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IN SEARCH OF THE FOREST PRIMEVAL:
DATA-DRIVEN APPROACHES TO MAPPING HISTORIC VEGETATION

A DISSERTATION APPROVED FOR THE
DEPARTMENT OF GEOGRAPHY

BY

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ACKNOWLEDGEMENTS

In late May 1989, I graduated from John Marshall High School in Oklahoma City, OK. Had I known then that I still had 20 years of schooling ahead of me (give or take the handful of stray years away from formal education), I may seriously have contemplated a different "career" path. For better or for worse, I stayed the course and have now arrived at one (but certainly not the final) of the destinations in this wayward journey. Although I have never traveled alone, it would be difficult to personally thank all whom I encountered along the way. To all of these giants on whose shoulders I have stood, enabling me to see beyond the scope of my own limited vision, thank you. This includes: all family and friends; acquaintances and even some strangers; mentors and colleagues; collaborators, agitators, and provocateurs; and anyone else I may have inadvertently omitted.

I would be remiss if I did not acknowledge several by name. My circuitous route to the academic discipline of geography came through a rather innocuous suggestion from my high school friend, David Lowther. David has remained a steadfast friend throughout the past 20 plus years and it is not an understatement to say it is highly unlikely I would be in the position I am in today had he not recommended, over several pints of beer, geography as my new academic foray. To blame David for the misery entailed in the completion of this dissertation would be a bit harsh, so I will instead offer him my kindest words of gratitude.

When I took David's advice, I certainly had no intentions (or even the remotest thoughts) of eventually pursuing a Ph.D. in geography. My primary goal was to find a stepping stone from which I could leap into more fulfilling endeavors, such as understanding and working towards sustaining this wondrous blue marble we call Earth. At the recommendation of Dr. Karen Humes, I decided to pursue a Master's in this fascinating discipline called geography. As chance would have it, Dr. Humes left the University of Oklahoma the semester I was to begin my graduate work. Ironically, I thank Karen both for her encouragement and for her departure. Her absence left me not only without an advisor, but also without a real direction in my academic paths. However, after several discussions with various professors, I was bowled over by the research conducted by Dr. Bruce Hoagland: historical vegetation reconstructions; landscape ecology; and biogeography. I had found my calling. I only needed the chance and circumstance to get me there.

Bruce has been a phenomenal advisor and friend throughout my graduate studies. This dissertation is truly a collaborative effort and I owe him a debt of gratitude that cannot be adequately expressed in words. Nonetheless, I would like to thank Bruce not only for his guidance on this research, but for all things, large and small, he has done for me over the years (especially knowing my fondness for Fat Tire beer).

Having invested so many years in this pursuit, I have seen many mentors and committee members come and go. All of these individuals also deserve recognition by name. First, I would like to thank all of my erstwhile committee members: Dr. Gavin Bridge, Dr. Soe Myint, and Dr. May Yuan. Additionally, thank you to Dr. Wayne Elisens and Dr. Aondover Tarhule for bearing with me throughout the duration of this journey. I owe a special debt of gratitude to Dr. J. Scott Greene and Dr. Robert

Rundstrom for kindly agreeing to join my committee at the 11th hour in order to fill two unexpected vacancies. Dr. Karl Offen, as the graduate liaison, has also been invaluable to me during the final stint of my Ph.D. Finally, Dr. Tarek Rashed deserves special recognition for both introducing me to one of the modeling techniques that I make extensive use of in my research and for offering valuable assistance in the early days of this research.

Despite the many fellow travelers who have endured this journey with me through the years, there is one that stands above all others. She pushed me when I needed a push; she pulled me when I needed a pull; she encouraged me when I needed it most; and, most importantly, she endured me when I was intolerable, as anyone who has struggled through a dissertation can undoubtedly become. Thank you to Traci Jane Quick, my lovely wife, my friend, my grief counselor, my drinking buddy, and the 1,001 other roles she plays despite the fact they were not clearly defined in our civil contract. The fact that she has yet to strangle me is testament to her greatness.

