woody cover, woody plant encroachment, nonlinear quantile regression, MODIS VCF

Introduction

Savanna ecosystems are characterized by the coexistence of woody and herbaceous vegetation (Frost et al., 1986). They exist across a wide range of conditions in terms of climate (e.g. rainfall), soil nutrient content, fire regimes and herbivory level, covering about 20% of the Earth’s terrestrial surface (Ramankutty & Foley, 1999). Mainly found in tropics and subtropics, savannas are home to a large proportion of human population, livestock and wildlife of the world. Moreover, savanna ecosystems play a critical role in global land-atmosphere energy balance, as well as carbon, nutrient, and water cycles (Scholes & Walker, 1993; Lal, 2004).

Many theories have been advanced to explain the coexistence and relative abundance of woody and herbaceous components in savannas, which can be categorized into two broad classes (Walter, 1971; van Langevelde et al., 2003; Higgins et al., 2000).

While one is based upon the competitive interactions between the two contrasting life forms, the other focuses exclusively on tree establishment and persistence restricted by demographic bottlenecks (Sankaran et al., 2004). However, both positive and negative evidence exists for each category of those theories, and none of them is generalizable across all types of savannas (Scholes & Archer, 1997; Jeltsch et al., 2000). Other than that, savanna dynamics have been debated with regard to equilibrium, non-equilibrium, and disequilibrium dynamics (Ellis & Swift, 1988; Sullivan & Rohde, 2002). As for savanna modelling community, the validity of traditional succession models versus state-and-transition models needs further investigation (Fowler & Simmons, 2008).

Furthermore, the phenomenon of woody plant encroachment, defined as the directional increase of woody plants at the expense of herbaceous vegetation, commends the relevance of illuminating the above ‘savanna questions’. This is because that the encroachment has been observed in southern United States (Archer et al., 1995; Creamer et al., 2013) and many other parts of the world (Cabral et al., 2003; Soliveres & Eldridge, 2014; Coetsee et al., 2013). And it has adversely affected the ecosystem production and function, and largely reduced species diversity (Hughes et al., 2006; Van Auken, 2009; Alofs & Fowler, 2010). A thorough understanding of the aforementioned alternative mechanisms and dynamics is urgently required for woody encroachment management, especially in consideration of changing climate and land use patterns anticipated to worsen the scenario (Sala et al., 2000; House et al., 2003; IPCC, 2014). Potential woody cover - the maximum realizable woody cover that a given site can support - would provide insights into these ‘savanna questions’.

Background

During the past several decades, substantial increase in woody plants has been observed on the Edwards Plateau of Texas, USA (Archer, 1989; Taylor, 2008; Alofs & Fowler, 2010). The encroachment was attributed to the expansion of existing woody species and establishment of new woody species, accompanied by a significant amount of temporal and spatial heterogeneity in fire regimes and herbivory level (González, 2010; Alofs & Fowler, 2013). Being unfavorable to the dominant herbivores in this region (domestic livestock and deer), the encroaching species of Ashe juniper and red berry juniper now dominate much of the plateau, largely reducing livestock production and regional plant diversity (Fowler & Simmons, 2008; Creamer et al., 2013).

Facing the huge encroachment, both conservation managers and research ecologists are concerned about the potential woody cover (the hypothetical degree of encroachment), as well as the alternative of succession models and state-and-transition models for savanna dynamics modelling. If potential woody cover is well below canopy closure, woody plant encroachment will be a bounded process (Sankaran et al., 2005). Otherwise, savannas may switch to a wooded state as a result of the encroachment, and disturbances such as fire and herbivory will be necessary for the persistence of woody and herbaceous vegetation. While succession models emphasize an ordered series of states during the development of savannas (Fowler & Simmons, 2008), the state-and-transition models consider reversible stable states (Briske et al., 2005; Bestelmeyer et al., 2009). If succession models fit Texas savanna dynamics, the encroachment will persist and the savanna will develop toward a more and more woody state. Otherwise, if the state-and-transition models fit better, the encroachment will be a reversible process with or without human manipulation and it will be a much easier task to combat with the encroachment.

It is hypothesized that the potential woody cover that a given site can support is predominantly limited by water availability (Frost et al., 1986; Sankaran et al., 2008). Research also suggests that, if water availability plays the primary role in determining woody cover in savannas, the potential woody cover would show a gradual increasing trend with mean annual precipitation (MAP) (Walker & Noy-Meir, 1982; Sankaran et al., 2004, 2005). But if factors such as fire and herbivory play the primary roles, an abrupt increase in potential woody cover would be observed over rainfall gradient. That is, a dominance of grassland will be found in areas below a MAP threshold, while woody canopy closure would occur in areas above that threshold sufficient for woody plant growth (Frost et al., 1986; Jeltsch et al., 2000).

Sankaran et al. (2005) analyzed the potential woody cover in African savannas applying the above MAP-based scheme. However, analogous research in other savanna regions has been rarely seen. And the pattern of the potential woody cover of other savanna ecosystems remains to be established, which could be different from that of the African savannas due to the relatively unexplored factors such as soil characteristic and climate seasonality (Kulmatiski & Beard, 2013). Given so, this study was designed to investigate the potential woody cover across broad environmental gradients in Texas savanna. While field sites were restricted to a fine scale of 0.25 to 0.5 ha in the African research, a coarse scale study would enrich the theory of scale-dependency of woody cover observation (Gillson, 2004; Wiegand et al., 2006).

Methodology

Study area

This study was tested on the Edwards Plateau of Texas, USA (Figure 1.1). The plateau is a unique ecoregion of Texas, characterized by juniper-oak savanna and mesquite-Acacia savanna with middle to short herbaceous vegetation (Küchler, 1964; Fowler & Simmons, 2008). It is adjacent with dry plains on its western border, and moist prairies and woods to the east. The plateau is roughly an oblong region in which a large rainfall gradient is present, with mean annual precipitation ranging from ~360 mm to ~950 mm in the west-east direction (Figure 1.2).

Data acquisition

MODIS Vegetation Continuous Fields (VCF) is an annual product that estimates the proportion of tree cover, non-tree vegetation and bare ground of global land surface at MODIS pixel level (DiMiceli et al., 2011). The VCF product has been widely used in a variety of research and application (Bucini & Hanan, 2007; Song et al., 2014). As the only large scale and proportional tree cover dataset available, the MODIS VCF tree cover layer is able to provide us a very large sample to examine the pattern of potential woody cover over broad environmental gradients that is difficult to discern by a small number of observations. The latest MODIS VCF tree cover of 2013 (250m resolution) was utilized in this research (Figure 3.1).

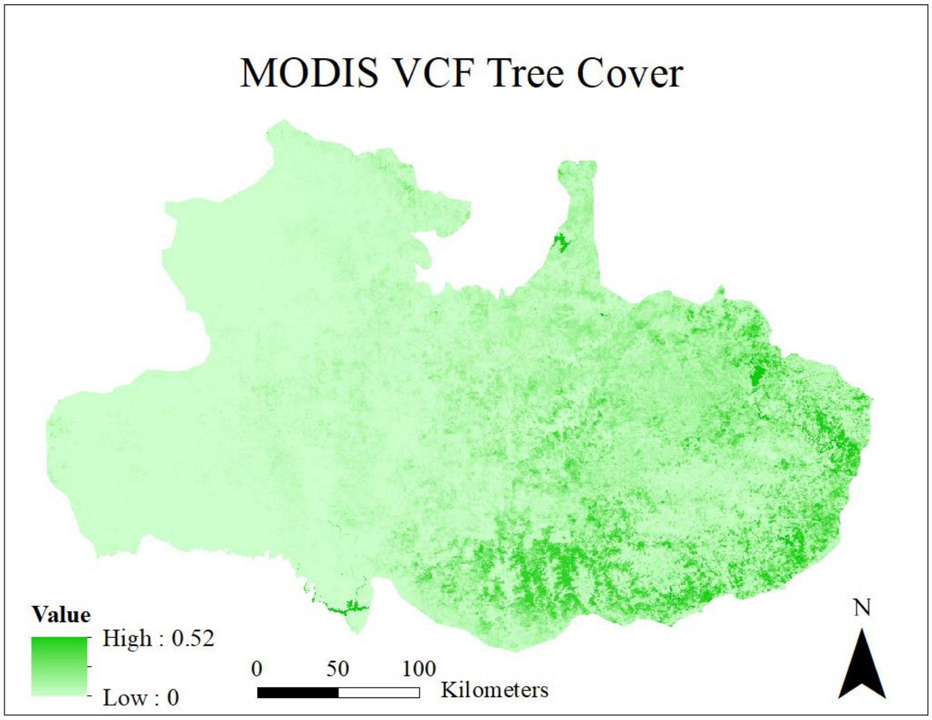


Figure 3.1: MODIS VCF tree cover product of 2013 (250m).

Precipitation data was acquired from Southern Regional Climate Center. MAP from 1981 to 2010 was calculated in millimeters for 51 rain gauge stations within this study area. Thereafter, a continuous MAP surface was created at 800m resolution (Figure 1.2). The interpolation method of Kriging was applied, which proves more realistic than other methods in rainfall interpolation (Ly et al., 2013).

Data sampling

Spatial random sampling was performed across the study area with the MODIS VCF tree cover layer in ArcGIS 10.3, creating a total of 10,000 random pixels. Corresponding proportional tree cover and MAP values were extracted for the sample. Pixels with tree cover values greater than 100% (due to water, cloud, shadow, or filled value) were excluded. The scatterplot of MODIS proportional tree cover vs. MAP is exhibited in Figure 3.2.

Data analysis

Quantile regression

Regression analysis has long been used in ecology study for investigation of relationships between ecological processes and associated factors (Cade & Noon, 2003; Hegyi & Garamszegi, 2011). While traditional regression analysis focuses on the mean of the response variable distribution, quantile regression is capable of estimating the relationship between measured factors and all parts of the response variable distribution (Koenker & Bassett, 1978). Thus, quantile regression is able to provide a more complete insight into the possible causes of ecological processes (Koenker et al., 1994; Cade & Guo, 2000; Dunham et al., 2002; Brown & Peet, 2003).

Specifically, many ecologists choose to fit the upper boundary of the conditional distribution of ecological responses to the factors of interest (Cade & Guo, 2000). It is due to that, though only a portion of the associated factors are measured and included in most ecology studies, the upper limit set by the measured factors cannot be exceeded even when other potential factors are included (Cade & Noon, 2003). Though a parametric form of the relationship is assumed for quantile regression, no hypothesis is made about the distributional form (e.g. normal, Poisson) of the random error portion of the analysis.

Potential woody cover modelling

Within Figure 3.2, an overall increasing trend of proportional woody cover with MAP is evident. To explore the pattern of potential woody cover, a nonlinear quantile regression was performed between the observed proportional woody cover and MAP, with the package '*quantreg*' in software R. The potential woody cover was represented by the 99th quantile of the observed proportional woody cover (Sankaran et al., 2005). While various functions were tested, the exponential function $y = a + c * \exp(-\exp(-b * (x - m)))$ fits the scatterplot best, confirmed by an additional linear b-spline quantile regression. In this exponential model, y represents potential woody cover, x represents mean annual precipitation, a, b, c, and m are the parameters to be estimated. The fitted curve is displayed in red in Figure 3.2. The details of the fitted function are summarized in Table 3.1.

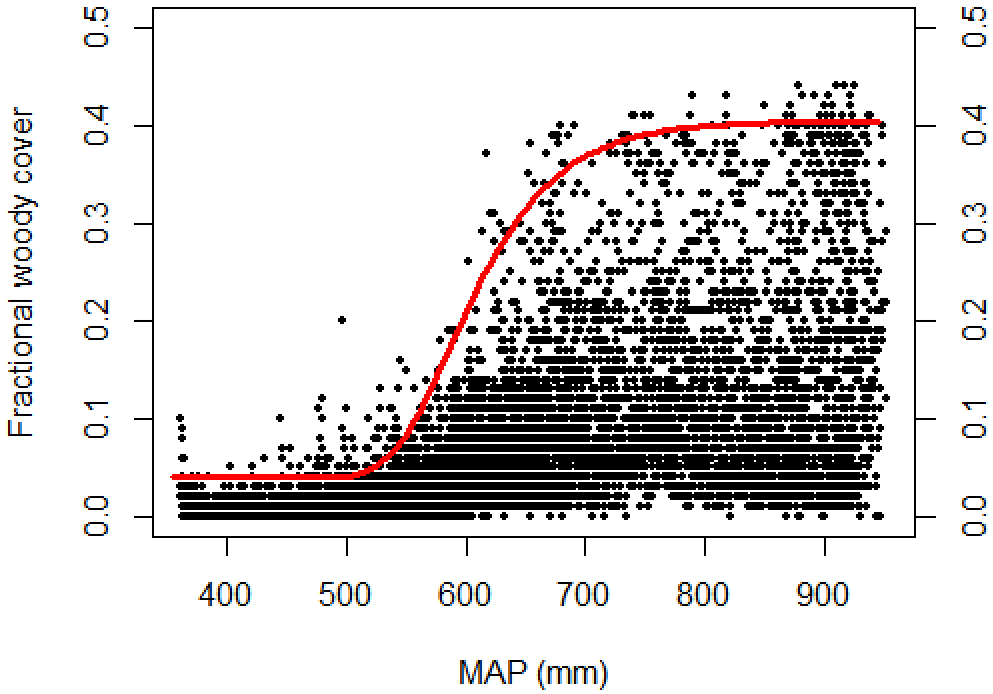


Figure 3.2: The scatterplot of MODIS tree cover vs. MAP and the modelled potential woody cover pattern (red curve).

Table 3.1: Details of MODIS tree cover-based potential woody cover pattern.

Variable	Value	Standard error	t value	Pr (>| t |)
a	0.04000	0.00549	7.28517	0.00000
b	0.01996	0.00188	10.62572	0.00000
c	0.36430	0.00760	47.96431	0.00000
m	586.90362	4.25957	137.78480	0.00000

Result and discussion

Result

As shown in Figure 3.2, the pattern of the potential woody cover at MODIS scale is in a sigmoid shape, suggesting a segmented relationship between potential woody cover and MAP in Texas savannas. The potential woody cover starts with a fixed and very low level till 500 mm MAP, followed by an approximate linear relationship with MAP by about 650 mm. From 650 mm on, the potential woody cover stays on a plateau value of about 42%.

It has to be noted that the MODIS VCF tree cover product does not include woody plants less than 5 meters height in their calibration data, while a lot of short woody plants exist in Texas savanna (DiMiceli et al., 2011; Sexton et al., 2013). Though it does not mean that the small woody plants don’t appear in the imagery with similar spectral implications, underestimation may occur with the tree cover product within this study area. It coincided with our visual estimation from Google Earth high resolution imagery, which indicates a higher upper bound than that of 42%. Even though further research is needed on the upper bound value, the segmented relationship between potential woody cover and mean annual precipitation can provide us a lot of insights into woody encroachment management and the mechanisms of tree-grass interactions in Texas savannas.

Discussion

This study follows the research by Sankaran et al. (2005) that suggests a similar potential woody cover pattern but a much higher upper bound in African savannas (about 80%). Besides the potential underestimation of the MODIS tree cover product, the discrepancy may be attributed to several other aspects. First of all, compared to the fine scale (0.25 to .05 ha) in the African study, the MODIS scale (6.25 ha) is much less sensitive to local heterogeneity and thus less likely to capture high woody cover of local dense locations.

Secondly, different soil characteristics would take part of the responsibility (Bucini & Hanan, 2007). Developed from limestone, soil in Texas savannas is shallow and coarse-textured (Schmid, 1969). It is suggested by the inverse texture hypothesis that coarse-textured soil supports less woody plants in wetter climates than fine-textured soil (Noy-Meir, 1973). With this in mind, the soil in African savannas is mushy in its long wet season. On the other hand, the soil in the dry season of African savannas is very porous and dry. This type of soil facilitates natural fires that fertilize the soil through the reintegration of ash, and consequently sustains plant growth.

Lastly, climate seasonality such as temperature, timing and intensity of precipitation can also affect potential woody cover through their effect on water partitioning between woody and herbaceous plants (Kulmatiski & Beard, 2013). For example, rainfall mainly occurs in May/June and September in Texas savannas, while the wet season stretches from May to November in African savannas (Mistry & Beradi, 2014). It is possible that the longer wet season in African savannas facilitates woody plant growth.

The gradual increasing trend of potential woody plant cover with MAP further confirmed the hypothesis of the primary determinant role of water availability in savanna woody cover in a northern hemisphere savanna. In the relatively dry areas (with MAP below the threshold value of 650 mm), potential woody cover is limited by water availability. Increased water availability in these areas will increase their potential in supporting tree growth and facilitating woody plant encroachment. Therefore, any changes that lead to increased water availability for woody plants such as changes in precipitation regimes and soil properties should be a concern for woody encroachment management.

In savanna dynamics, the distinction between independent (constraints or disturbances) and dependent (interactive) environmental factors depends on observation scale (Skarpe, 1992). Moreover, the distinction is also environment-specific. According to this study, woody plant growth in the relatively dry areas in Texas savannas is constrained by water availability, suggesting that MAP acts as an independent factor in savanna dynamics. In mesic areas with MAP above 650 mm, rainfall is sufficient for woody plant growth and is more likely a part of the interactive mechanisms of the savanna dynamics. It also indicates that a combination of competition-based theories and demographic-bottleneck theories is necessary for a full understanding of the savanna dynamics.

Research shows how the increasing woody plants in Texas savannas will persist under present conditions without mechanical removing (Fowler & Simmons, 2008). The successional process of woody plant encroachment in Texas savannas indicates that traditional succession models characterized by transient dynamics may better depict its present dynamics, compared to the widely used state-and-transition models with reversible alternate stable states. Since the successional process continues until a climax point is reached, the process of woody plant encroachment will not stop until its potential woody cover is realized.

Conclusion

The result of this study unveils the pattern of potential woody cover over broad environmental gradients in Texas savannas, further confirming the hypothesis of the primary role of water availability in determining savanna woody cover in a relatively understudied US-located savanna. In addition, this project's findings highlight the role of factors other than MAP such as soil characteristic and climate seasonality in affecting potential woody cover. Due to the scale dependency of woody cover observation, future studies at finer scales would provide a more complete picture of the pattern of potential woody cover in Texas savannas.

Above all, this study further unveils the fundamental nature of savanna ecosystems and serves as a baseline for further work concerning savanna management and restoration. It is important to note that the usage of MODIS VCF tree cover product was critical. Despite of the aforementioned potential bias, this dataset in particular, as well as satellite-based regional-scale earth observation techniques in general, exhibit great potential in uncovering the nature of global environmental systems.

Chapter 4: Multi-scale analysis of potential woody cover in Texas savannas

Abstract

The characteristic tree-grass coexistence of savanna ecosystems necessarily implies due consideration of spatial scale at which the coexistence occurs. However, most research on savanna questions are spatial scale-free, resulting in mutually exclusive theories on tree-grass coexistence. This study aims to dissect those conflicts, particularly taking multi-scale analysis of potential woody cover as a new perspective into the dynamics of savanna ecosystems. It was tested in Texas savannas of a wide rainfall gradient in west-east direction, with mean annual precipitation increasing from 360 mm to 950 mm. A 99th quantile regression was performed between observed fractional woody cover and mean annual precipitation (MAP) at Landsat and MODIS scales respectively. Here we show that potential woody cover at Landsat scale increases linearly with MAP over the rainfall gradient, whereas it is in a prominent piecewise-linear relationship with MAP at MODIS scale. The discrepancy of the potential woody cover patterns at Landsat and MODIS scales corroborates the scale dependence of the primary determinants of savanna tree density, indicating that the existing theories are not necessarily mutually exclusive. Moreover, Texas savannas could be divided into sub-regions of arid-savanna, semi-arid savanna and mesic savanna according to the two threshold MAP values in the MODIS scale potential woody cover pattern. Furthermore, the MODIS scale potential woody cover pattern confirms the feasibility of patch dynamics perspective in arid and semi-arid savannas.