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Abstract

Biogeography is the study of the spatial distribution of biota. It is a comparative and observational science that seeks to describe the variations in the spatial patterns of biodiversity through the examination of historical (e.g. vicariance, speciation, and extinction) and ecological (e.g. climate, edaphic, and topographic) factors. Additionally, researchers are increasingly recognizing the role that anthropogenic disturbance regimes have played in shaping current biogeographic patterns. Indeed, in many parts of the world, humans have become the dominant force in alterations to biotic distributions. Since human activities can influence biotic patterns for many years, the interpretation of biogeographic phenomenon without consideration of human influence may lead to erroneous conclusions.

This research is built upon the broad supposition that evaluation of current biogeographic patterns must be predicated on antecedent conditions, typically prior to widespread anthropogenic disturbance regimes. To this end, this research utilizes historical data to create baselines from which subsequent changes in biogeographic patterns can be measured. In a narrow sense, this dissertation focuses on land use, land cover, and woody plant compositional changes in the Arbuckle Mountains of south-central Oklahoma during a period of rapid demographic change (circa 1870 to 1898). In this regard, this research seeks to provide insight into the ecological processes of habitat fragmentation, woody plant encroachment, and mesophication that are believed to have occurred subsequent to the periods under investigation in this research.

In a broader context, this research is an evaluation of how anthropogenic alterations in landscape pattern and processes may affect the distributions of individual woody plant taxon. Though the datasets utilized in this research are unique to the region, the methods employed in this study should be transferable to other areas of interest. Additionally, the patterns and processes under investigation are not unique to the region under investigation. The results of this research, therefore, should be placed within the context of anthropogenic change that has occurred throughout the eastern deciduous forests of North America, particularly in the western cross timbers, in the period following European settlement.

In order to accomplish these goals, this dissertation is divided into two broad research themes. The first employs repeat Public Land Survey System (PLS) data from the 1870s and 1890s, respectively, to quantify changes in landscape structure, woody taxa assemblages, and anthropogenic markers in the Arbuckle Mountains during this period of rapid demographic transition. The second utilizes a Bayesian method known as weights-of-evidence to address the problem of coarse sampling structure of PLS records. The results of this research indicate that the landscape of the Arbuckle Mountains became increasingly fragmented during the approximately 27 years between the two surveys, primarily due to land clearance for agriculture, transportation networks, and anthropogenic structures. Additionally, there were changes in stand composition between the two surveys, implying that these anthropogenic disturbance regimes may be responsible for shifts in biogeographic patterns. The weights-of-evidence method proved to be a statistically valid method to map individual taxon distributions at finer resolutions than afforded from traditional methods of mapping PLS data. These findings will help further elucidate subsequent distributional shifts in these taxa, thereby providing a better understanding of contemporary biogeographic patterns.

CHAPTER 1: INTRODUCTION

Contextualization

Biogeography occupies a unique position in contemporary geography. It is neither a social nor physical science, the traditional purviews of geography (Gaile and Wilmott 2003). Rather, it is a biological science inspired by and interacting with both the physical and social sciences (Young 2002). The fundamental endeavor of biogeography is understanding the distribution of biota, both past and present (Quammen 1996; MacDonald 2003). This pursuit necessarily entails an analysis of the distribution of biota in terms of their relationship with the physical environment (MacArthur 1972). Similarly, many contemporary biogeographic patterns are inextricably linked to past anthropogenic activities (Spellerberg and Sawyer 1999; Cox and Moore 2000; Dupouey et al. 2002; MacDonald 2003). Indeed, the study of the biogeographic phenomena without explicit inclusion of the human dimension may lead to erroneous conclusions (Mielke 1989; Spellerberg and Sawyer 1999).

Biogeography is an interdisciplinary study (Veblen 1989; Young et al. 2003) practiced not only by geographers, but by botanists, zoologists, geologists, paleontologists, systematists, and many others (Figure 1.1). It is an assemblage of several discreet but related systematic and integrative studies, relying heavily on data and theory from evolutionary and population biology, systematics, physiology, the earth sciences, and, of course, geography. Whereas there are numerous and varied approaches to the practice of biogeography (Lomolino and Heaney 2004), biogeography as practiced by geographers is similar to contemporary ecology. However, unlike traditional ecological inquiry, biogeography is more inclusive of the anthropogenic contribution to biotic distributions (Veblen 1989).