Key words: savanna, potential woody cover, multi-scale, encroachment, quantile regression

Introduction

Savannas are ecologically, economically, and culturally important ecosystems, characterized by the coexistence of woody and herbaceous vegetation as well as distinct dry season (Scholes & Archer, 1997). The coexistence of woody and herbaceous vegetation implies the inherent issue of spatial scale at which the coexistence occurs. For instance, though the coexistence expands as large as 33 million km^2 (approximately 20%) of the earth's terrestrial surface (Ramankutty & Foley, 1999), it does not occur within an area as small as a square centimeter.

Wu and Loucks (1995) proposed the Hierarchical Patch Dynamics Paradigm (HPDP) as a combination of the hierarchy theory and the patch dynamics perspective to understand the complex nature of ecosystems. The HPDP is centered on the concepts of heterogeneity, sub-systems, and patches (Wu, 1999; Wu and David, 2002), offering an appropriate way to link ecological pattern and process to spatial scale (Levin, 1992; Wu & Loucks, 1995). Later, Gillson (2004) tested the paradigm in savanna ecosystems through a comparison of the patterns of vegetation change over hundreds of years at micro, local, and landscape scales by palaeoecological techniques. Research results suggest a scale dependency of the ecological processes that dominate tree density.

Wiegand et al (2006) and Meyer et al (2009) proposed a scale-explicit mechanism of patch dynamics to explain the coexistence of woody and herbaceous vegetation as well as woody plant encroachment in arid and semi-arid savannas. Under this mechanism, arid and semi-arid savannas are composed of a spatial mosaic of discrete patches at different stages of the same cyclical succession between woody and herbaceous dominance. The succession is supposed to be driven by variable rainfall and inter-tree competition in arid savanna, while mainly by precipitation conditions in semi-arid savanna. Evidence was found for this hypothesis in a variety of empirical field studies (Wiegand et al., 2006; Meyer et al, 2009; Levick & Rogers, 2011; Cipriotti & Aguiar, 2015).

With regard to that savanna ecosystems span a wide range of conditions in terms of precipitation, soil nutrient content, fire regime and herbivory level (Ramankutty & Foley, 1999), the role of these factors on savanna structure was suggested to vary across diverse types of savannas (arid, semi-arid, and mesic) (Sankaran, et al., 2005, 2008). Given so, a multi-scale approach and incorporation of broad environmental gradients are necessary for a full understanding of savanna ecosystems.

Potential woody cover, the maximum realizable woody cover that a site of certain size can support under given environmental and climatic conditions, has a strong implication on the dynamics of savanna ecosystems (Sankaran et al., 2005; Yang et al., 2016). Among others, it defines the end-point of the globally observed woody plant encroachment – the directional increase of woody plants in cover, density, and biomass at the expense of herbaceous vegetation. If potential woody cover is well below canopy closure, the encroachment process will stop at a certain woody plant density below canopy closure. Otherwise, the encroachment can continue till canopy closure. In the latter case, disturbances would be necessary to maintain the coexistence of woody and herbaceous vegetation (Sankaran et al., 2005). Moreover, potential woody cover may help elucidate the debated equilibrium, non-equilibrium, and disequilibrium dynamics in savanna ecosystems (Ellis & Swift, 1988; Sullivan & Rohde, 2002). Furthermore, the pattern of potential woody cover would provide insights into the validity of the patch-dynamics perspective in arid and semi-arid savannas.

However, study on potential woody cover thus far has been focusing on single spatial observation scale (Sankaran et al., 2005; Yang et al., 2016), despite of the aforementioned spatial scale issue. This research aims to fill the void and analyze the pattern of potential woody cover at multiple observation scales and over broad environmental gradients. It is expected that this multi-scale research will provide fresh insights into the dynamics of savanna ecosystems.

Background

Woody cover in savanna ecosystems is prone to the processes of seed dispersal and germination, seedling establishment, aging and mortality, which are under the effect of multiple factors like rainfall, soil nutrient contents, disturbance (e.g., fire, herbivory) over various spatial and temporal scales (Gillson, 2004). As for potential woody cover, the maximum realizable woody cover that a given site can support, it is predominantly limited by water availability (Frost et al., 1986; Sankaran et al., 2008). Research also suggests that, if water availability plays the primary role in determining savanna woody cover, the potential woody cover would show a gradual increasing trend with it (Walker & Noy-Meir, 1982; Bucini & Hanan, 2007; Good & Caylor, 2011; Yang et al., 2016). However, if factors other than water availability such as fire and herbivory play the primary role, the potential woody cover would jump from grassy dominance to woody dominance by certain water availability sufficient for woody plant growth (Frost et al., 1986; Jeltsch et al., 2000; Sankaran et al., 2004, 2005).

Rigorous research on potential woody cover has been very rare seen due to limited availability of fractional woody cover product over large areas (Yang et al., 2016). Sankaran et al. (2005) collected field data of fractional woody cover from several sources for sample plots across African savannas, and analyzed the potential woody cover by the above MAP-based scheme. However, whether the conclusions from the African savannas hold in other savannas, especially in the relatively understudied northern Hemisphere savannas, remains unclear. The answer could be negative due to the relatively underexplored factors such as woody species, soil characteristic, and climate seasonality (Kulmatiski & Beard, 2013; Stevens et al., 2017). Moreover, the sample plots in the Africa study are not strictly uniform in size and range from 0.25 ha to 0.5 ha, which may have biased the result when referring to the aforementioned scale dependency of woody cover observation (Gillson, 2004; Wiegand et al., 2006). Furthermore, the plots were not randomly sampled, not to mention distribution balance in terms of water availability, and may not be representative of the study area.

Yang et al. (2016) overcame the above weaknesses of plot size variation and unbalanced sampling through utilization of the MODIS Vegetation Continuous Fields (VCF) tree cover product (DiMiceli et al., 2011). It assessed the pattern of potential woody cover in Texas savannas over the present rainfall gradient at MODIS scale (250m). A piecewise linear relationship was revealed between potential woody cover and water availability (represented by mean annual precipitation) over the rainfall gradient, providing fundamental insight into woody plant encroachment management and biodiversity conservation in Texas savannas. However, the MODIS VCF tree cover product is targeted at trees over 5m in height, while many short woody plants exist in Texas savannas. Though small woody plants may appear in the imagery with similar spectral implications, underestimation could occur with this tree cover product in Texas savannas. Hereafter, further research is in need on the exact value of potential woody cover. Other than that, the single spatial observation scale of woody cover in this research limits its scientific significance.

Thus, a multi-scale assessment of potential woody cover pattern over broad environmental gradients would make a critical material and theoretical contribution to savanna ecology. The availability of the nationwide 1m resolution Digital Orthophoto Quarter Quads (DOQQs) provides n great opportunity for this kind of research, especially in terms of remote areas inaccessible for field survey. Particularly, it makes fractional woody cover derivation possible at multiple observation scales and allows for a balanced sampling of plots in terms of factors of interest. Given so, this study was designed to investigate the pattern of potential woody cover over the wide rainfall gradient in Texas savannas at both Landsat scale (30m) and MODIS scale (500m).

Study area

This study was tested in Texas savannas located on the Edwards Plateau ecological region in central Texas (Figure 1.1). It is roughly in an oblong shape and expansive enough to encapsulate a meaningful precipitation gradient. The expanse of this area could avoid artifacts associated with prior potentially idiosyncratic site-specific findings. The rainfall gradient lies in the west-east direction, where mean annual precipitation (MAP) increases from about 360 mm to 950 mm (Figure 1.2). The plateau is mainly occupied by juniper-oak savanna and mesquite-Acacia savanna, interspersed with middle to short herbaceous vegetation (Küchler 1964).

Methodology

Sampling strategy

Since potential woody cover is suggested to be limited by water availability, a MAP-based stratified random sampling of MODIS pixels (500m) was performed for a full representation of the study area. Specifically, the study area was divided into 10 rainfall zones of equal MAP interval and about 150 MODIS pixels were randomly sampled within each rainfall zone, resulting in a total of 1553 MODIS pixels (Figure 4.1).

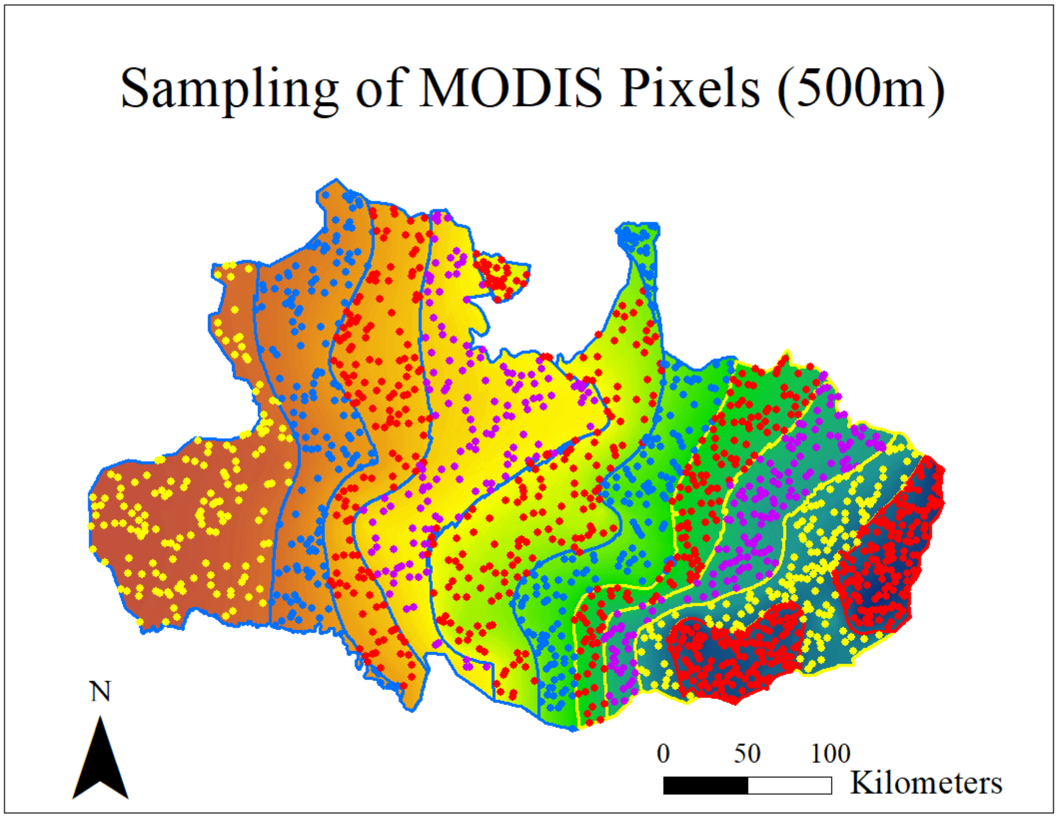


Figure 4.1: MAP-based stratified random sampling of MODIS pixels (500m).

A systematic sampling of Landsat pixels (30m) was conducted within each of the above MODIS pixels. The centroid of each MODIS pixel was captured first. Points 60m, 120m and 180m away from the centroid in the west, east, north and south direction were created respectively (Figure 4.2). The corresponding Landsat pixels of these 13 points within each MODIS pixel were retrieved from the Web-Enabled Landsat Data (WELD). As a result, 13 groups of Landsat pixels were obtained in terms of their relative location to the centroid of each MODIS pixel (Figure 4.2).

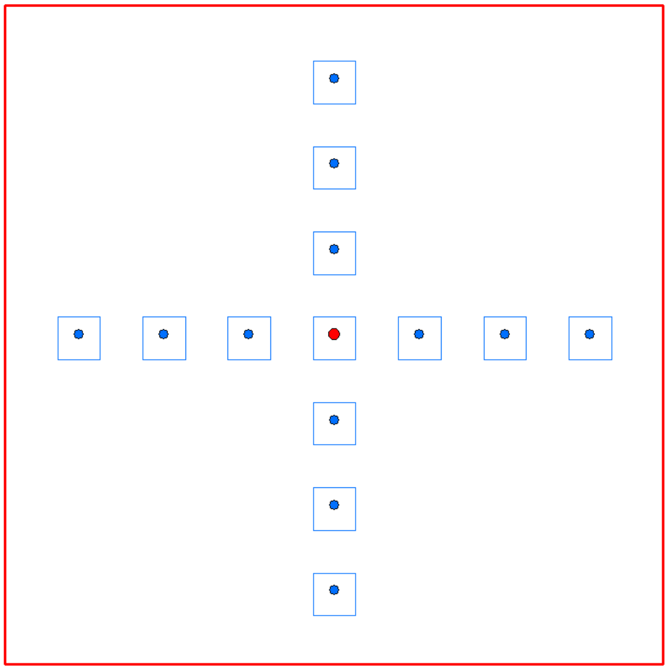


Figure 4.2: The relative location of MODIS pixel (red polygon, 500m) and Landsat pixels (blue polygons, 30m).

Data

Fractional woody cover of the area covered by Landsat and MODIS pixels was derived from 1m resolution Digital Orthophoto Quarter Quads (DOQQs) of 2012, provided by Texas Natural Resources Information System. The multi-spectral bands of the DOQQs (red, green, blue, and near infrared) and the imaging time of growing season greatly facilitate the distinguishment of woody plants of various heights from the background. The corresponding DOQQ image of each MODIS pixel was classified into 10 thematic classes by unsupervised pixel-based classification. Each class was attributed as woody plant or non-woody plant, taking true- and false-color composites as reference.

The corresponding fractional woody cover of the Landsat pixels was then derived from the above classified binary image of woody plant vs. non-woody plant with Zonal Statistics tool in ArcGIS.

In consideration of the uniformity of soil type across the plateau (Schmid, 1969), water availability was represented by mean annual precipitation (MAP), provided by Southern Regional Climate Center. There are 51 rain gauge stations within the study area and the MAP of 1981 to 2010 is available for each station. A continuous MAP surface was created at 800m resolution with the interpolation method of Kriging (Figure 1.2).

Quantile regression

Regression analysis has been popular in ecology study in exploring response of ecological processes to associated factors (Cade & Noon, 2003; Yang et al., 2016). Traditional, regression analysis focuses on the mean of the response variable distribution. Quantile regression, a special kind of the regression analysis, is able to link all parts of the response variable distribution to factors of interest (Koenker & Bassett, 1978; Koenker, 2006). Compared to the traditional regression analysis, quantile regression can provide a more complete insight into the possible causes of ecological processes (Koenker et al., 1994; Dunham et al., 2002; Brown & Peet, 2003).

In practice, many ecologists are interested in the upper boundary (e.g. 99th quantile) of the conditional distribution of ecological responses (Cade & Guo, 2000). It is because that usually not all associated factors can be measured or included in ecology studies, while the upper limit set by the measured ones cannot be exceeded by inclusion of other possible factors (Cade & Noon, 2003). In terms of quantile regression modelling, an assumed parametric form of the relationship is required, but no hypothesis is made on the distributional form (e.g. normal, Poisson) of the random error portion of the analysis.

Multi-scale potential woody cover modelling

The scatterplot of fractional woody cover vs. MAP of the 1553 random MODIS pixels is shown in Figure 4.3. It is evident that the upper boundary of the fractional woody cover over the rainfall gradient is in a segmented shape. To quantify the potential woody cover pattern, a nonlinear 99th quantile regression was performed with package '*quantreg*' in the freeware R, with regard to that potential woody cover could be represented by 99th quantile of the observed fractional woody cover (Sankaran et al., 2005). Among others, the exponential function $y = a + c * \exp(-\exp(-b * (x - m)))$ proves the best fit to the scatterplot, which is confirmed by additional b-spline linear quantile regression. In this exponential function, y denotes potential woody cover, x denotes mean annual precipitation, a, b, c, and m are the parameters to be estimated. The fitted curve is overlaid on the scatterplot in red in Figure 4.3, and the details of the fitted exponential function are summarized in Table 4.1.

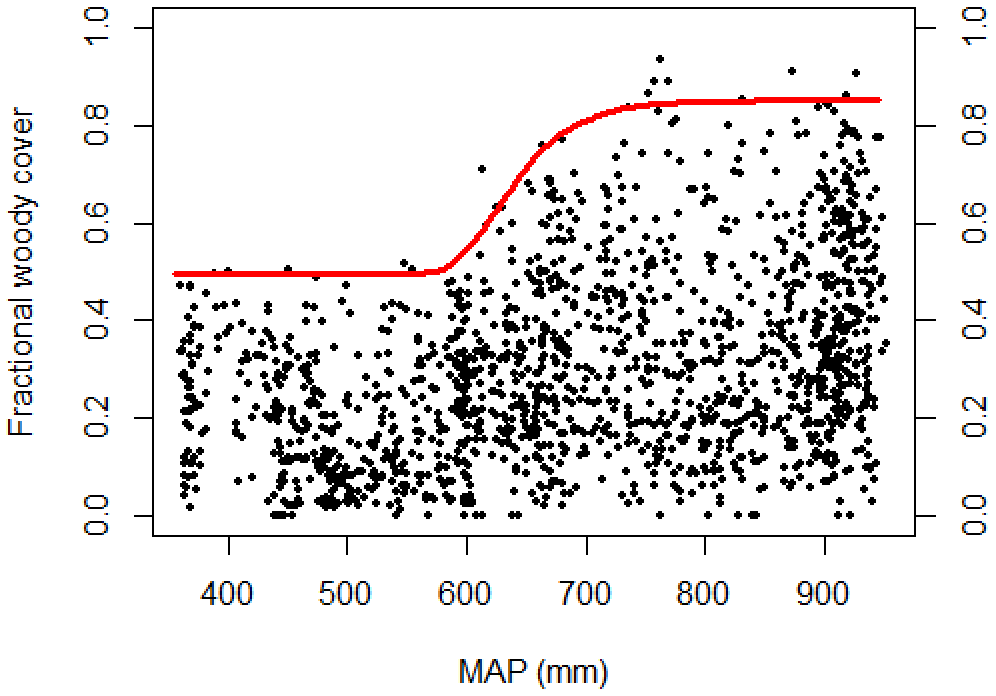


Figure 4.3: The scatterplot of fractional woody cover vs. MAP and the modelled potential woody cover pattern at MODIS scale (500m).

Table 4.1: Details of potential woody cover pattern at 500m scale.

Variable	Value	Standard error	t value	Pr (>| t |)
a	0.49591	0.01185	41.84749	0.00000
b	0.02797	0.01312	2.13148	0.03865
c	0.35510	0.02442	14.54305	0.00000
m	625.06304	12.21592	51.16789	0.00000

As mentioned before, 13 groups of Landsat pixels were retrieved. Each group of Landsat pixels correspond to a scatterplot of Landsat scale fractional woody cover vs. MAP. These scatterplots unanimously suggest an increasing upper boundary of fractional woody cover over the rainfall gradient. 1 of the 13 scatterplots is displayed in Figure 4.4, and all the other 12 scatterplots are displayed in the Appendix.