Though there are many biogeography subfields (Figure 1.1), biogeography can be broadly divided into two primary approaches. The first is often termed classical biogeography (Veblen 1989) or historical biogeography (MacDonald 2003; Lomolino and Heaney 2004). Historical biogeography is typically practiced by systematists (Veblen 1989) and attempts to reconstruct the origin, dispersal, and extinction of taxa and biota. By and large, these biogeographers are concerned with the classification, taxonomic affinities, and evolutionary histories of organisms, employing techniques such as phylogentic and paleontological reconstructions to describe past and present distribution of biota.

The second approach to biogeography is often referred to as ecological biogeography (Lomolino et al. 2006). This approach attempts to account for contemporary biotic distributions in terms of an organism's (or group of organisms') interaction with the physical environment and/or other biotic factors. In particular, ecological biogeography seeks to explain the distribution of organism in terms of habitat area, environmental gradients, and interactions with other organisms, including humans.

The two broad approaches are not mutually exclusive. The past distributions of organisms were influenced by biotic and abiotic interactions, while current biogeographic patterns are the products of past events. An integrative historic-ecological approach is, therefore, necessary to properly understand the contemporary biogeography of a given region. As used here, though, the term "historical" may take on a different meaning than has been traditionally employed in biogeography as the periods under investigation may be measured in decades and centuries, rather than millennia.

The purpose of this dissertation is two-fold. First, it utilizes repeat Public Land Survey data to provide insight into anthropogenic disturbance regimes that occurred during a period of rapid demographic transition. Second, it documents the role that these anthropogenic alterations of landscape pattern and process have had on the distributions of individual woody plant taxon. These are accomplished through an exploration of the past biogeography of the Arbuckle Mountains of Oklahoma, a biologically diverse, mid-continent transition zone where dramatic land cover and biotic changes occurred during the second half of the nineteenth century.

The Arbuckle Mountains occur within an area characterized by the congruence of prairie, savanna, woodland, and forest vegetation types. This region, known collectively as the cross timbers (Hoagland et al. 1999), resides on the western edge of the eastern deciduous forest and the eastern edge of the Great Plains. Consequently, the Arbuckle Mountains are home to a diversity of flora and fauna, including a number of species of concern from a conservation perspective, including *Alnus maritima*, *Epipactis gigantea*, *Penstemon oklahomensis*, *Psoralea reverchonii*, and *Aquila chrysaetos* (see Table 5.1 for a complete list). This diversity in land cover types and biota make the Arbuckle Mountains a prime natural laboratory for the study of numerous ecological patterns and processes.

Evidence suggests that the Arbuckle Mountains have undergone rapid ecological changes during the period of widespread European resettlement. In particular, fire suppression and other land use practices have led to increases in *Juniperus* spp. at the expense of grasslands and are believed to have contributed to increases in density of savannas, woodlands, and forests. Additionally, habitat fragmentation, i.e. the reduction of the areal extent of a continuous land cover type into smaller patches, has led to a decrease of native habitats and an increase of anthropogenic land cover types.

Despite some understanding of these ecological transformations, there is a dearth of quantitative research on the biotic conditions prior to these anthropogenic changes. The Arbuckle Mountains' position within the boundaries of the Chickasaw Nation (Figure 1.2) provide two quantitative, historical datasets, one preceding widespread European settlement, the other immediately following a substantial resettlement. These repeat datasets allow a unique analysis of these anthropogenic dynamics and their ecological consequences and may provide greater insight into similar dynamics that have occurred elsewhere.

Specialization

In addition to the introductory and concluding chapters, this dissertation is composed of four primary components: three chapters and the appendices. Each of the chapters is designed as a stand-alone manuscript that can be read independently of the others. Nonetheless, the chapters are bound together by common themes, namely the exploration of methods to reconstruct past biogeographies and the biogeographic consequences of various anthropogenic disturbance regimes.