While various functions were tested for the 99th quantile regression, the simple linear function $y = a + b * x$ fits the upper boundary of Landsat scale fractional woody cover best, which was corroborated by segmented linear quantile regression. In this simple linear function, y represents potential woody cover, x represents mean annual precipitation, while a and b are the parameters to be estimated. The fitted lines are overlaid on the scatterplots in red in Figure 4.4 and in the Appendix, followed by details of the quantile regression.

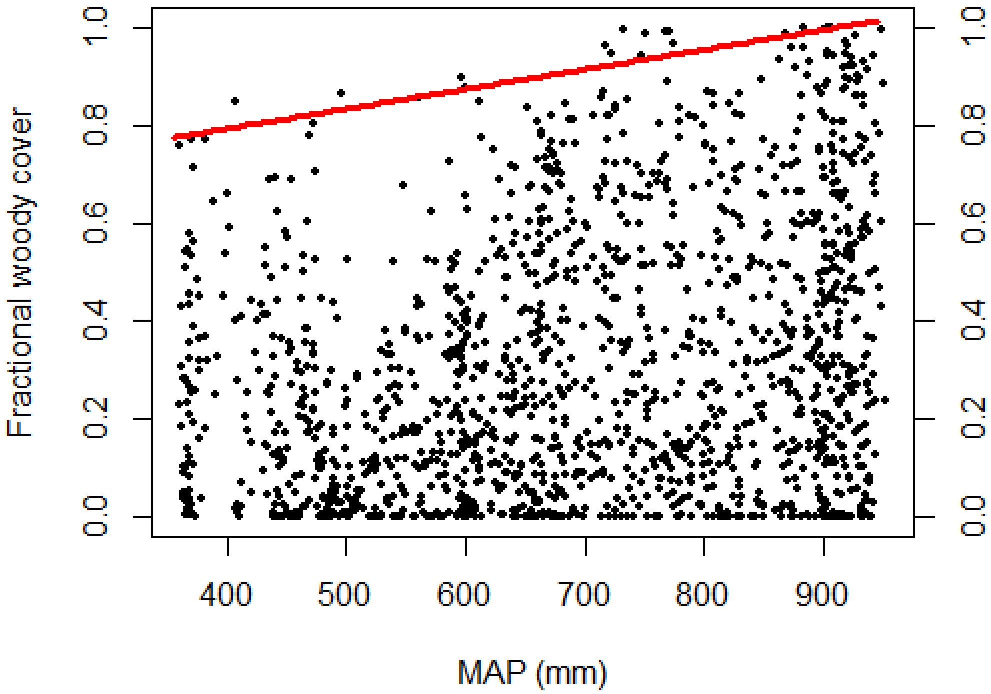


Figure 4.4: The scatterplot of fractional woody cover vs. MAP and the modelled potential woody cover pattern at Landsat scale (30m).

Table 4.2: Details of potential woody cover pattern at 30m scale.

Variable	Value	Standard error	t value	Pr (>| t |)
a	0.63102	0.04315	14.62517	0.00000
b	0.00041	0.00005	7.66339	0.00000

Result and discussion

Result

As shown in Figure 4.3, the curve of the potential woody cover at MODIS scale (500m) is in a sigmoid shape, suggesting a segmented relationship between potential woody cover and MAP (water availability) at MODIS scale in Texas savannas. The potential woody cover stays at a fixed level of about 50% below 600mm MAP, followed by an approximate positive linear relationship with MAP by 735mm MAP. From 735mm MAP on, the potential woody cover stays on a plateau value of about 87%. According to the threshold MAP values of 600mm and 735mm, Texas savannas could be divided into three sub-regions of arid savanna, semi-arid savanna, and mesic savanna (Figure 4.5).

As displayed in Figure 4.4 and the figures in appendix, analysis of the 13 sets of Landsat scale data unanimously suggests a positive linear relationship between potential woody cover and MAP at Landsat scale (30m). That is, potential woody cover increases linearly from about 80% to 100% over the rainfall gradient of 360 mm to 950 mm MAP.

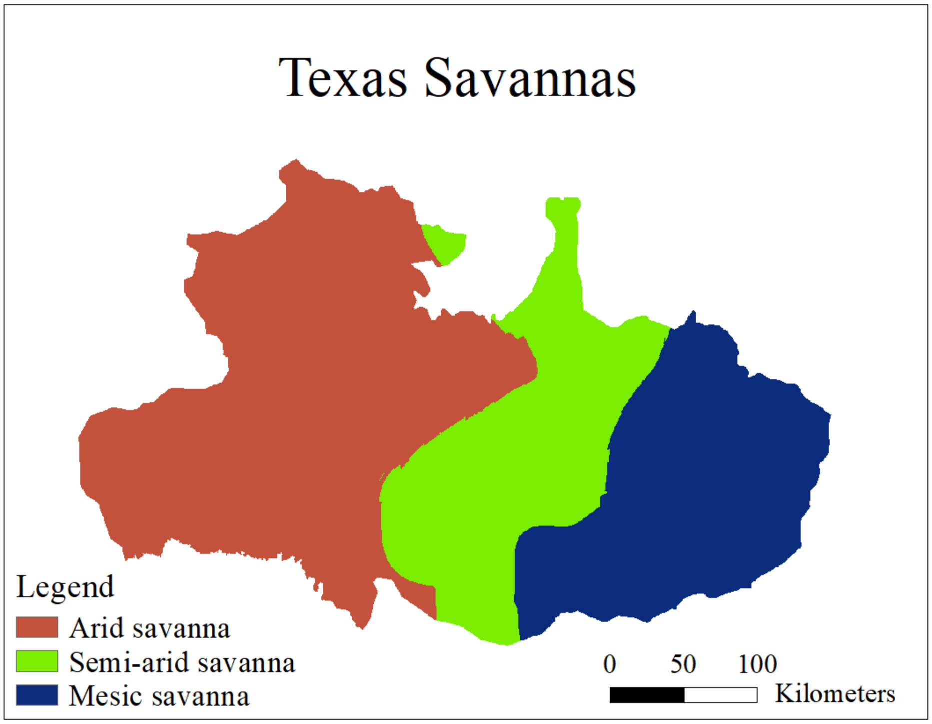


Figure 4.5: Division of Texas savannas into arid savanna, semi-arid savanna, and mesic savanna.

Discussion

This study explored the pattern of potential woody cover at both Landsat scale (10^2 m^2, micro-scale) and MODIS scale (10^{-1} km^2, local scale) over the rainfall gradient present in Texas savannas. While the potential woody cover increases linearly with MAP at Landsat scale, it exhibits a three-segment relationship with MAP at MODIS scale. This discrepancy corroborates the scale dependency of the primary determinants of savanna woody plant density (Gillson, 2004). At Landsat (micro) scale, woody plant density is susceptible to seed germination, plant interactions, and disturbances (e.g., selective herbivory, trampling) (Gillson, 2004). As for potential woody cover, it is suggested by this study that water availability is the primary determinant at Landsat (micro) scale.

At the MODIS (local) scale, woody plant density is suggested susceptible to patterns of seedling recruitment, which is more under the effect of factors such as disturbance than water availability (Gillson, 2004). It is further confirmed in this study by the pattern of potential woody cover at MODIS scale. Within the first and third segments of the rainfall gradient (360-600mm MAP, 735-950mm MAP), the potential woody cover does not increase with MAP (water availability), which suggests that potential woody cover at MODIS scale is also limited by other factors than water availability.

While potential woody cover is supposed to define the end-point of woody plant encroachment (Sankaran et al., 2005), the choice of appropriate spatial observation scale(s) is important, given the scale dependency of woody cover observation. It is illustrated by the discrepancy of the potential woody cover patterns at Landsat and MODIS scales. The choice of appropriate spatial scale(s) could be enlightened by the patch dynamics perspective, which considers that arid and semi-arid savannas are composed of discrete patches of a few hectares or smaller in size. While the exact size of the patches is constrained by the patchiness of rainfall, each patch cycles between woody and herbaceous dominance (Wiegand et al., 2006; Meyer et al., 2009). As for potential woody cover observation, the spatial scale should be large enough to consider all the effect factors but also small enough for operability. In comparison, MODIS scale is more reasonable than Landsat scale for potential woody cover observation. It is because that potential woody cover at MODIS scale is also under the effect of other factors than water availability, as discussed in the above paragraph.

The pattern of potential woody cover at MODIS scale also confirms the feasibility of patch dynamics perspective in arid and semi-arid savannas from a unique angle. In areas with MAP below 600mm, the potential woody cover is limited to 50%. It excludes the possibility of woodland formation and ensures the possibility of cyclical succession between woody and herbaceous dominance.

The MODIS scale (0.25 ha) in this study is close to the observation scale of the similar Africa study (0.25-0.5 ha) by Sankaran et al. (2005). However, while potential woody cover at MODIS scale exhibits a three-segment relationship with MAP in Texas savannas, it is in a two-segment relationship over a even wider rainfall gradient in African savannas. This discrepancy highlights the importance of the relatively underexplored factors such as woody species, soil characteristic, and climate seasonality (Yang et al., 2016).

Utilizing the MODIS VCF tree cover product, Yang et al. (2016) reveals a similar potential woody cover pattern with a much lower magnitude at 250m observation scale, compared to the MODIS scale (500m) pattern in this study. This similar pattern confirms the three-segment relationship between potential woody cover and MAP at MODIS scale in Texas savannas. It is also indicated that short woody plants in savanna ecosystems do appear in remote sensing imagery to some extent with similar spectral implication, though not included in the calibration data of the MODIS tree cover product. On the other hand, the much lower magnitude of potential woody cover by the MODIS tree cover product reveals its inefficiency in capturing short woody plants in savanna ecosystems. Furthermore, the comparison of potential woody cover patterns suggests a novel way for assessing the accuracy of MODIS tree cover product.

Conclusion

This study reveals the pattern of potential woody cover in Texas savannas at Landsat (micro) and MODIS (local) scales. The discrepancy at Landsat and MODIS scales corroborates the scale dependency of the primary determinants of woody plant density in savanna ecosystems. In comparison, however, MODIS scale is more reasonable for potential woody cover observation. Moreover, the discrepancy of the potential woody cover patterns in African savannas and Texas savannas highlights the role of the relatively understudied factors in controlling woody plant density such as woody species, soil characteristic, and climate seasonality. It is hinted as well that the pattern of potential woody cover could vary from region to region.

Different from the suggestion that long-term data are necessary for understanding the dynamics of savanna ecosystems (Gillson, 2004), this multi-scale analysis provides fresh insights into the dynamics of savanna ecosystems with static remote sensing data. It is important to note that the usage of the nationwide DOQQs was critical for this study. This study also exhibits the great potential of remote sensing and statistical analysis techniques in understanding the nature of complex ecosystems.

Chapter 5: The rate and effect factors of woody plant encroachment: a case study of Ashe juniper in Texas savannas

Abstract

Woody plant encroachment – the directional increase of trees, shrubs, and bushes in density, biomass and cover – has been observed worldwide in savanna ecosystems. While a lot of studies have been devoted to understanding the underlying mechanism of this phenomenon, many of them conclude exclusively in terms of the encroachment rate and relative importance of effect factors. Literature review suggests that these conflicts could be attributed to the variability of the existing studies in study area extent, woody species and life stages, spatial observation scale, and initial woody plant density of sample plots. Analysis targeted at specific woody species and life stages and over broad environmental gradients would provide more pertinent strategy for woody plant encroachment management. This research aims to analyze the encroachment rate of Ashe juniper at its early life stage at a hectare observation scale in Texas savannas, and analyze the role of mean annual precipitation (MAP) and woody plant density in the encroachment process. Remote sensing and statistical analysis techniques were applied. Research results suggest that MAP has a significant positive effect on the encroachment rate in the semi-arid region of Texas savannas (600mm < MAP < 735mm), but no significant effect in the mesic region (MAP > 735mm). It is revealed in the mesic region that the encroachment rate increases with woody plant density by a threshold density, then starts decreasing with woody plant density. This research demonstrates the varying role of the effect factors of woody plant encroachment. It is also indicated that the existing theories on tree-grass coexistence are not necessarily exclusive.

Key words: savanna, woody plant encroachment, mean annual precipitation, woody plant density, rainfall gradient, Ashe juniper

Introduction

Savanna ecosystems

Savannas are ecologically, economically, and culturally important ecosystems, characterized by the coexistence of woody and herbaceous vegetation as well as distinct dry season (Scholes & Archer, 1997). They cover about 33 million km^2 (approximately 20%) of the earth's terrestrial surface and exist across a wide range of conditions in terms of precipitation, soil nutrient content, fire regime, and herbivory level (Ramankutty & Foley, 1999). Mainly found in tropics and subtropics, savannas are home to a large proportion of human population, livestock and wildlife. Moreover, their net primary production (NPP) accounts for 30% of the whole terrestrial system (Grace et al., 2006). Furthermore, savanna ecosystems play an important role in global land-atmosphere energy balance, and in water, carbon, and nutrient cycles (Lal, 2004; Poulter et al., 2014; Liu et al., 2015). It has to be noted that the balance between woody and herbaceous components in savanna ecosystems is critical to their livestock production, biodiversity, and many other ecosystem functions (Sankaran et al., 2005).

Woody plant encroachment

Woody plant encroachment – the directional increase of woody plants (trees, shrubs, and bushes) at the expense of herbaceous vegetation in grassland and savanna communities – has been documented in many parts of the world, including Southern United States (Hobbs & Mooney, 1986; Archer, 1995; Fowler & Simmons, 2009; Creamer et al., 2013), South America (Cabral et al., 2003; Anadon et al., 2014), Australia (Murphy et al., 2014; Soliveres & Eldridge, 2014), and Africa (Van Vegten, 1984; Mitchard et al., 2011; Coetsee et al., 2013; O'Connor et al., 2014). It occurs across multiple land uses such as commercial ranches and reserved areas, and across different levels of precipitation (Fensham et al., 2005). The encroaching woody species vary among continents in terms of architectural traits and biological characteristics (Dantas & Pausas, 2013; Moncrieff et al., 2014). For instance, while African savannas are dominated by N-fixing woody species, N-fixing species only account for about 10% of South America savanna, and none of the dominant encroaching woody species was found N-fixing in Australian savannas (Stevens et al., 2017). In addition, trees of certain stem diameter in African savannas have twice canopy width of that in Australian savannas (Moncrieff et al., 2014).

Along with the encroachment, the allocation of plant biomass shifts from belowground to aboveground (McKinley et al., 2008). Moreover, it brings a lot of negative consequences to savanna ecosystems, in terms of livestock carrying capacity (Angassa & Baars, 2000; Anadon et al., 2014), species diversity (Ratajczak et al., 2012), ground water recharge (Gray & Bond, 2013), soil nutrient distribution (Throop & Archer, 2008), and soil carbon storage (Berthrong et al., 2012; Blaser et al., 2014). Both the scientific community and stakeholders such as residents, ranchers, and government/NGO agencies are concerned about the encroachment. A thorough understanding of the underlying mechanism of this phenomenon is urgently required for savanna management and restoration, especially given future changing climate and land use anticipated to worsen the scenario (Sala et al., 2000; House et al., 2003; Stocker, 2014).

Rate and effect factors of woody plant encroachment

Numerous effect factors were found to affect savanna structure and function (Scholes, 1993). Among them, climate (e.g. rainfall), soil nutrient content, fire regime, and herbivory level are recognized as 'key determinants', while all the other factors are related to these four key determinants and work through them (Frost et al., 1986; Walker, 1987; Skarpe, 1991; House et al., 2003). The manifested increase of woody plants in savannas is a response to the alteration of those biotic and abiotic factors (Roberts et al., 1987; Sankaran et al., 2008).

The rate and magnitude of woody plant encroachment were found to vary significantly across regions and continents (Stevens et al., 2017). The most rapid encroachment was observed in savannas of South America with reduced fire frequency and fragmented landscape. In the contrary, Australian savannas experienced the lowest level of encroachment. Under the same land management strategy, the encroachment rate observed in African savannas is two and a half times that of Australian savannas. The discrepancy of the encroachment rate and magnitude among regions and continents was supposed associated with factors such as fire regimes, stocking rate, and soil nutrient contents (Stevens et al., 2017).

Background

Many existing studies on woody plant encroachment conclude differently on the encroachment rate and relative importance of effect factors (House et al., 2003; Sankaran et al., 2004; Stevens et al., 2017). Literature review suggests that these conflicts could be attributed to the variation of those studies in study area extent, focus of woody species and life stages, observation scale, and initial status of sample plots (e.g., woody cover). The potential effects of these variations are discussed below.

Study area extent

The existing theories usually arise from small-scale or site-specific studies that focus on specific environmental processes and factors that are important under a given condition (House et al., 2003), which may not occur across all sites, gradients, or expanses. Given the wide range of geographic occurrence and the diversity of bioclimatic conditions of savanna ecosystems, it is possible that the role of the effect factors varies across different types of savannas (arid, semi-arid, and mesic) (Ramankutty & Foley, 1999). For instance, greater fluctuation in woody cover has been documented in sites receiving higher rainfall (Lehmann et al., 2009).

Woody species

The functional traits of woody plants such as architecture and N-fixing ability were suggested to determine their responsiveness to the biotic and abiotic factors and thus influence their encroachment rate (Stevens et al., 2017). For instance, trees with higher ratio of canopy diameter to stem diameter is supposed to have higher rates of woody cover increase than trees with a lower ratio under the same condition (Moncrieff et al., 2014). N-fixing species was found to encroach faster with increasing CO_2 concentration than other species (Stevens et al., 2017). Other than that, the length of growing season vary between deciduous and evergreen woody species (Bowman & Prior, 2005; Buitenwerf et al., 2015; Stevens et al., 2017), which is supposed to affect the encroachment rate.

Life stages of woody plants

Woody plants usually experience various life stages of seedling, juvenile, adulthood and mortality, and respond differently to external disturbance at different life stages (Sankaran et al., 2004; Wiegand et al., 2006). For instance, while fire is able to kill seedling and juvenile junipers, it has very minimal effect on mature junipers (Lyons et al., 2009). Moreover, it is evident that the rate of woody cover increase varies among those life stages. However, most of the existing research on woody plant encroachment does not take the life stages into account (Sankaran et al., 2008; Skowno et al., 2016; Devine et al., 2017), which may have biased their conclusion.

Observation scale

The coexistence of woody and herbaceous vegetation inherently implies the due consideration of spatial scale at which the coexistence occurs. For instance, though savanna spans over 33 million km^2 (approximately 20%) of the earth’s terrestrial surface (Ramankutty & Foley, 1999), the two contrasting life forms rarely coexist within a square decimeter. Moreover, the primary determinants of tree density were found to be scale-dependent (Gillson, 2004). Thus, it is possible that the encroachment rate and the relative importance of different effect factors are susceptible to the observation scale. And an explicit observation scale is necessary for comparability of different studies. However, the spatial issue was not taken into consideration thus far in most research addressing savanna questions (Sankaran et al., 2004).

Woody plant density

Initial woody cover is supposed to influence the process of woody plant encroachment through their effect on woody plant competition for water and soil nutrients (Walter, 1971). A negative relationship was found between initial woody cover and encroachment rate. That is, the highest encroachment rate was observed at sites of low initial woody cover, and the encroachment rate decreases with increasing woody cover (Roques et al., 2001). This relationship is supposed to be due to density dependence (Lehmann et al., 2014). Thus, initial woody cover should be taken into account when talking about woody encroachment rate.

Research objective

This research aims to overcome the aforementioned shortcomings of existing studies and draw more pertinent conclusion for savanna management. Specifically, it endeavors to understand the encroachment rate of Ashe juniper at its early life stage at a hectare scale, as well as the role of rainfall and initial woody cover in the encroachment process, over the broad rainfall gradient of Texas savannas.

Study area

This study will be tested in Texas savannas, located on the Edwards Plateau ecological region in central Texas (Figure 1.1). The Edwards Plateau is one of the important ecoregions of Texas, bordered with dry plains in west and moist prairies and woods in east. It is roughly in an oblong shape, and has thick and flat bedrock of hard early Cretaceous limestone. Soils are shallow (less than 10 inches) and rich in clay contents due to the origin of limestone (Schmid, 1969). The meaningful rainfall gradient in west-east direction is expansive enough to avoid artifacts associated with prior potentially idiosyncratic site-specific findings (Figure 1.2). Drought occurs periodically in this region, exhibiting long term effect on habitat resources and wildlife populations (Schmid, 1969).

During the past several decades, the highly undesirable Ashe juniper and redberry juniper (commonly called cedar) encroached much of the plateau (Archer, 1989; Fowler & Simmons, 2009; Creamer et al., 2013). The encroachment includes the expansion of existing woody plants and establishment of new woody plants (González, 2010).

Moreover, the encroachment raises broad and complex concerns in terms of livestock carrying capacity, species diversity, wildlife habitat, and rainfall effectiveness (Russell & Fowler, 1999, 2002, 2004; Taylor, 2008; Alofs & Fowler, 2010). For instance, the forage production of a closed juniper canopy is as little as one sixth of an open land. The “cedar break” has also greatly reduced plant diversity (Alofs & Fowler, 2010).

Ashe juniper and effect factors of encroachment

Ashe juniper, also called blueberry cedar, is selected as the study woody species. It is mostly found in the eastern and southern parts of the Edwards Plateau, and featured by a single trunk and rounded growth form (Lyons et al., 2009). Each tree has a gender of male or female and does not re-sprout after top killing. It pollinates in December, January, and February, whereas berry starts dispersing from November till April. Its berry production is prone to precipitation.

Ashe juniper contains volatile oils, which defends against herbivore and makes it minimally palatable to livestock (Lyons et al., 2009). Due to low its nutritional quality, Ashe juniper (berries and foliage) is only fairly fed on by deer when desirable browse is depleted (Lyons et al., 2009). It is vulnerable to fire at an early stage of less than 4 feet height. However, fire occurrence, especially wildland fire, has been very rare in this area during the past several decades (Archer, 1989; Fowler & Simmons, 2009). It is partially corroborated by MODIS burned area product (MCD45) since 2000. Previous research suggests that soil type has no significant effect on woody plant encroachment (Roques et al., 2001).

With regard to that herbivore, fire, and soil type have very minimal effect on Ashe juniper in Texas savannas, they are not investigated in this study. Instead, rainfall and initial woody cover could play a significant role in the encroachment process of Ashe juniper through their effect on seedling establishment and woody plant vigor (O'Connor, 1995; Roques et al., 2001). Given so, rainfall and initial woody cover are the focus of this study.

Methodology

Study period

Woody plant encroachment is suggested to be a successional and relatively slow process, which occurs over a decadal time scale (Archer, 1989; Hudak & Wessman, 1998). In consideration of the availability of 1m resolution Digital Orthophoto Quarter Quads (DOQQs) of the study area, the whole study period was set as 1996-2014. However, the encroachment of Ashe juniper will be observed in the two time periods of 1996-2004 and 2004-2014 respectively.

In terms of life stage, the stages of seedling establishment and young tree growth are the main focus of this study, which are also the key stages of woody plant encroachment. The duration of the study period of 1996-2014 is roughly a good match to that of seedling establishment and young tree growth (Lyons et al., 2009).

Field survey and plots sampling

Since most Texas land is privately owned and fenced, access to Ashe juniper plots is limited to roadside. Fortunately, Google Earth offers an effective alternative for plots sampling. The very high spatial resolution imagery and the multi-angle view in Google Earth provide an almost onsite view of the trees. Moreover, the successive images across seasons can filter deciduous woody species from Ashe juniper, which is evergreen. Furthermore, the architectural traits of Ashe juniper such as isolated and rounded growth form easily distinguish them from other species.

Initially, a cognitive procedure was performed. That is, roadside Ashe juniper plots were located across the study area in Google Earth. These roadside plots were then validated by field survey. Then based on the experience and knowledge, Ashe juniper plots were sampled across the semi-arid savanna and mesic savanna in Texas.

Several criteria were applied in the sampling of Ashe juniper plots. Firstly, the topography of the plots is relatively flat, ensuring the representativeness of local rainfall as water availability. Secondly, the size of the plots is limited to around one hectare, ensuring uniform observation scale. Thirdly, woody cover of the plots at the starting point of observation (in 1996) is limited to a low level, ensuring the focus on early life stages. Fourthly, the plots were free of human cultivation, during the observation period of 1996-2004 or 2004-2014. This criterion was reached by checking through the successive very high spatial resolution imagery in Google Earth that dates back to 1995. The distribution of sample plots across the semi-arid savanna and mesic savanna in each time period is displayed in Figure 5.1 and Figure 5.2 respectively, and the number of sample plots is summarized in Table 5.1.

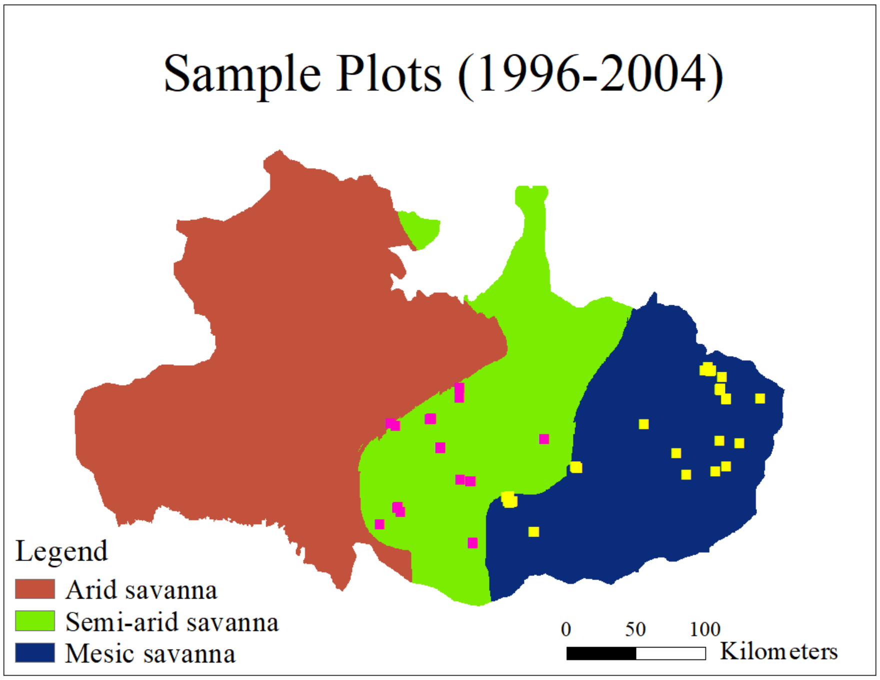


Figure 5.1: The distribution of sample plots for the time period 1996-2004.

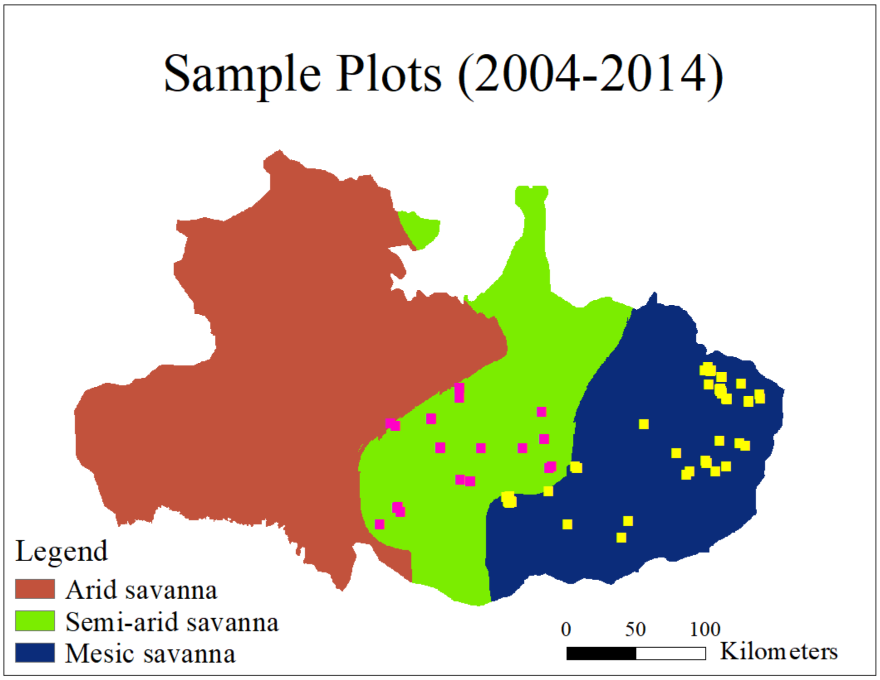


Figure 5.2: The distribution of sample plots for the time period 2004-2014.

Table 5.1: Number of sample plots.

	1996-2004	2004-2014
Semi-arid area	28	27
Mesic area	42	67

Data

Dependent variable

The 1m resolution Digital Orthophoto Quarter Quads (DOQQs) of 1996 (color-infrared imagery), 2004 (color-infrared imagery), and 2014 (natural-color/color-infrared imagery) were utilized. They were obtained from Texas Natural Resources Information System (TNRIS). The multi-spectral bands of the DOQQs as well as the imaging time of growing season greatly facilitate the classification of woody plants of various heights from the background. Moreover, the consistent 1m spatial resolution ensures the comparability of woody cover classification across time (Laliberte et al., 2004).

Images of 1996, 2004, and 2014 of each plot were clipped out of the DOQQs. Each image was classified into 10 thematic classes by unsupervised pixel-based classification. Each class was then attributed as woody plant or non-woody plant, taking the natural-color or color-infrared imagery as reference. Based on the classification results, mean annual encroachment rate was calculated for each sample plot, for the time period of 1996-2004 or 2004-2014. The mean annual encroachment was standardized into the unit of mean annual encroachment per hectare (m^2 $year^{-1}$/ha).

Independent variables

Initial woody cover (woody cover in 1996 for time period 1996-2004, woody cover in 2004 for time period 2004-2014) was calculated for each plot in percentage (%). Mean annual precipitation of 1981 to 2010 was used as an approximation of water availability in this area (Figure 1.2)

Analysis and result

The analysis was conducted in semi-arid savanna and mesic savanna separately to test the varying role of water availability and woody plant density. Moreover, to avoid temporal autocorrelation, the analysis was performed for the two time periods of 1996-2004 and 2004-2014 separately. The standardized mean annual encroachment rate (m^2 year^{-1}/ha) was related to (1) mean annual precipitation (MAP), and (2) initial woody cover (%).

The role of MAP in woody plant encroachment

In semi-arid savanna

The scatterplots of standardized mean annual encroachment rate vs. MAP in the semi-arid savanna are displayed in Figure 5.3. The encroachment rate ranges from 34 m^2 year^{-1}/ha to 365 m^2 year^{-1}/ha in the time period of 1996-2004, while it ranges from 78 m^2 year^{-1}/ha to 430 m^2 year^{-1}/ha in 2004-2014. Linear regression analysis suggests that mean annual precipitation has a significant positive effect on the encroachment rate in both time periods.

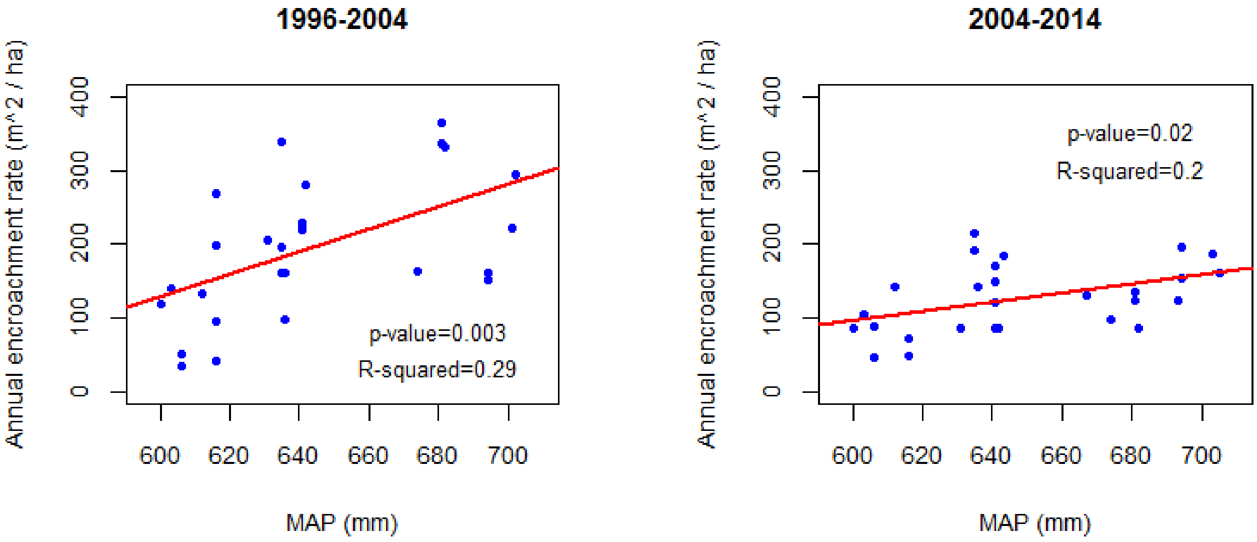


Figure 5.3: The role of MAP in woody plant encroachment in semi-arid savanna.

In mesic savanna

The scatterplots of standardized mean annual encroachment rate vs. MAP in the mesic savanna are displayed in Figure 5.4. The encroachment rate ranges from 46 m^2 $year^{-1}$/ha to 214 m^2 $year^{-1}$/ha in the time period of 1996-2004, while it ranges from 114 m^2 $year^{-1}$/ha to 318 m^2 $year^{-1}$/ha in 2004-2014. Linear regression analysis suggests that there is no significant relationship between the encroachment rate and mean annual precipitation in both time periods.

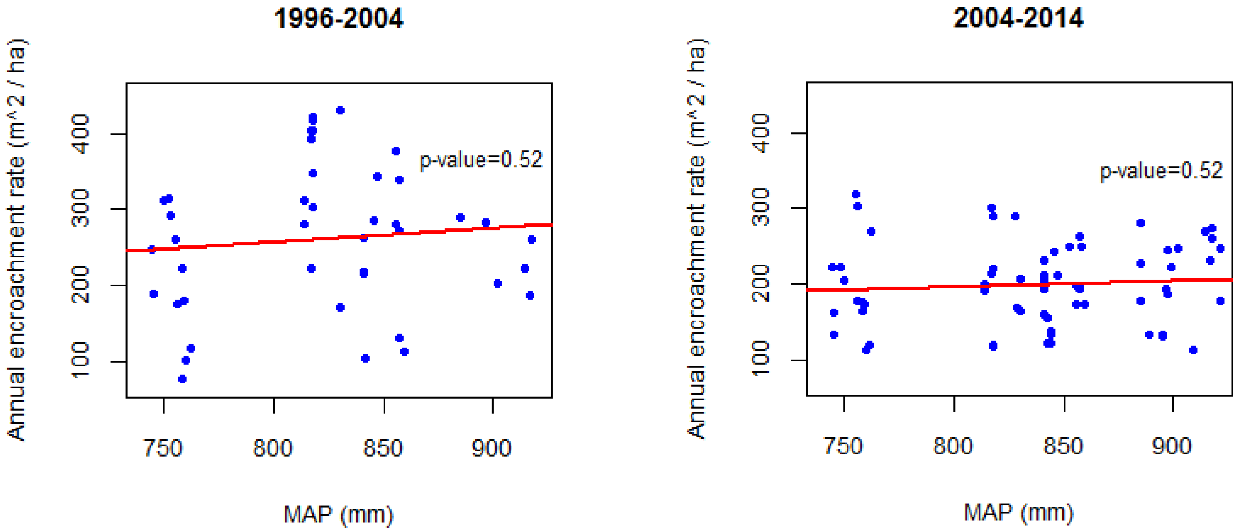


Figure 5.4: The role of MAP in woody plant encroachment in mesic savanna.

The role of woody plant density in woody plant encroachment

In semi-arid savanna

The scatterplots of standardized mean annual encroachment rate vs. initial woody cover (density) in the semi-arid savanna are displayed in Figure 5.5. Statistical analysis suggests that there is no significant relationship between the encroachment rate and initial woody cover in both time periods in the semi-arid savanna.

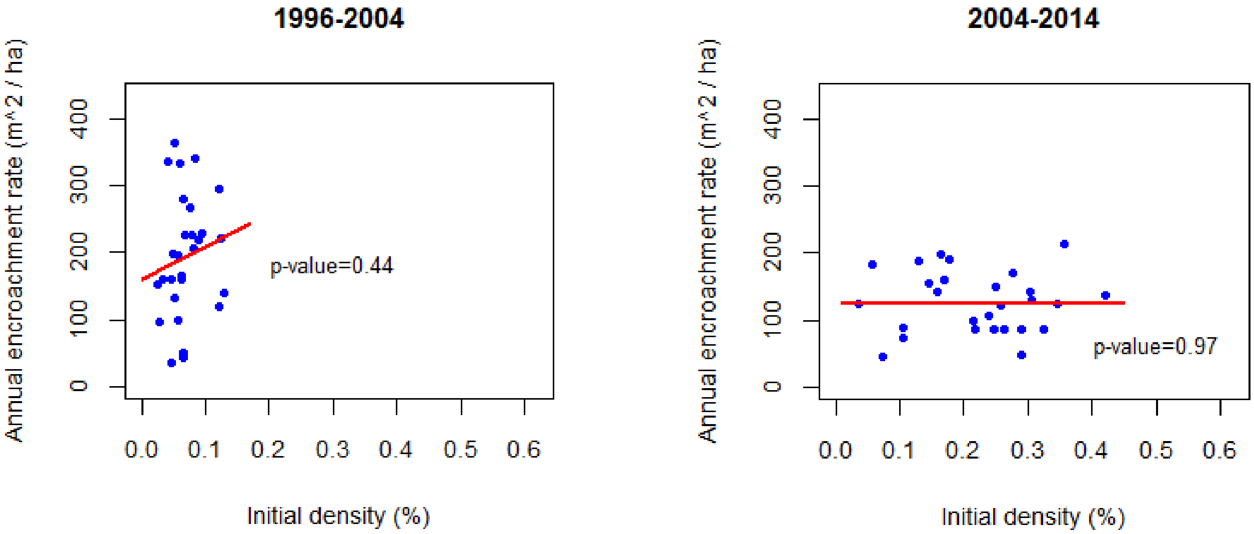


Figure 5.5: The role of woody plant density in woody plant encroachment in semi-arid savanna.

In mesic savanna

The scatterplots of standardized mean annual encroachment rate vs. initial woody cover (density) in the mesic savanna are displayed in Figure 5.6. It is evident in both scatterplots that the encroachment rate increases with woody plant density till a threshold density, and then starts decreasing with woody plant density. A quadratic function was fitted between the encroachment rate and initial woody plant density in each scatterplot. The fitted curves and details are overlaid on the scatterplots.