During the past two decades, there has been an ever expanding body of work that utilizes the records of the Public Land Survey (PLS) of the General Land Office (GLO) to reconstruct past environments. Chapter 2 is a comprehensive literature review, through approximately January 2009, of the uses of PLS data in historical vegetation reconstructions. The chapter is not only an exploration of *where* these studies have occurred, but also an analysis of *how* these data have been used in these vegetation reconstructions. Two broad conclusions from this analysis can be made in regards to the overall focus of this dissertation. First, despite an apparent uniqueness in the PLS datasets for the area now known as Oklahoma, there are but a few examples of the uses of these data for historical vegetation reconstructions or similar purposes within this geographic domain (Shutler 2001; Shutler and Hoagland 2004; Watkins 2004; Watkins 2007). Second, despite the widespread use of PLS data in general, there are numerous shortcomings in these data that have inhibited their broader use in biogeographic analysis.

The U.S. General Land Office conducted two separate surveys in a portion of present-day state of Oklahoma during a relatively short time span. In contrast, the GLO typically conducted a single survey in most states, with each survey often requiring a period of multiple years, even decades to complete. For instance, surveying of the state of Wisconsin occurred over a 34-year period (Shulte and Mladenoff 2001), while the surveys of Michigan's Upper Peninsula occurred over a 16 year period (Zhang et al. 2000). As a result of the duration of these surveys, researchers have found differences resulting from temporal processes (e.g. both natural and anthropogenic) in adjacent townships surveyed in different years (Shulte and Mladenoff 2001), thereby limiting their overall effectiveness in vegetation reconstructions.

Evaluation of the degree of change in a given area requires multiple observations through time. While, the GLO began the PLS in 1785, the earliest change detection studies using PLS records date from approximately the mid-twentieth century and relied on data collected at least half a century after the original surveys (e.g. Fassett 1944; Curtis 1956). However, many ecological processes occur at rates that exceed the availability of quantitative data (Hoch and Briggs 1999; Briggs et al. 2002). While a comparison of the state of vegetation at the discrete times of data availability is possible, it is not possible to determine the nature of the vegetation at any intermittent point.

The U.S. federal government surveyed the lands of the Chickasaw Nation (Figure 1.2) beginning in the early 1870s. The first survey of the Arbuckle Mountains (see Figure 3.2), the study area for this dissertation, occurred between November 1870 and February 1872. In 1895, the United States Congress appropriated $200,000 for the survey of all tribal lands in Indian Territory, including those that had been previously surveyed in the 1870s (Gibson 1981; Carter 1999). As a result, the GLO surveyed the Arbuckle Mountains again between November 1897 and December 1898. Overall, there was an average of 26.6 years (26 years, 7 months) between the original survey and the resurvey.

The period between the two surveys is marked by rapid demographic changes in the resurveyed areas (Gibson 1981). Assuming fidelity in these data, the PLS records from the 1870s characterize the vegetation immediately prior to extensive European resettlement, while the data from the 1890s characterize the vegetation following the first major influx of European settlers into the region. While the two datasets only represent the vegetation of the area at two discrete time periods, the PLS data for Oklahoma, nonetheless, offer a rare glimpse at the changes that occurred during these demographic shifts. Chapter 3, therefore, is an exploration of the PLS data for the Arbuckle Mountains from these two surveys and represents the most comprehensive change-detection analysis using repeat PLS data to date.

There are numerous limitations to these datasets (Bourdo 1956; Maines et al. 2001). One persistent problem related to PLS data in ecological analysis relates to the coarse sampling structure of the data--tree data were only collected along section lines at 0.8 km (0.5 mi.) intervals. In order to compensate for this, several researchers have attempted to convert discrete PLS point data into continuous surfaces using various interpolation methods (e.g. Brown 1998; Batek et al. 1999; He et al. 2000; Wang and Larsen 2006). However, these methods typically fail to consider the numerous covariates that can influence the distribution of individual species. Instead these methods treat PLS witness tree data as numeric without consideration of the underlying ecological processes that can influence the distribution of individual taxon. In Chapter 4, I employ a method known as weights-of-evidence to convert discrete PLS data into probabilistic surfaces based on known associations with several environmental covariates.