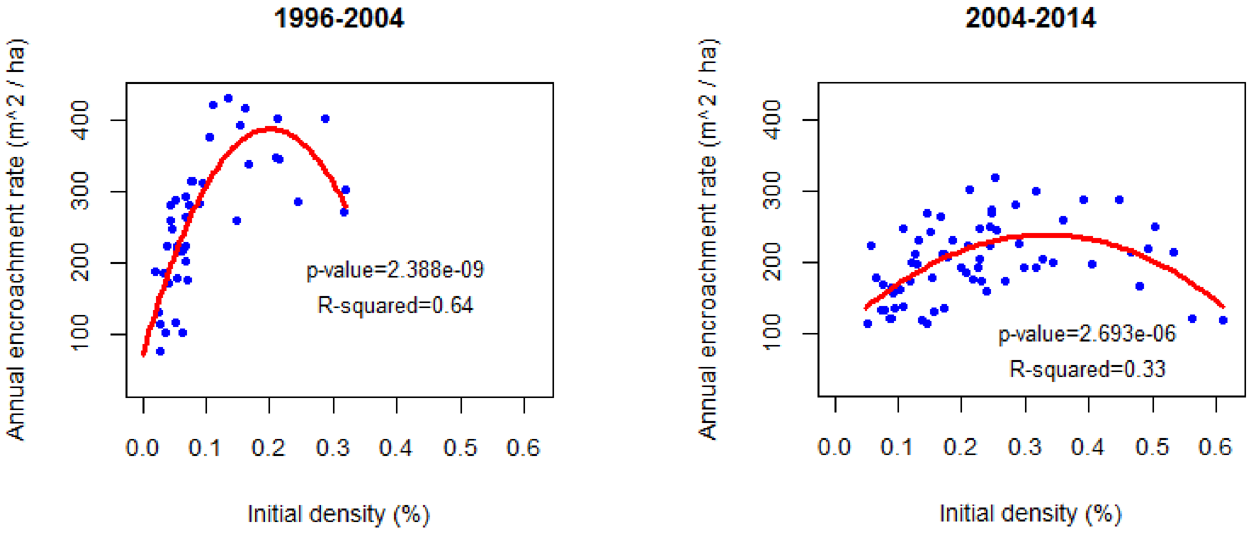


Figure 5.6: The role of woody plant density in woody plant encroachment in mesic savanna.

Discussion and conclusion

The standardized mean annual encroachment rate of Ashe juniper varies from 34 m^2 year^{-1}/ha to 430 m^2 year^{-1}/ha across the semi-arid savanna and mesic savanna, under different conditions of mean annual precipitation and woody plant density. While the lowest encroachment rate was observed in the semi-arid savanna in the time period of 1996-2004, the most rapid rate was observed in the mesic savanna in the same period. The variation of the role of water availability (MAP) and woody plant density in woody plant encroachment across semi-arid and mesic savannas is summarized in Table 5.1.

Table 5.2: Variation of the role of water availability (MAP) and woody plant density in woody plant encroachment across semi-arid savanna and mesic savanna.

	Semi-arid savanna	Mesic savanna
Water availability	Significant	Non-significant
Woody plant density	Non-significant	Significant

With regard to the role of mean annual precipitation in the encroachment process, it varies over the rainfall gradient. That is, while it imposes a significant positive effect on the encroachment rate in the semi-arid savanna (Figure 5.3), it has no significant effect in the mesic savanna (Figure 5.4). It agrees with the conclusion of chapter 4 that water availability is a limiting factor of woody plant growth in semi-arid savanna, but not in the mesic savanna.

In comparison of the two R-squared values of the fitted lines in Figure 5.3, mean annual precipitation exhibits a stronger effect in the time period 1996-2004 than that in 2004-2014. As shown in Figure 5.5, the initial woody cover is much lower in 1996-2004 than that in 2004-2014. It is thus indicated that Ashe juniper encroachment is more susceptible to water availability in earlier life stage.

With regard to the role of woody plant density in the encroachment process, it varies as well. In the semi-arid savanna, there is no significant relationship between the encroachment rate and initial woody cover (Figure 5.5). In the mesic savanna, however, the encroachment rate increases with woody plant density till a threshold density, and then starts decreasing with woody plant density (Figure 5.6). It is hinted that facilitative effect dominates among woody plants at lower density, while it shifts to competition by a certain point of woody plant density with woody plant encroachment.

In comparison of the two scatterplots in Figure 5.6, the one of 2004-2014 shows a higher average woody plant density than that of 1996-2004, while the fitted curve in 1996-2004 has a much higher R-squared value than that in 2004-2014. It is indicated that Ashe juniper encroachment is more susceptible to woody plant density in earlier life stage. In comparison, the scatterplot of 1996-2004 reaches a higher peak at a lower woody plant density. This could be attributed to the shorter duration of the time period 1996-2004. That is, the longer duration of the time period 2004-2014 flattens the average encroachment rate.

In conclusion, this research documented one example of Ashe juniper encroachment in Texas savannas. Importantly, this research quantified the rate of Ashe juniper encroachment, as well as the role of water availability (MAP) and woody plant density in the encroachment. It is suggested that the rate and potential causes of woody plant encroachment are savanna regions-specific (Stevens et al., 2017). Regional context such as rainfall and biological traits of woody species is critical to understand the trend of woody plant encroachment (Lehmann et al., 2009).

This research provides more well-targeted insight into the dynamics of Texas savannas. It should also be noted that the research methods are generic and can be applied in cases of different encroaching woody species or savanna ecosystems. Moreover, it highlights the application of remote sensing and statistical analysis techniques in understanding the dynamics of complex ecosystems.

Chapter 6: Conclusion

With the phenomenon of woody plant encroachment being observed worldwide in savanna ecosystems, this dissertation research aims to improve our understanding of the dynamics of savanna ecosystems and provide insights on savanna management and restoration. It was tested in Texas savannas in central Texas, featured by a wide rainfall gradient. It centers on three themes: (1) methodology exploration of fractional woody cover mapping at fine spatial scale (Landsat scale), for close and continuous woody plant encroachment monitoring, (2) potential woody cover (*maximum realizable woody cover that a given site can support*) modelling over the present rainfall gradient, for implication of the end-point of woody plant encroachment, (3) analysis of the rate and effect factors of woody plant encroachment, for pertinent management strategy. This dissertation research highlights the application of remote sensing, GIS, and statistical analysis in understanding the dynamics of complex ecosystems.

Contribution of this dissertation research

This dissertation contributes to the literature in the following areas.

Fractional woody cover mapping in savanna ecosystems

Compared to traditional discrete classification scheme, fractional coverage mapping of landscape components is more accurate and can better depict spatially complex landscapes. It has greater potential in land use/land cover study. This is especially true for savanna ecosystems, which are featured by the mixture of woody plants, herbaceous vegetation, and barren land. This study sets up protocols for close and continuous monitoring of woody plant encroachment in savanna ecosystems by medium to coarse spatial resolution remote sensing data, as verified through high resolution (1m) digital orthophotos. It may also contribute to best practices of landscape components mapping over large areas in other ecosystems with these and other sensor systems. Moreover, the success of this study demonstrates the potential and advantage of the Web-Enabled Landsat Data (WELD) in land use/land cover study. The occurrence of overestimation in sparse woody area and underestimation in dense woody area informs the direction of critically needed next steps in research, notably in structurally complex regions and in systems where a high percentage of short woody plants exists.

Potential woody cover modelling in savanna ecosystems

This study reveals the pattern of potential woody cover over the present rainfall gradient in Texas savannas at Landsat (30m) and MODIS (500m) scales respectively. While potential woody cover exhibits a positive linear relationship with mean annual precipitation (MAP) at Landsat scale, it is in a three-segment relationship with MAP at MODIS scale. This discrepancy corroborates the scale dependency of the primary determinants of savanna woody plant density. In comparison, MODIS scale is more pertinent for savanna management since it is expansive enough to consider all the effect factors but also small enough for operability. Moreover, the discrepancy of the potential woody cover patterns in African savannas and Texas savannas highlights the role of relatively understudied factors in savanna woody plant density, including woody species, soil characteristic, and climate seasonality. It is thus possible that the pattern of potential woody cover would vary across regions and continents. Opposed from the suggestion that long-term data are necessary for understanding the dynamics of savanna ecosystems (Gillson, 2004), this multi-scale analysis provides fresh insights into savanna dynamics with static remote sensing data.

Woody plant encroachment analysis in savanna ecosystems

This study documents one example of Ashe juniper encroachment in semi-arid and mesic regions of Texas savannas. It analyzes the rate of Ashe juniper encroachment, as well as the role of water availability (MAP) and woody plant density in the encroachment. It is suggested that water availability has a significant positive effect on the encroachment rate in the semi-arid savanna, but no significant effect in the mesic savanna. While the rate of woody plant encroachment is susceptible to woody plant density in mesic savanna, it is not in semi-arid savanna.

This study suggests that the rate and potential causes of woody plant encroachment are savanna regions-specific (Stevens et al., 2017). Regional context such as rainfall and biological traits of woody species is critical to understand the trend of woody plant encroachment (Lehmann et al., 2009). It should be noted that the research methods are generic and can be applied in cases of different encroaching woody species or savanna ecosystems.

Future research direction

In the future, I expect to further this dissertation research in the following areas.

Fractional woody cover mapping in savanna ecosystems

Single-date images, repeatedly composited data (*e.g. monthly maximum NDVI*) and annual multi-temporal metrics (*e.g., maximum annual near-infrared value*) (Hansen et al., 2002) derived from time series remote sensing data (*e.g., MODIS*) will be tested in landscape components (e.g., woody plants, herbaceous vegetation) mapping in savanna and other ecosystems. The advantages and disadvantages of each data format will be illustrated, to enlighten the choice of appropriate data under a specific scenario.

Though fragmentation information of landscape components is supposed to improve their fractional mapping (Hansen et al., 2002), it is rarely tested. In future research, I will incorporate the fragmentation information derived from fine spatial resolution data (*e.g., Landsat*) to model the fractional coverage of landscape components at coarse scale (*e.g., MODIS scale*).

Thus far, various statistical approaches have been applied in fractional landscape components mapping (Schwarz & Zimmermann, 2005; Brandt et al., 2016). Among others, decision trees, linear mixture models, and generalized linear models have been popular in literature. In future research, the strengths and weaknesses of those three approaches will be tested. Texas savannas, featured by a wide rainfall gradient and an accompanying woody cover gradient, provide a comprehensive laboratory for this test.

Potential woody cover modelling in savanna ecosystems

In response to the scale dependency of woody cover observation, my future research would further investigate the scale dependency of potential woody cover in savanna ecosystems by modelling potential woody cover pattern over rainfall gradient at other spatial observation scales (*e.g., 100m*, *250m*). The scale dependency of potential woody cover pattern would enrich our understanding of the dynamics of savanna ecosystems and enrich the scale-pattern-process literature in ecology study.

As discussed before, the potential woody cover pattern of Texas savannas differs from that of African savannas. The discrepancy could be attributed to the relatively understudied factors such as woody species, soil characteristic, and climate seasonality. With that regard, the variations in these factors across regions and continents underscore the necessity of species- or soil type-specific analysis of potential woody cover pattern, which would enhance our understanding of the complex nature of savanna ecosystems.

Woody encroachment analysis in savanna ecosystems

The rate and effect factors of woody plant encroachment are supposed to vary among woody species and life stages (Lyons et al., 2009; Stevens et al., 2017). In that regard, different conclusions could be expected in future research on woody plant encroachment that targets at different woody species at different life stages. These woody species- and life stages-specific conclusions will provide more pertinent strategy on savanna management and restoration.

Appendices

The other 12 of the 13 scatterplots of Chapter 4 of Landsat scale fractional woody cover vs. mean annual precipitation, and the modelled potential woody cover patterns (red lines) are displayed here. Each modelled pattern is followed by the details of the 99th quantile regression of function $y = a + b*x$. In this simple linear function, y represents potential woody cover, x represents mean annual precipitation, while a (intercept) and b (coefficient of x) are the parameters to be estimated.

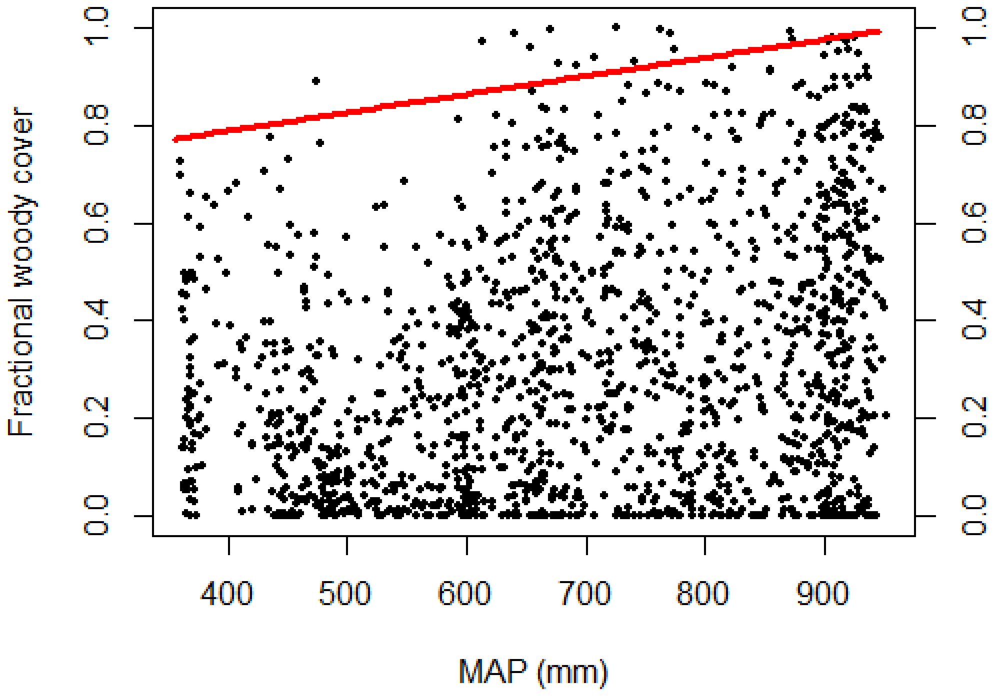


Figure A.1: The second of the 13 scatterplots and modelled potential woody cover pattern.

Table A.1: Details of the second modelled potential woody cover pattern.

Variable	Value	Standard error	t value	Pr (>| t |)
a	0.63823	0.10011	6.37565	0.00000
b	0.00038	0.00012	3.19343	0.00143

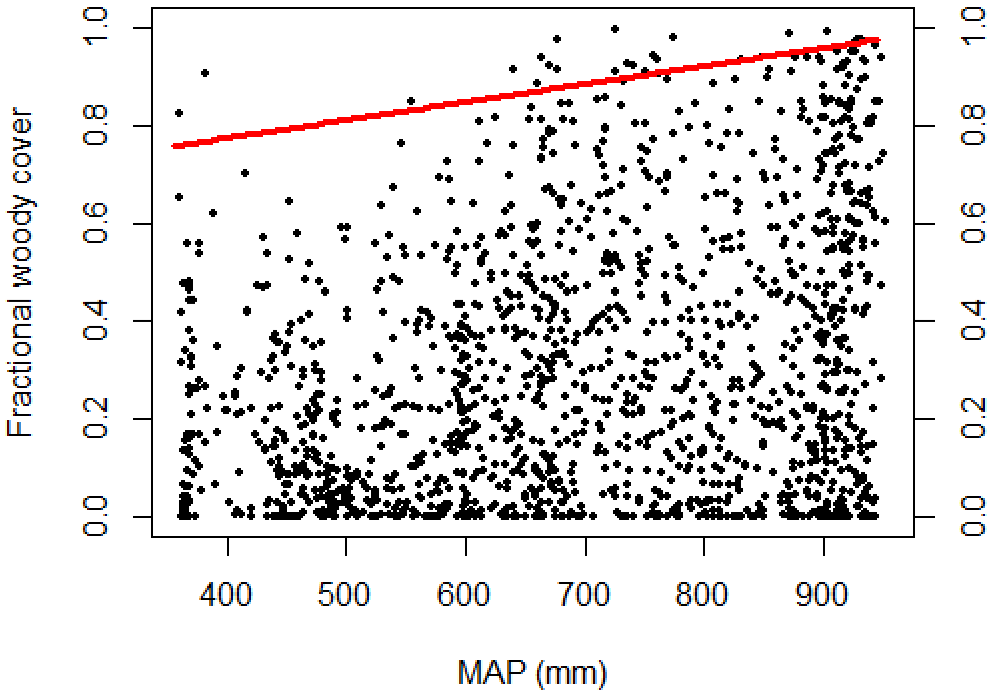


Figure A.2: The third of the 13 scatterplots and modelled potential woody cover pattern.

Table A.2: Details of the third modelled potential woody cover pattern.

Variable	Value	Standard error	t value	Pr (>| t |)
a	0.62584	0.11547	5.41979	0.00000
b	0.00037	0.00014	2.61754	0.00894

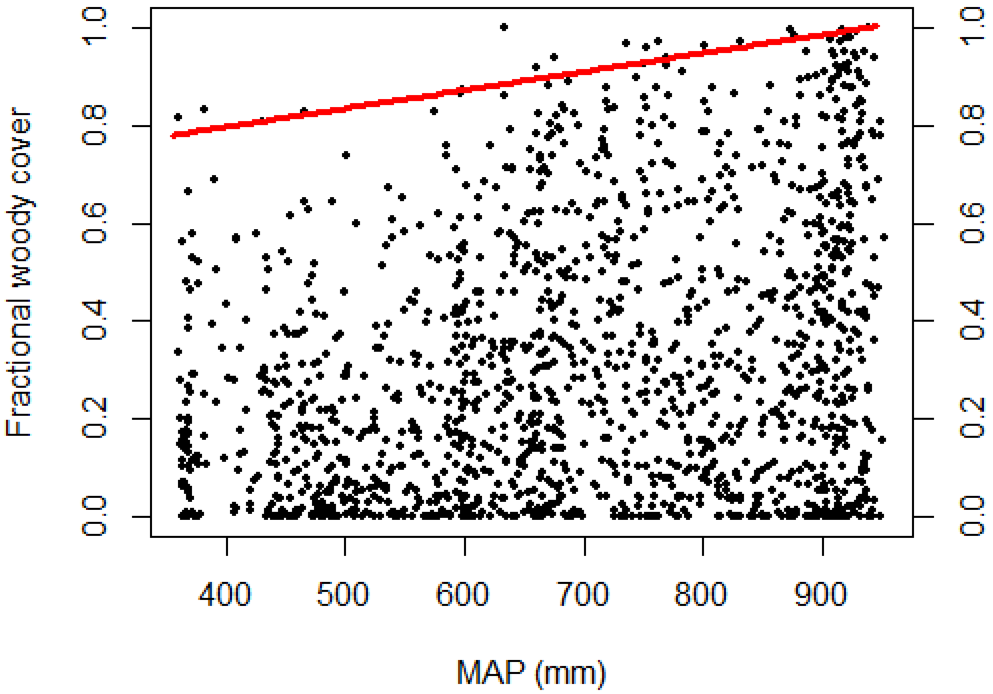


Figure A.3: The fourth of the 13 scatterplots and modelled potential woody cover pattern.