Structure

Each of the two research chapters (chapters 3 and 4) is formatted for submission to specific journals. Chapter 3 is formatted for the *Annals of the Association of American Geographers* and/or *The Professional Geographer*, while Chapter 4 is formatted for the *Journal of Biogeography*. An earlier version of Chapter 2 was published in *The North American Geographer*. However, the version presented here has been revised, updated, and expanded to reflect advances in research using PLS data since the article was originally published. Nonetheless, Chapter 2 remains formatted following the guidelines of *The North American Geographer*.

All tables and figures appear at the end of each respective chapter immediately following the literature cited section. Because there is a limited number of tables and figures that can be submitted to journals for publication, I have included two appendices of additional tables and figures that are apropos to the dissertation, but which had to be omitted from any manuscript I wish to submit for publication.

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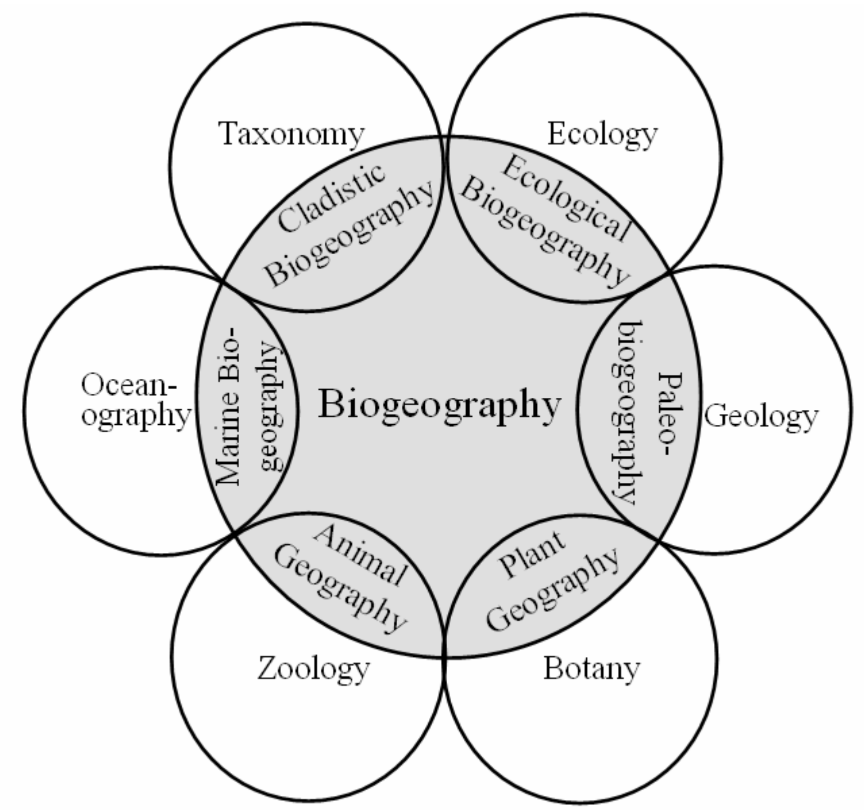
Figure 1.1. The circumference of biogeography. Inspired by Holt-Jensen (1999)