Table A.3: Details of the fourth modelled potential woody cover pattern.

Variable	Value	Standard error	t value	Pr (>| t |)
a	0.64588	0.06789	9.51304	0.00000
b	0.00038	0.00008	4.62871	0.00000

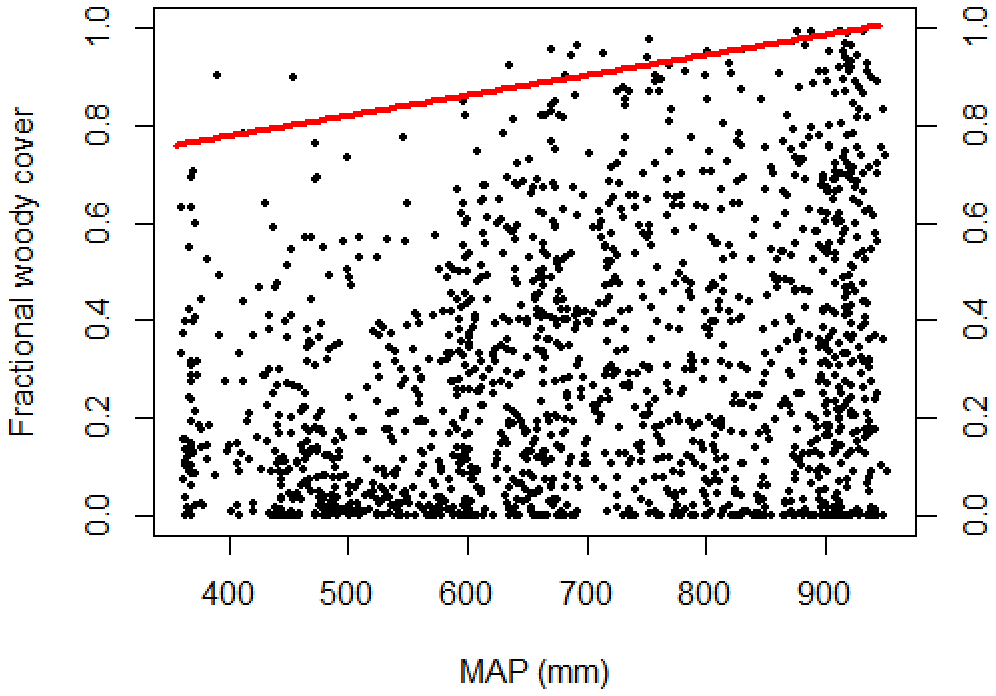


Figure A.4: The fifth of the 13 scatterplots and modelled potential woody cover pattern.

Table A.4: Details of the fifth modelled potential woody cover pattern.

Variable	Value	Standard error	t value	Pr (>| t |)
a	0.61205	0.09711	6.30242	0.00000
b	0.00042	0.00011	3.69401	0.00023

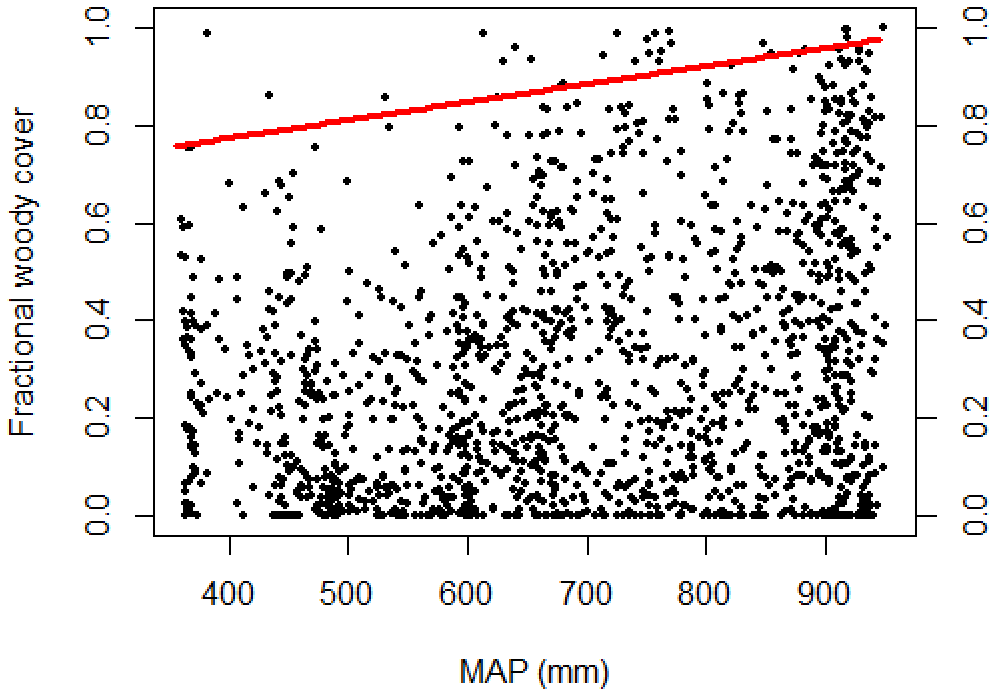


Figure A.5: The sixth of the 13 scatterplots and modelled potential woody cover pattern.

Table A.5: Details of the sixth modelled potential woody cover pattern.

Variable	Value	Standard error	t value	Pr (>| t |)
a	0.62584	0.10243	6.10987	0.00000
b	0.00037	0.00013	2.94977	0.00323

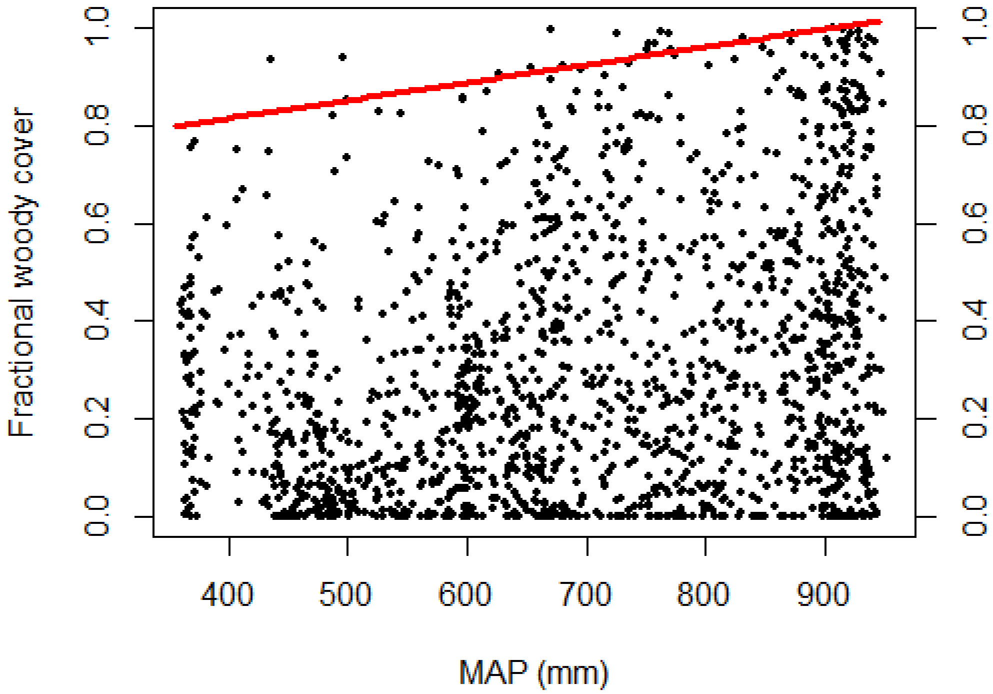


Figure A.6: The seventh of the 13 scatterplots and modelled potential woody cover pattern.

Table A.6: Details of the seventh modelled potential woody cover pattern.

Variable	Value	Standard error	t value	Pr (>| t |)
a	0.66820	0.07871	8.48992	0.00000
b	0.00037	0.00009	3.88193	0.00011

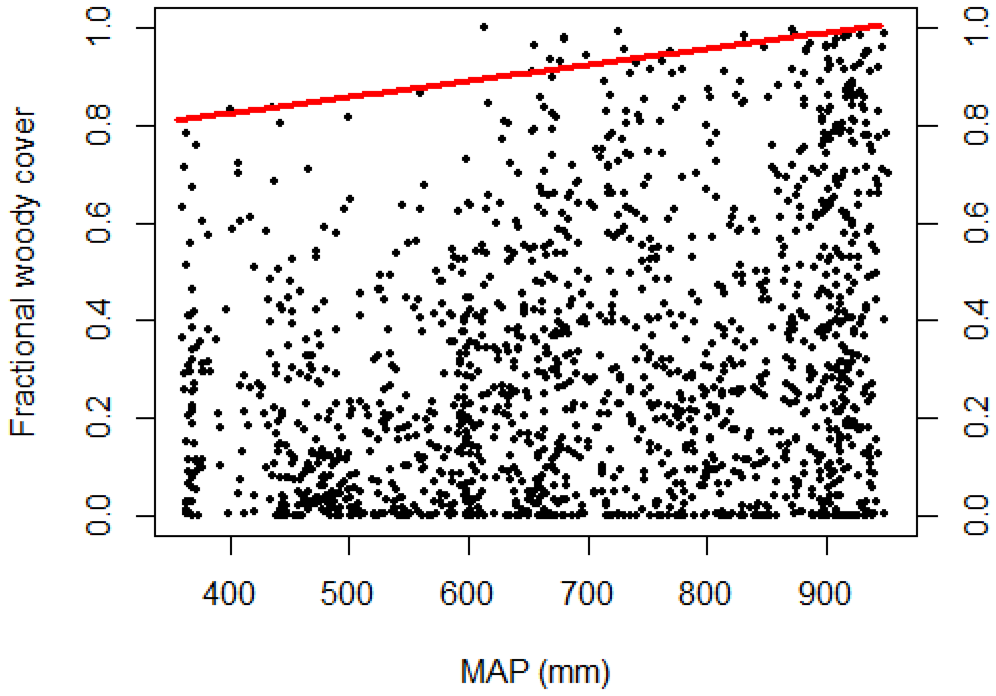


Figure A.7: The eighth of the 13 scatterplots and modelled potential woody cover pattern.

Table A.7: Details of the eighth modelled potential woody cover pattern.

Variable	Value	Standard error	t value	Pr (>| t |)
a	0.69231	0.03996	17.32303	0.00000
b	0.00033	0.00005	6.75456	0.00000

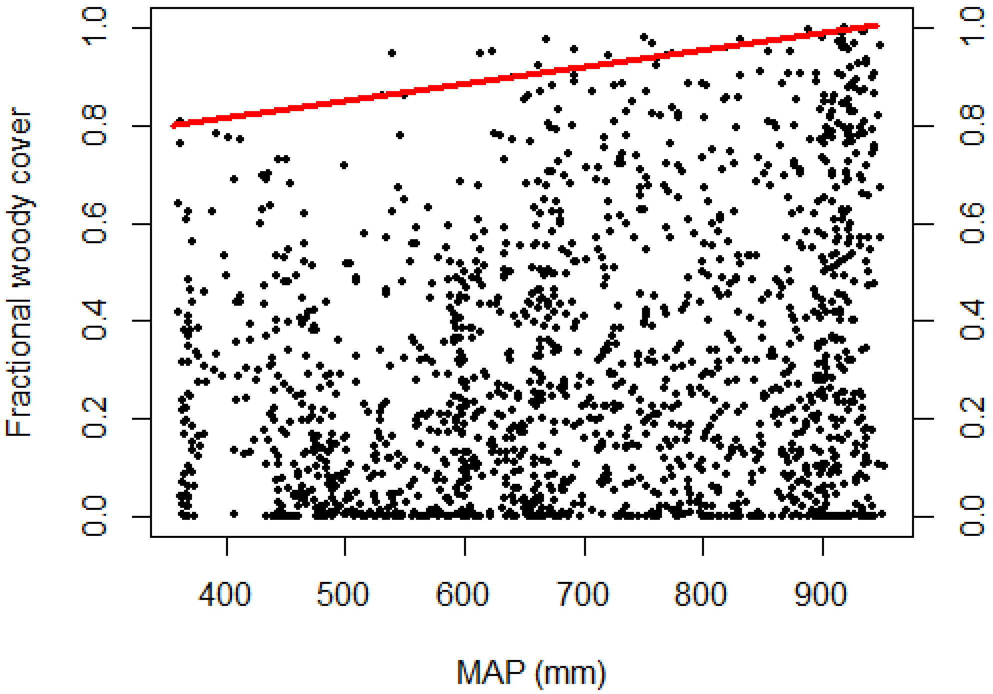


Figure A.8: The ninth of the 13 scatterplots and modelled potential woody cover pattern.

Table A.8: Details of the ninth modelled potential woody cover pattern.

Variable	Value	Standard error	t value	Pr (>| t |)
a	0.67664	0.04479	15.10654	0.00000
b	0.00035	0.00005	6.36626	0.00000

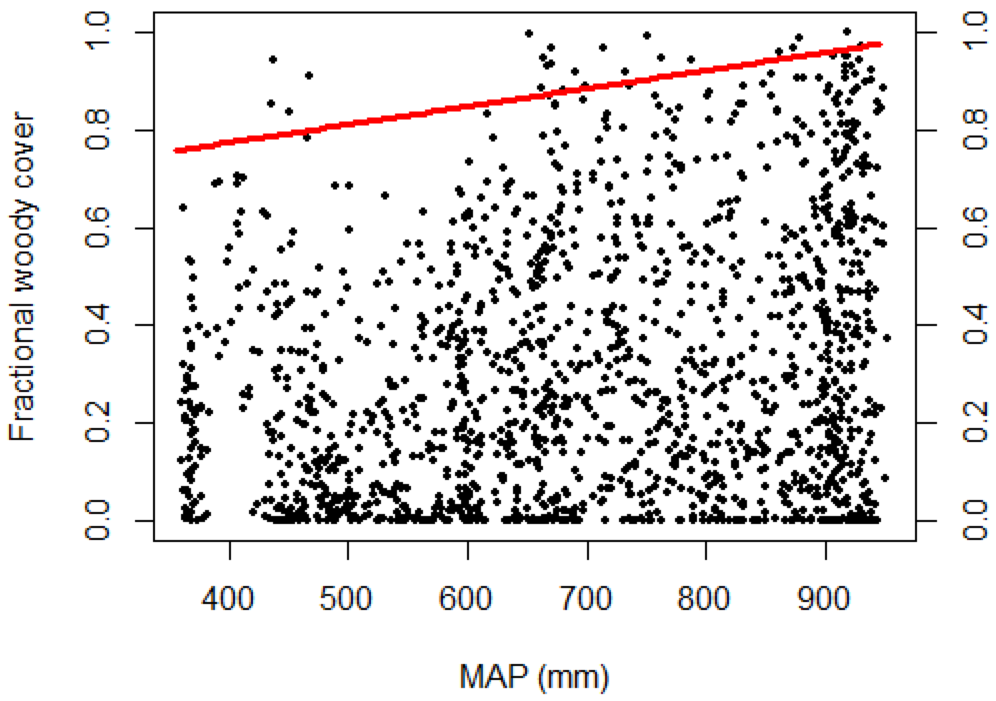


Figure A.9: The tenth of the 13 scatterplots and modelled potential woody cover pattern.

Table A.9: Details of the tenth modelled potential woody cover pattern.

Variable	Value	Standard error	t value	Pr (>| t |)
a	0.62584	0.10527	5.94531	0.00000
b	0.00037	0.00013	2.85333	0.00438

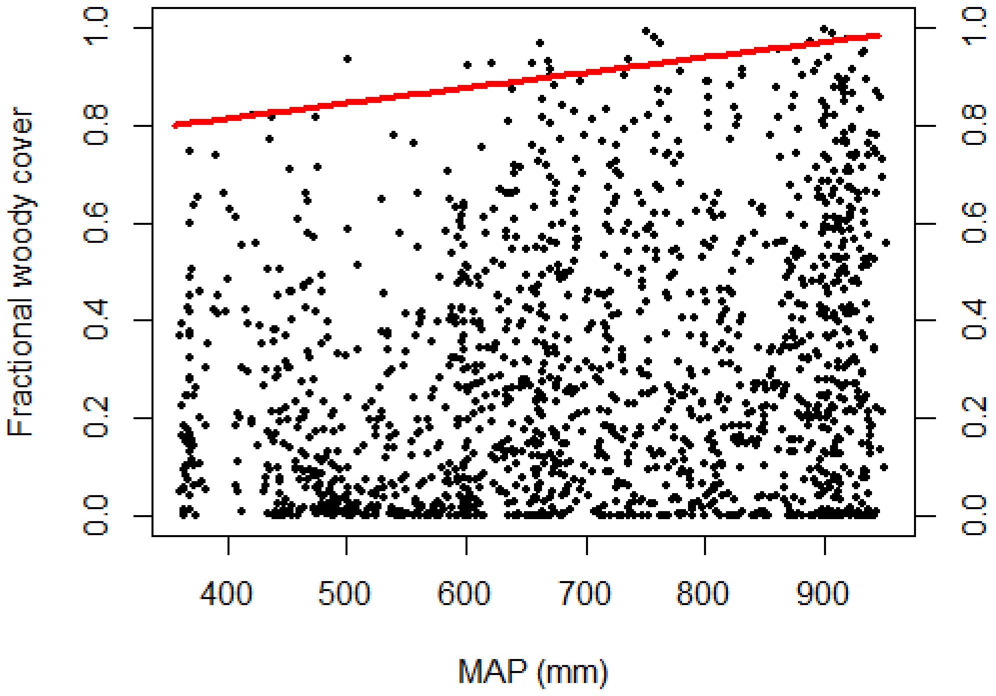


Figure A.10: The eleventh of the 13 scatterplots and modelled potential woody cover pattern.

Table A.10: Details of the eleventh modelled potential woody cover pattern.

Variable	Value	Standard error	t value	Pr (>| t |)
a	0.68865	0.06361	10.82656	0.00000
b	0.00031	0.00008	3.98164	0.00007

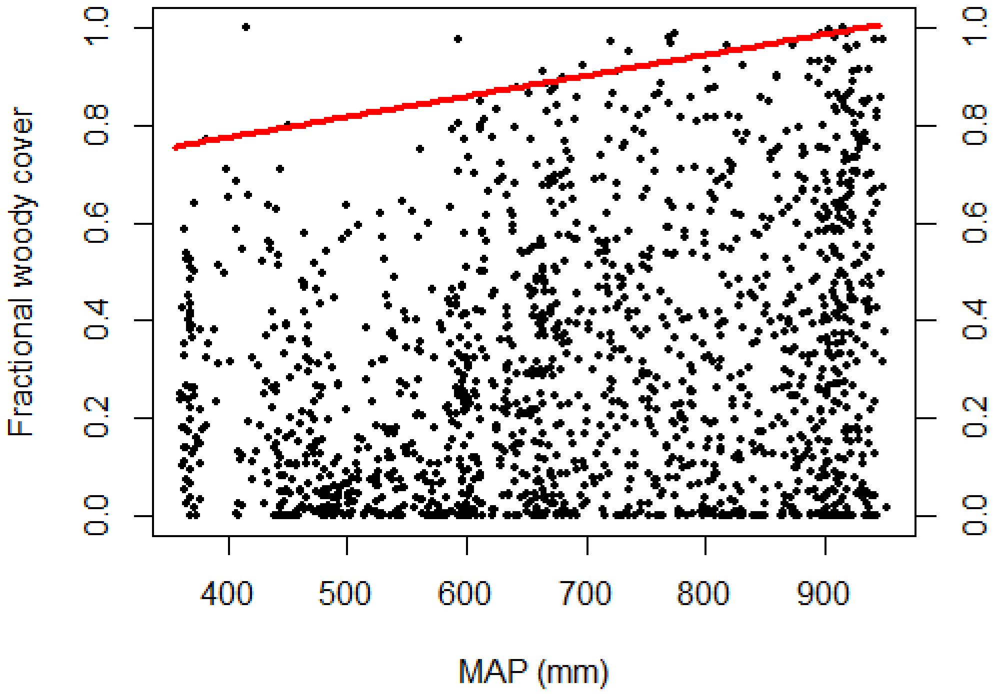


Figure A.11: The twelfth of the 13 scatterplots and modelled potential woody cover pattern.

Table A.11: Details of the twelfth modelled potential woody cover pattern.

Variable	Value	Standard error	t value	Pr (>| t |)
a	0.60540	0.06431	9.41377	0.00000
b	0.00042	0.00008	5.33438	0.00000

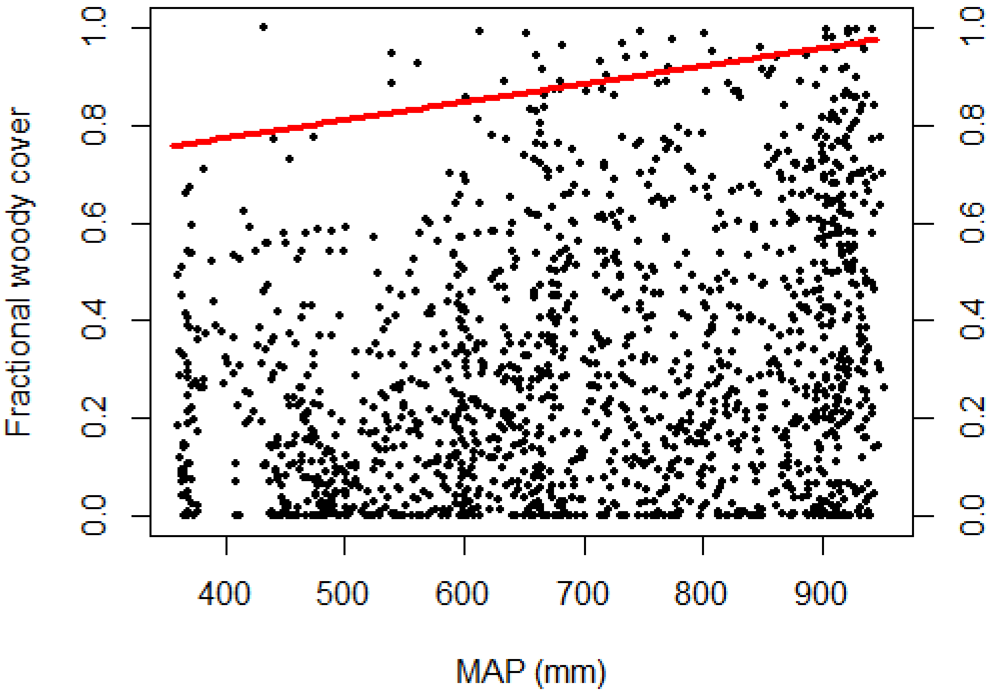


Figure A.12: Thirteenth of the 13 scatterplots and modelled potential woody cover pattern.

Table A.12: Details of the thirteenth modelled potential woody cover pattern.

Variable	Value	Standard error	t value	Pr (>| t |)
a	0.62584	0.09584	6.52996	0.00000
b	0.00037	0.00011	3.40483	0.00068

References

Allen-Diaz, B., and J. W. Bartolome. 1998. SAGEBRUSH–GRASS VEGETATION DYNAMICS: COMPARING CLASSICAL AND STATE-TRANSITION MODELS. *Ecological Applications* 8 (3):795–804.

Alofs, K. M., and N. L. Fowler. 2010. Habitat fragmentation caused by woody plant encroachment inhibits the spread of an invasive grass. *Journal of Applied Ecology* 47 (2):338–347.

Alofs, K. M., and N. L. Fowler. 2013. Loss of native herbaceous species due to woody plant encroachment facilitates the establishment of an invasive grass. *Ecology* 94 (3):751–760.

Anadon, J. D., O. E. Sala, and F. T. Maestre. 2014. Climate change will increase savannas at the expense of forests and treeless vegetation in tropical and subtropical Americas. *Journal of Ecology* 102 (6):1363–1373.

Angassa, A., and R. M. Baars. 2000. Ecological condition of encroached and non-encroached rangelands in Borana, Ethiopia. *African Journal of Ecology* 38 (4):321–328.

Archer, S. 1989. Have southern Texas savannas been converted to woodlands in recent history? *The American Naturalist* 134 (4):545–561.

Archer, S. 1995. Tree-grass dynamics in a Prosopis-thornscrub savanna parkland: reconstructing the past and predicting the future. *Ecoscience* 2 (1):83–99.

Archer, S., D. S. Schimel, and E. A. Holland. 1995. Mechanisms of shrubland expansion: land use, climate or CO2? *Climatic Change* 29 (1):91–99.

Augustine, D. J., and S. J. McNaughton. 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. The Journal of wildlife management :1165–1183.

Berthrong, S. T., G. PIneiro, E. G. Jobbágy, and R. B. Jackson. 2012. Soil C and N changes with afforestation of grasslands across gradients of precipitation and plantation age. *Ecological Applications* 22 (1):76–86.

Bestelmeyer, B. T., A. J. Tugel, G. L. Peacock, D. G. Robinett, P. L. Shaver, J. R. Brown, J. E. Herrick, H. Sanchez, and K. M. Havstad. 2009. State-and-transition models for heterogeneous landscapes: a strategy for development and application. *Rangeland Ecology & Management* 62 (1):1–15.

Blaser, W. J., G. K. Shanungu, P. J. Edwards, and H. Olde Venterink. 2014. Woody encroachment reduces nutrient limitation and promotes soil carbon sequestration. *Ecology and evolution* 4 (8):1423–1438.

Bond, W. J., and B. W. Van Wilgen. 1996. Fire and Plants (population and community biology series 14). Population and Community Biology 263.

Bond, W. J., and J. E. Keeley. 2005. Fire as a global ‘herbivore’: the ecology and evolution of flammable ecosystems. Trends in ecology & evolution 20 (7):387–394.

Bowman, D., and L. D. Prior. 2005. Why do evergreen trees dominate the Australian seasonal tropics? *Australian Journal of Botany* 53 (5):379–399.

Brandt, M., P. Hiernaux, T. Tagesson, A. Verger, K. Rasmussen, A. A. Diouf, C. Mbow, E. Mougin, and R. Fensholt. 2016. Woody plant cover estimation in drylands from Earth Observation based seasonal metrics. *Remote Sensing of Environment* 172:28–38.

Breiman, L., J. Friedman, C. J. Stone, and R. A. Olshen. 1984. *Classification and regression trees*. CRC press.

Briggs, J. M., A. K. Knapp, and B. L. Brock. 2002. Expansion of woody plants in tallgrass prairie: a fifteen-year study of fire and fire-grazing interactions. The American Midland Naturalist 147 (2):287–294.

Briske, D. D., S. D. Fuhlendorf, and F. E. Smeins. 2005. State-and-transition models, thresholds, and rangeland health: a synthesis of ecological concepts and perspectives. *Rangeland Ecology & Management* 58 (1):1–10.

Brown, J. R., and S. Archer. 1989. Woody plant invasion of grasslands: establishment of honey mesquite (Prosopis glandulosa var. glandulosa) on sites differing in herbaceous biomass and grazing history. Oecologia 80 (1):19–26.

Brown, R. L., and R. K. Peet. 2003. Diversity and invasibility of southern Appalachian plant communities. Ecology 84 (1):32–39.

Bucini, G., and N. P. Hanan. 2007. A continental-scale analysis of tree cover in African savannas. *Global Ecology and Biogeography* 16 (5):593–605.

Buitenwerf, R., L. Rose, and S. I. Higgins. 2015. Three decades of multi-dimensional change in global leaf phenology. *Nature Climate Change* 5 (4):364–368.

Cabral, A. C., J. M. Miguel, A. J. Rescia, M. F. Schmitz, and F. D. Pineda. 2003. Shrub encroachment in Argentinean savannas. *Journal of Vegetation Science* 14 (2):145–152.

Cade, B. S., and B. R. Noon. 2003. A gentle introduction to quantile regression for ecologists. *Frontiers in Ecology and the Environment* 1 (8):412–420.

Cade, B. S., and Q. Guo. 2000. Estimating effects of constraints on plant performance with regression quantiles. Oikos 91 (2):245–254.

Chander, G., B. L. Markham, and D. L. Helder. 2009. Summary of current radiometric calibration coefficients for Landsat MSS, TM, ETM+, and EO-1 ALI sensors. *Remote sensing of environment* 113 (5):893–903.

Change, I. P. on C. 2014. *Climate Change 2014–Impacts, Adaptation and Vulnerability: Regional Aspects*. Cambridge University Press.

Coetsee, C., E. F. Gray, J. Wakeling, B. J. Wigley, and W. J. Bond. 2013. Low gains in ecosystem carbon with woody plant encroachment in a South African savanna. *Journal of Tropical Ecology* 29 (01):49–60.

Coughenour, M. B. 1985. Graminoid responses to grazing by large herbivores: adaptations, exaptations, and interacting processes. Annals of the Missouri Botanical Garden :852–863.

Creamer, C. A., T. R. Filley, D. C. Olk, D. E. Stott, V. Dooling, and T. W. Boutton. 2013. Changes to soil organic N dynamics with leguminous woody plant encroachment into grasslands. *Biogeochemistry* 113 (1–3):307–321.

Dantas, V. de L., and J. G. Pausas. 2013. The lanky and the corky: fire-escape strategies in savanna woody species. *Journal of Ecology* 101 (5):1265–1272.

Daubenmire, R., and others. 1968. Plant communities: a textbook of plant synecology. *Plant communities: a textbook of plant synecology.*

Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. Journal of ecology 88 (3):528–534.

DeFries, R. S., C. B. Field, I. Fung, C. O. Justice, S. Los, P. A. Matson, E. Matthews, H. A. Mooney, C. S. Potter, K. Prentice, and others. 1995. Mapping the land surface for global atmosphere-biosphere models: Toward continuous distributions of vegetation's functional properties. *Journal of Geophysical Research: Atmospheres* 100 (D10):20867–20882.

DeFries, R. S., M. C. Hansen, J. R. G. Townshend, A. C. Janetos, and T. R. Loveland. 2000. A new global 1-km dataset of percentage tree cover derived from remote sensing. *Global Change Biology* 6 (2):247–254.

DeFries, R., M. Hansen, M. Steininger, R. Dubayah, R. Sohlberg, and J. Townshend. 1997. Subpixel forest cover in central Africa from multisensor, multitemporal data. *Remote Sensing of Environment* 60 (3):228–246.

Devine, A. P., R. A. McDonald, T. Quaife, and I. M. Maclean. 2017. Determinants of woody encroachment and cover in African savannas. *Oecologia* 183 (4):939–951.

DiMiceli, C. M., M. L. Carroll, R. A. Sohlberg, C. Huang, M. C. Hansen, J. R. G. Townshend, and others. 2011. Annual global automated MODIS vegetation continuous fields (MOD44B) at 250 m spatial resolution for data years beginning day 65, 2000–2010, collection 5 percent tree cover. *University of Maryland, College Park, MD, USA.*

Dunham, J. B., B. S. Cade, and J. W. Terrell. 2002. Influences of spatial and temporal variation on fish-habitat relationships defined by regression quantiles. Transactions of the American Fisheries Society 131 (1):86–98.

Ellis, J. E., and D. M. Swift. 1988. Stability of African pastoral ecosystems: alternate paradigms and implications for development. *Journal of Range Management Archives* 41 (6):450–459.

Fensham, R. J., R. J. Fairfax, and S. R. Archer. 2005. Rainfall, land use and woody vegetation cover change in semi-arid Australian savanna. *Journal of Ecology* 93 (3):596–606.

Fowler, N. L., and M. T. Simmons. 2009. Savanna dynamics in central Texas: just succession? *Applied Vegetation Science* 12 (1):23–31.

Frost, C. C., J. Walker, and R. K. Peet. 1986. Fire-dependent savannas and prairies of the Southeast: Original extent, preservation status and management problems. *Wilderness and natural areas in the eastern United States: a management challenge. Nacogdoches, TX: Stephen F. Austin State University, School of Forestry, Center for Applied Studies* :348–357.

Frost, P. G. H., and F. Robertson. 1985. FIRE THE ECOLOGICAL EFFECTS OF FIRE IN SAVANNAS. In Presentations made by savanna researchers at a workshop in Harare, Zimbabwe, December 1985, 93.

Fuhlendorf, S. D., F. E. Smeins, and W. E. Grant. 1996. Simulation of a fire-sensitive ecological threshold: a case study of Ashe juniper on the Edwards Plateau of Texas, USA. Ecological Modelling 90 (3):245–255.

Gillson, L. 2004. Testing non-equilibrium theories in savannas: 1400 years of vegetation change in Tsavo National Park, Kenya. *Ecological Complexity* 1 (4):281–298.

Gillson, L. Evidence of hierarchical patch dynamics in an east African savanna? *Landscape Ecology* **19,** 883–894 (2005).

González, A. V. 2010. Dynamics of woody plant encroachment in Texas savannas: density dependence, environmental heterogeneity, and spatial patterns. Hanan, N. P., A. T. Tredennick, L. Prihodko, G. Bucini, and J. Dohn. 2014. Analysis of stable states in global savannas: is the CART pulling the horse? *Global Ecology and Biogeography* 23 (3):259–263.

Grace, J., J. S. Jose, P. Meir, H. S. Miranda, and R. A. Montes. 2006. Productivity and carbon fluxes of tropical savannas. *Journal of Biogeography* 33 (3):387–400.

Gray, E. F., and W. J. Bond. 2013. Will woody plant encroachment impact the visitor experience and economy of conservation areas? *Koedoe* 55 (1):00–00.

Hanan, N. P., A. T. Tredennick, L. Prihodko, G. Bucini, and J. Dohn. 2014. Analysis of stable states in global savannas: is the CART pulling the horse? *Global Ecology and Biogeography* 23 (3):259–263.

Hansen, M. C. 2016. Personal communication (email), 26 November 2016.

Hansen, M. C., A. Egorov, D. P. Roy, P. Potapov, J. Ju, S. Turubanova, I. Kommareddy, and T. R. Loveland. 2011. Continuous fields of land cover for the conterminous United States using Landsat data: First results from the Web-Enabled Landsat Data (WELD) project. *Remote Sensing Letters* 2 (4):279–288.

Hansen, M. C., D. P. Roy, E. Lindquist, B. Adusei, C. O. Justice, and A. Altstatt. 2008. A method for integrating MODIS and Landsat data for systematic monitoring of forest cover and change in the Congo Basin. *Remote Sensing of Environment* 112 (5):2495–2513.

Hansen, M. C., J. R. Townshend, R. S. DeFries, and M. Carroll. 2005. Estimation of tree cover using MODIS data at global, continental and regional/local scales. *International Journal of Remote Sensing* 26 (19):4359–4380.

Hansen, M. C., R. S. DeFries, J. R. G. Townshend, M. Carroll, C. Dimiceli, and R. A. Sohlberg. 2003. Global percent tree cover at a spatial resolution of 500 meters: First results of the MODIS vegetation continuous fields algorithm. *Earth Interactions* 7 (10):1–15.

Hansen, M. C., R. S. DeFries, J. R. G. Townshend, R. Sohlberg, C. Dimiceli, and M. Carroll. 2002. Towards an operational MODIS continuous field of percent tree cover algorithm: examples using AVHRR and MODIS data. *Remote Sensing of Environment* 83 (1):303–319.

Hegyi, G., and L. Z. Garamszegi. 2011. Using information theory as a substitute for stepwise regression in ecology and behavior. Behavioral Ecology and Sociobiology 65 (1):69–76.

Heiskanen, J., and S. Kivinen. 2008. Assessment of multispectral,-temporal and-angular MODIS data for tree cover mapping in the tundra–taiga transition zone. *Remote Sensing of Environment* 112 (5):2367–2380.

Heisler, J. L., J. M. Briggs, A. K. Knapp, J. M. Blair, and A. Seery. 2004. Direct and indirect effects of fire on shrub density and aboveground productivity in a mesic grassland. Ecology 85 (8):2245–2257.

Higgins, S. I., W. J. Bond, and W. S. Trollope. 2000. Fire, resprouting and variability: a recipe for grass–tree coexistence in savanna. *Journal of Ecology* 88 (2):213–229.

Hill, M. J., and N. P. Hanan. 2010. *Ecosystem function in savannas: Measurement and modelling at landscape to global scales*. CRC Press.

Hobbs, N. T. 1996. Modification of ecosystems by ungulates. The Journal of Wildlife Management :695–713.

Hobbs, N. T., D. S. Schimel, C. E. Owensby, and D. S. Ojima. 1991. Fire and grazing in the tallgrass prairie: contingent effects on nitrogen budgets. Ecology 72 (4):1374–1382.

Hobbs, R. J., and H. A. Mooney. 1986. Community changes following shrub invasion of grassland. *Oecologia* 70 (4):508–513.

Hoffmann, W. A., W. Schroeder, and R. B. Jackson. 2002. Positive feedbacks of fire, climate, and vegetation and the conversion of tropical savanna. Geophysical Research Letters 29 (22).

Holben, B. N. 1986. Characteristics of maximum-value composite images from temporal AVHRR data. *International journal of remote sensing* 7 (11):1417–1434.

House, J. I., S. Archer, D. D. Breshears, and R. J. Scholes. 2003. Conundrums in mixed woody–herbaceous plant systems. *Journal of biogeography* 30 (11):1763–1777.

Hudak, A. T., and C. A. Wessman. 1998. Textural analysis of historical aerial photography to characterize woody plant encroachment in South African savanna. *Remote sensing of environment* 66 (3):317–330.

Hughes, R. F., S. R. Archer, G. P. Asner, C. A. Wessman, C. McMurtry, J. I. M. Nelson, and R. J. Ansley. 2006. Changes in aboveground primary production and carbon and nitrogen pools accompanying woody plant encroachment in a temperate savanna. *Global Change Biology* 12 (9):1733–1747.

Jeltsch, F., G. E. Weber, and V. Grimm. 2000. Ecological buffering mechanisms in savannas: a unifying theory of long-term tree-grass coexistence. *Plant Ecology* 150 (1–2):161–171.

Koenker, R. & Bassett Jr, G. Regression quantiles. *Econometrica: journal of the Econometric Society* 33–50 (1978).

Koenker, R. 2006. Quantile regresssion. Encyclopedia of environmetrics.

Koenker, R., P. Ng, and S. Portnoy. 1994. Quantile smoothing splines. Biometrika 81 (4):673–680.

Kraaij, T., and D. Ward. 2006. Effects of rain, nitrogen, fire and grazing on tree recruitment and early survival in bush-encroached savanna, South Africa. Plant Ecology 186 (2):235–246.