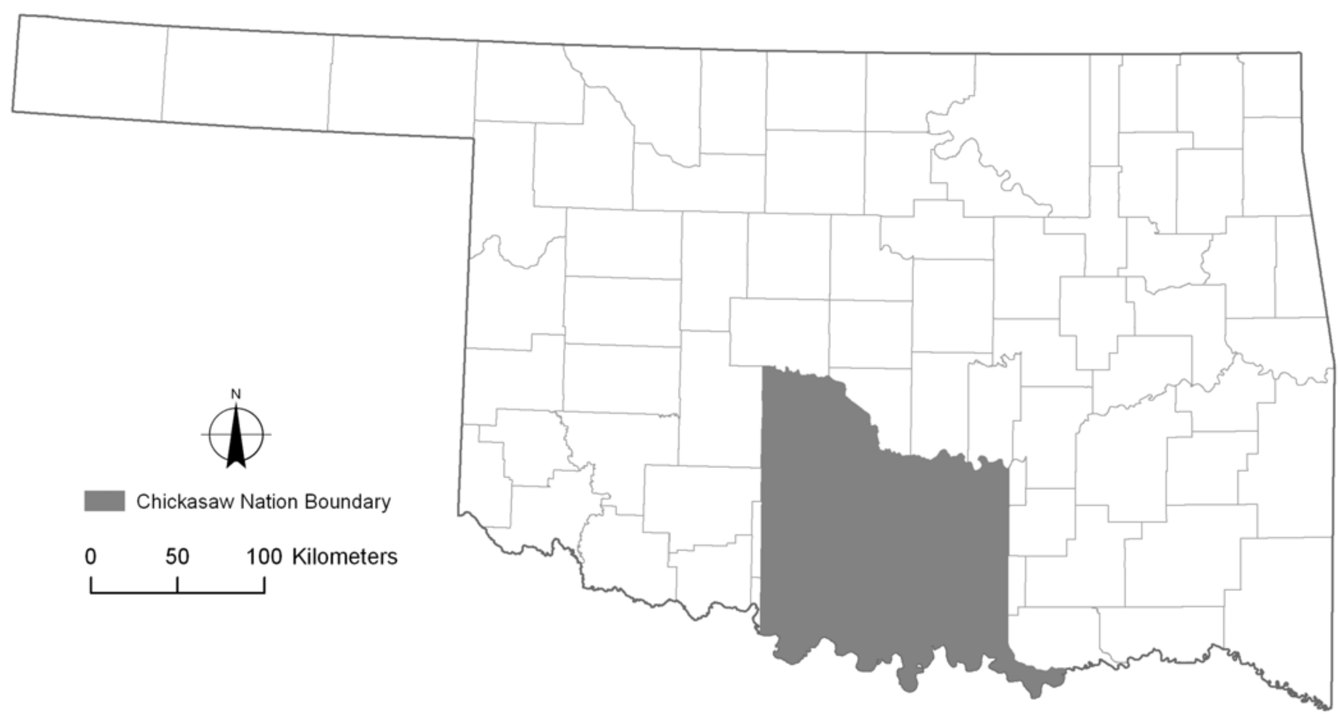


Figure 1.2. The Chickasaw Nation, 1855 to present.

CHAPTER 2:

THE USE OF LAND SURVEY RECORDS IN RECONSTRUCTING PAST LANDSCAPES AND EVALUATING HUMAN IMPACT

Introduction

Environmental transformation by human agency has impacted many regions of the Earth (Goudie and Viles 1997). Though environmental change proceeds in the absence of human activity, human-induced transformations have become a principal force altering the surface of the earth (Mannion 1998; Meyer and Turner 1997; Sauer 1969; Turner and Meyer 1991). Several sub-fields in geography are engaged in the study of human transformation of the environment. Among them, biogeography strives to understand the spatial and temporal distribution of biota and biotic assemblages (Cox and Moore 1993). As a discipline, biogeographers rely heavily on theory and approaches from evolutionary and population biology, systematics, physiology, and the earth sciences (Brown and Lomolino 1998). Often, it is difficult to distinguish from ecology (Veblen 1989). However, biogeography, as practiced by geographers, is more inclusive of human dimensions than traditional ecological inquiry (Taylor 1984).

Human alterations of biota are diverse and include introduction and extinction of species (Cox and Moore 1993; Spellerberg and Sawyer 1999; Veblen 1989), plant and animal domestication (Mielke 1989; Simmons 1980; Veblen 1989), alteration of biogeochemical cycles (Mannion 1998; Turner and Meyer 1991), habitat fragmentation and destruction (Saunders et al. 1991), and modifications of the land surface (Forman and Godron 1986; Meyer and Turner 1997). Since past human activities can influence biotic patterns for many years (Christensen 1989; Dupouey et al. 2002), the interpretation of biogeographic phenomenon without consideration of human influence may lead to erroneous conclusions (Mielke 1989; Spellerberg and Sawyer 1999).