Krehbiel, C., T. Jackson, and G. M. Henebry. 2015. Using Web-enabled Landsat Data time series to analyze the impacts of urban areas on remotely sensed vegetation dynamics. In *Urban Remote Sensing Event (JURSE), 2015 Joint,* 1–4. IEEE

Küchler, A. W. 1964. *Potential natural vegetation of the conterminous United States*. American Geographical Society.

Kulmatiski, A., and K. H. Beard. 2013. Woody plant encroachment facilitated by increased precipitation intensity. *Nature Climate Change* 3 (9):833–837.

Lal, R. 2004. Carbon sequestration in dryland agriculture. *Challenges and Strategies of Dryland Agriculture* (challengesandst):315–334.

Lal, R. 2004. Soil carbon sequestration impacts on global climate change and food security. *science* 304 (5677):1623–1627.

Laliberte, A. S., A. Rango, K. M. Havstad, J. F. Paris, R. F. Beck, R. McNeely, and A. L. Gonzalez. 2004. Object-oriented image analysis for mapping shrub encroachment from 1937 to 2003 in southern New Mexico. *Remote Sensing of Environment* 93 (1):198–210.

Laliberte, A. S., E. L. Fredrickson, and A. Rango. 2007. Combining decision trees with hierarchical object-oriented image analysis for mapping arid rangelands. *Photogrammetric Engineering & Remote Sensing* 73 (2):197–207.

Laycock, W. A. 1991. Stable states and thresholds of range condition on North American rangelands: a viewpoint. *Journal of Range Management* :427–433.

Lee, D. S., J. C. Storey, M. J. Choate, and R. W. Hayes. 2004. Four years of Landsat-7 on-orbit geometric calibration and performance. *IEEE Transactions on Geoscience and Remote Sensing* 42 (12):2786–2795.

Lehmann, C. E., J. Ratnam, and L. B. Hutley. 2009. Which of these continents is not like the other? Comparisons of tropical savanna systems: key questions and challenges. *New Phytologist* 181 (3):508–511.

Lehmann, C. E., T. M. Anderson, M. Sankaran, S. I. Higgins, S. Archibald, W. A. Hoffmann, N. P. Hanan, R. J. Williams, R. J. Fensham, J. Felfili, and others. 2014. Savanna vegetation-fire-climate relationships differ among continents. *Science* 343 (6170):548–552.

Levin, S. A. The problem of pattern and scale in ecology: the Robert H. MacArthur award lecture. *Ecology* **73,** 1943–1967 (1992).

Litvak, M. E., S. Schwinning, and J. L. Heilman. 2011. Woody plant rooting depth and ecosystem function of savannas: a case study from the Edwards Plateau Karst, Texas. Ecosystem Function in Savannas 117:134.

Liu, Y. Y., A. I. Van Dijk, R. A. De Jeu, J. G. Canadell, M. F. McCabe, J. P. Evans, and G. Wang. 2015. Recent reversal in loss of global terrestrial biomass. *Nature Climate Change* 5 (5):470–474.

Ly, S., C. Charles, and A. Degré. 2013. Different methods for spatial interpolation of rainfall data for operational hydrology and hydrological modelling at watershed scale. A review. *Biotechnologie, Agronomie, Société et Environnement* 17 (2):392.

Lyons, R. K., M. K. Owens, R. V. Machen, and others. 2009. Juniper biology and management in Texas. *Texas FARMER Collection*.

Mazía, N., J. Moyano, L. Perez, S. Aguiar, L. A. Garibaldi, and T. Schlichter. 2016. The sign and magnitude of tree–grass interaction along a global environmental gradient. *Global Ecology and Biogeography* 25 (12):1510–1519.

McKinley, D. C., C. W. Rice, and J. M. Blair. 2008. Conversion of grassland to coniferous woodland has limited effects on soil nitrogen cycle processes. *Soil Biology and Biochemistry* 40 (10):2627–2633.

McNaughton, S. J. 1988. Mineral nutrition and spatial concentrations of African ungulates. Nature 334 (6180):343–345.

McNaughton, S. J. 1990. Mineral nutrition and seasonal movements of African migratory ungulates. Nature 345 (6276):613–615.

McNaughton, S. J. 1992. The propagation of disturbance in savannas through food webs. Journal of Vegetation Science 3 (3):301–314.

McNaughton, S. J., F. F. Banyikwa, and M. M. McNaughton. 1997. Promotion of the cycling of diet-enhancing nutrients by African grazers. Science 278 (5344):1798–1800.

Meyer, K. M., K. Wiegand, and D. Ward. 2009. Patch dynamics integrate mechanisms for savanna tree–grass coexistence. *Basic and Applied Ecology* 10 (6):491–499.

Mistry, J., and A. Beradi. 2014. *World savannas: ecology and human use*. Routledge.

Mitchard, E. T., S. S. Saatchi, S. L. Lewis, T. R. Feldpausch, I. H. Woodhouse, B. Sonké, C. Rowland, and P. Meir. 2011. Measuring biomass changes due to woody encroachment and deforestation/degradation in a forest–savanna boundary region of central Africa using multi-temporal L-band radar backscatter. *Remote Sensing of Environment* 115 (11):2861–2873.

Moncrieff, G. R., C. E. Lehmann, J. Schnitzler, J. Gambiza, P. Hiernaux, C. M. Ryan, C. M. Shackleton, R. J. Williams, and S. I. Higgins. 2014. Contrasting architecture of key African and Australian savanna tree taxa drives intercontinental structural divergence. *Global ecology and biogeography* 23 (11):1235–1244.

Moncrieff, G. R., S. Scheiter, W. J. Bond, and S. I. Higgins. 2014. Increasing atmospheric CO2 overrides the historical legacy of multiple stable biome states in Africa. *New Phytologist* 201 (3):908–915.

Montesano, P. M., R. Nelson, G. Sun, H. Margolis, A. Kerber, and K. J. Ranson. 2009. MODIS tree cover validation for the circumpolar taiga–tundra transition zone. *Remote Sensing of Environment* 113 (10):2130–2141.

Murphy, B. P., C. E. Lehmann, J. Russell-Smith, and M. J. Lawes. 2014. Fire regimes and woody biomass dynamics in Australian savannas. *Journal of Biogeography* 41 (1):133–144.

Noy-Meir, I. 1973. Desert ecosystems: environment and producers. *Annual review of ecology and systematics*:25–51.

O’connor, T. G. 1995. Acacia karroo invasion of grassland: environmental and biotic effects influencing seedling emergence and establishment. *Oecologia* 103 (2):214–223.

O’Connor, T. G., J. R. Puttick, and M. T. Hoffman. 2014. Bush encroachment in southern Africa: changes and causes. *African Journal of Range & Forage Science* 31 (2):67–88.

Ouaidrari, H., and E. F. Vermote. 1999. Operational atmospheric correction of Landsat TM data. *Remote Sensing of Environment* 70 (1):4–15.

Poulter, B., D. Frank, P. Ciais, R. B. Myneni, N. Andela, J. Bi, G. Broquet, J. G. Canadell, F. Chevallier, Y. Y. Liu, and others. 2014. Contribution of semi-arid ecosystems to interannual variability of the global carbon cycle. *Nature* 509 (7502):600–603.

Pressland, A. J. 1973. Rainfall partitioning by an arid woodland (Acacia aneura F. Muell.) in south-western Queensland. *Australian Journal of Botany* 21 (2):235–245.

Ramankutty, N., and J. A. Foley. 1999. Estimating historical changes in global land cover: Croplands from 1700 to 1992. *Global biogeochemical cycles* 13 (4):997–1027.

Rasmussen, M. O., F.-M. Göttsche, D. Diop, C. Mbow, F.-S. Olesen, R. Fensholt, and I. Sandholt. 2011. Tree survey and allometric models for tiger bush in northern Senegal and comparison with tree parameters derived from high resolution satellite data. *International Journal of Applied Earth Observation and Geoinformation* 13 (4):517–527.

Ratajczak, Z., J. B. Nippert, and S. L. Collins. 2012. Woody encroachment decreases diversity across North American grasslands and savannas. *Ecology* 93 (4):697–703.

Roberts, B. R., L. R. Wilson, J. J. Cascino, and G. P. Smith. 1987. Autoradiographic studies of ethylenediurea distribution in woody plants. *Environmental Pollution* 45 (2):81–86.

Rodríguez-Iturbe, I., P. D’Odorico, A. Porporato, and L. Ridolfi. 1999. Tree-grass coexistence in Savannas: The role of spatial dynamics and climate fluctuations. Geophysical Research Letters 26 (2):247–250.

Roques, K. G., T. G. O’connor, and A. R. Watkinson. 2001. Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. *Journal of Applied Ecology* 38 (2):268–280.

Roy, D. P., J. Ju, K. Kline, P. L. Scaramuzza, V. Kovalskyy, M. Hansen, T. R. Loveland, E. Vermote, and C. Zhang. 2010. Web-enabled Landsat Data (WELD): Landsat ETM+ composited mosaics of the conterminous United States. *Remote Sensing of Environment* 114 (1):35–49.

Russell, F. L., and N. L. Fowler. 1999. Rarity of oak saplings in savannas and woodlands of the eastern Edwards Plateau, Texas. *The Southwestern Naturalist* :31–41.

Russell, F. L., and N. L. Fowler. 2002. Failure of adult recruitment in Quercus buckleyi populations on the eastern Edwards Plateau, Texas. *The American Midland Naturalist* 148 (2):201–217.

Russell, F. L., and N. L. Fowler. 2004. Effects of white-tailed deer on the population dynamics of acorns, seedlings and small saplings of Quercus buckleyi. *Plant Ecology* 173 (1):59–72.

Sala, O. E., F. S. Chapin, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. F. Huenneke, R. B. Jackson, A. Kinzig, and others. 2000. Global biodiversity scenarios for the year 2100. *science* 287 (5459):1770–1774.

Sankaran, M. *et al.* Determinants of woody cover in African savannas. *Nature* **438,** 846–849 (2005).

Sankaran, M., and T. M. Anderson. 2009. Management and restoration in African savannas: interactions and feedbacks. New models for ecosystem dynamics and restoration :136–155.

Sankaran, M., J. Ratnam, and N. Hanan. 2008. Woody cover in African savannas: the role of resources, fire and herbivory. *Global Ecology and Biogeography* 17 (2):236–245.

Sankaran, M., J. Ratnam, and N. P. Hanan. 2004. Tree–grass coexistence in savannas revisited–insights from an examination of assumptions and mechanisms invoked in existing models. *Ecology Letters* 7 (6):480–490.

Sankaran, M., N. P. Hanan, R. J. Scholes, J. Ratnam, D. J. Augustine, B. S. Cade, J. Gignoux, S. I. Higgins, X. Le Roux, F. Ludwig, and others. 2005. Determinants of woody cover in African savannas. *Nature* 438 (7069):846–849.

Scanlan, J. C., and S. Archer. 1991. Simulated dynamics of succession in a North American subtropical Prosopis savanna. *Journal of Vegetation Science* 2 (5):625–634.

Schmidt, J. A. The wild landscape of the Edwards Plateau of south central Texas-a study of developing livelihood patterns and ecological change: University of Chicago. *unpublished MS thesis* (1969).

Scholes, R. J. & Archer, S. R. Tree-grass interactions in savannas. *Annual review of Ecology and Systematics* 517–544 (1997).

Scholes, R. J. 1993. Nutrient cycling in semi-arid grasslands and savannas: its influence on pattern, productivity and stability. In *Proceedings of the XII International Grassland Congress*.

Scholes, R. J., and B. H. Walker. 1993. African savannas: an overview. *An African savanna: synthesis of the Nylsvley study*:2–16.

Scholes, R. J., and S. R. Archer. 1997. Tree-grass interactions in savannas 1. *Annual review of Ecology and Systematics* 28 (1):517–544.

Schwarz, M., and N. E. Zimmermann. 2005. A new GLM-based method for mapping tree cover continuous fields using regional MODIS reflectance data. *Remote Sensing of Environment* 95 (4):428–443.

Schwarz, M., N. E. Zimmermann, and L. T. Waser. 2004. MODIS based continuous fields of tree cover using generalized linear models. In *Geoscience and Remote Sensing Symposium, 2004. IGARSS'04. Proceedings. 2004 IEEE International*, 2377–2380.

Sexton, J. O., X.-P. Song, M. Feng, P. Noojipady, A. Anand, C. Huang, D.-H. Kim, K. M. Collins, S. Channan, C. DiMiceli, and others. 2013. Global, 30-m resolution continuous fields of tree cover: Landsat-based rescaling of MODIS vegetation continuous fields with lidar-based estimates of error. *International Journal of Digital Earth* 6 (5):427–448.

Skarpe, C. 1991. Impact of grazing in savanna ecosystems. *Ambio* :351–356.

Skarpe, C. 1992. Dynamics of savanna ecosystems. *Journal of vegetation Science* 3 (3):293–300.

Skowno, A. L., M. W. Thompson, J. Hiestermann, B. Ripley, A. G. West, and W. J. Bond. 2016. Woodland expansion in South African grassy biomes based on satellite observations (1990–2013): general patterns and potential drivers. *Global change biology*.

Solbrig, O. T., E. Medina, and J. F. Silva. 2013. *Biodiversity and savanna ecosystems processes: a global perspective*. Springer Science & Business Media.

Soliveres, S., and D. J. Eldridge. 2014. Do changes in grazing pressure and the degree of shrub encroachment alter the effects of individual shrubs on understorey plant communities and soil function? *Functional ecology* 28 (2):530–537.

Song, X.-P., C. Huang, M. Feng, J. O. Sexton, S. Channan, and J. R. Townshend. 2014. Integrating global land cover products for improved forest cover characterization: An application in North America. *International Journal of Digital Earth* 7 (9):709–724.

Stebbins, G. L. 1981. Coevolution of grasses and herbivores. Annals of the Missouri Botanical Garden :75–86.

Stevens, N., C. E. Lehmann, B. P. Murphy, and G. Durigan. 2017. Savanna woody encroachment is widespread across three continents. *Global change biology* 23 (1):235–244.

Stocker, T. 2014. *Climate change 2013: the physical science basis: Working Group I contribution to the Fifth assessment report of the Intergovernmental Panel on Climate Change*. Cambridge University Press.

Stuart-Hill, G. C., and N. M. Tainton. 1989. The competitive interaction between Acacia karroo and the herbaceous layer and how this is influenced by defoliation. *Journal of Applied Ecology* :285–298.

Su, H., W. Liu, H. Xu, Z. Wang, H. Zhang, H. Hu, and Y. Li. 2015. Long-term livestock exclusion facilitates native woody plant encroachment in a sandy semiarid rangeland. *Ecology and evolution* 5 (12):2445–2456.

Sullivan, S. & Rohde, R. On non-equilibrium in arid and semi-arid grazing systems. *Journal of Biogeography* **29,** 1595–1618 (2002).

Taylor Jr, C. A. 2008. Ecological consequences of using prescribed fire and herbivory to manage Juniperus encroachment. In *Western North American Juniperus Communities*, 239–252. Springer.

Taylor, C. A., and F. E. Smeins. 1994. A history of land use of the Edwards Plateau and its effect on the native vegetation. In Juniper symposium, 94–2.

Throop, H. L., and S. R. Archer. 2008. Shrub (Prosopis velutina) encroachment in a semidesert grassland: spatial–temporal changes in soil organic carbon and nitrogen pools. *Global Change Biology* 14 (10):2420–2431.

Thurow, T. L., W. H. Blackburn, and C. A. Taylor Jr. 1986. Hydrologic characteristics of vegetation types as affected by livestock grazing systems, Edwards Plateau, Texas. Journal of Range Management :505–509.

Toomey, R. S., M. D. Blum, and S. Valastro. 1993. Late Quaternary climates and environments of the Edwards Plateau, Texas. Global and planetary change 7 (4):299–320.

Townshend, J. R., and C. O. Justice. 1988. Selecting the spatial resolution of satellite sensors required for global monitoring of land transformations. *International Journal of Remote Sensing* 9 (2):187–236.

Urbazaev, M., C. Thiel, R. Mathieu, L. Naidoo, S. R. Levick, I. P. Smit, G. P. Asner, and C. Schmullius. 2015. Assessment of the mapping of fractional woody cover in southern African savannas using multi-temporal and polarimetric ALOS PALSAR L-band images. *Remote Sensing of Environment* 166:138–153.

Van Auken, O. W. 2009. Causes and consequences of woody plant encroachment into western North American grasslands. *Journal of Environmental Management* 90 (10):2931–2942.

Van Langevelde, F., C. A. Van De Vijver, L. Kumar, J. Van De Koppel, N. De Ridder, J. Van Andel, A. K. Skidmore, J. W. Hearne, L. Stroosnijder, W. J. Bond, and others. 2003. Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology* 84 (2):337–350.

Vegten, J. van. 1984. Thornbush invasion in a savanna ecosystem in eastern Botswana. *Plant Ecology* 56 (1):3–7.

Walker, B. H. 1987. A general model of savanna structure and function. *IUBS MONOGR. SER. 1987.*

Walker, B. H., and I. Noy-Meir. 1982. Aspects of the stability and resilience of savanna ecosystems. In *Ecology of tropical savannas*, 556–590. Springer

Walker, B. H., D. Ludwig, C. S. Holling, and R. M. Peterman. 1981. Stability of semi-arid savanna grazing systems. *The Journal of Ecology* :473–498.

Walter, H., D. MUELLER-DOMBOIS, and others. 1971. *Ecology of tropical and subtropical vegetation.* Edinburgh, UK, Oliver & Boyd.

Watt, A. S. 1947. Pattern and process in the plant community. *Journal of ecology* 35 (1/2):1–22.

White, M. A., J. D. Shaw, and R. D. Ramsey. 2005. Accuracy assessment of the vegetation continuous field tree cover product using 3954 ground plots in the south-western USA. *International Journal of Remote Sensing* 26 (12):2699–2704.

Wiegand, K., D. Saltz, and D. Ward. 2006. A patch-dynamics approach to savanna dynamics and woody plant encroachment–insights from an arid savanna. *Perspectives in Plant Ecology, Evolution and Systematics* 7 (4):229–242.

Wilcox, B. P., and Y. Huang. 2010. Woody plant encroachment paradox: Rivers rebound as degraded grasslands convert to woodlands. *Geophysical Research Letters* 37 (7).

Wilsey, B. J. 1996. Variation in use of green flushes following burns among African ungulate species: the importance of body size. African Journal of Ecology 34 (1):32–38.

Wu, J. & David, J. L. A spatially explicit hierarchical approach to modelling complex ecological systems: theory and applications. *Ecological Modelling* **153,** 7–26 (2002).

Wu, J. & Loucks, O. L. From balance of nature to hierarchical patch dynamics: a paradigm shift in ecology. *Quarterly review of biology* 439–466 (1995).

Wu, J. Hierarchy and scaling: extrapolating information along a scaling ladder. *Canadian journal of remote sensing* **25,** 367–380 (1999).

Yang, X., K. A. Crews, and B. Yan. 2016. Analysis of the pattern of potential woody cover in Texas savanna. *International Journal of Applied Earth Observation and Geoinformation* 52:527–531.

Yessoufou, K., T. J. Davies, O. Maurin, M. Kuzmina, H. Schaefer, M. Bank, and V. Savolainen. 2013. Large herbivores favour species diversity but have mixed impacts on phylogenetic community structure in an African savanna ecosystems. *Journal of Ecology* 101 (3):614–625.

Zeeman, B. J., I. D. Lunt, and J. W. Morgan. 2014. Can severe drought reverse woody plant encroachment in a temperate Australian woodland? *Journal of vegetation science* 25 (4):928–936.