Biogeographers have a number of resources at hand with which to address these questions, including palynological data, analysis of relict vegetation stands, analysis of land survey maps and notes, ethnographic surveys, analysis of repeat aerial and ground photography, and change detection analysis using geographic information systems (GIS) and remotely sensed data (Russell 1997). During the past decade, the use of land survey data has become one of the predominant methods for exploring the human dimensions of biogeographic change. This paper reviews the use of these data in the study of vegetation dynamics.

Land Survey Methodology

Documents generated by land surveys, conducted from the colonial era to the present, have proven to be useful for analysis of historical vegetation patterns. These records fill a critical gap in quantitative data available for the time prior to and immediately following European settlement. These data have been used to characterize the vegetation at the time of the survey, analyze plant/environment relationships, and the role of disturbance in structuring vegetation (Brothers 1991; Whitney 1994; Barrett et al. 1995; Predmore et al. 2007). Land surveys have been instrumental in aiding land managers and restoration ecologists in riparian, grassland, and Midwestern woodland habitat restoration (Nuzzo 1986; Galatowitsch 1990).

The earliest land surveys conducted in the United States employed the metes and bounds system, which has been criticized for lacking uniformity resulting in unequal areas and voids between adjacent parcels of land (White 1984). In an attempt to rectify these deficiencies, the Land Ordinance was passed by the Continental Congress in 1785, espousing survey before the settlement of Federal lands in the western territories and establishing the rectangular survey system (Stewart 1935). The Land Ordinance outlined a nationally integrated cadastral survey system, which utilized a unit of uniform shape and area (Cazier 1976; White 1984). The Public Land Survey (PLS) subdivided land into Townships of 36 square miles, which were further subdivided into sections of 1 square miles (Stewart 1935). The General Land Office (GLO), which was integrated with the Grazing Service to form the Bureau of Land Management in 1946, conducted surveys throughout the continental United States except for nineteen eastern and southern states, which were previously surveyed using the metes and bounds system (Stewart 1935).

Both PLS and metes and bounds surveys generated two datasets of interest to biogeographers—survey plats and bearing tree data. The first dataset was from surveyor notes about the features and vegetation types encountered along the survey lines. Upon returning from the field, these data were compiled into a plat from the area surveyed. While in the field, surveyors documented the general character of the soil, location of prominent physical features, such as barrens, prairies, scrublands, and forest, natural disturbances such as windfalls and erosion, and, in some instances, evidence of recent fires (Brothers 1991; Hutchison 1988; Whitney and DeCant 2001; Maclean and Cleland 2003). Soils were typically classified as first, second, or third rate for agricultural production. They also documented the location of agricultural fields, often with the landowners name provided, American Indian villages, and freedman settlements. Sawmills, coal mines, quarries, lime kilns, roads, and cattle trails are features of economic interest that were mapped as well. Thus, the plats produced by surveyors portray the spatial distribution of vegetation types, land use, and settlement patterns.

The second dataset provides quantitative data regarding the species of trees encountered along survey lines. These data were gathered in order to facilitate relocation of nodes (i.e. intersections of section lines, etc.) along the survey line by future surveyors, which were marked by cairns or other monuments. In the PLS surveys, at intersection of section lines, surveyors were required to record the distance and direction to and species and diameter of the nearest tree in each of four quadrants in order to relocate monuments. The same data were recorded for two individuals at the quarter section line (Bourdo 1956; Brothers 1991). Often, trees encountered along the survey line, referred to as lines trees, were also recorded (Batek et al. 1999). In metes-and-bounds surveys a single bearing tree was typically identified and measured at nodes along the survey line (McIntosh 1962; Siccama 1971). Although these data were not collected for ecological purposes, the process has provided a great deal of information on vegetation composition and structure. Witness tree data can be analyzed using plotless techniques, such as the point-center-quarter method to characterize vegetation composition (Cottam and Curtis 1956; Cole and Taylor 1995; Anderson et al. 2006; Bouldin 2008). Metrics of forest composition typically calculated using these data are stem density, frequency, and basal area. These metrics can be relativized and summed into an importance value for each species (Nelson 1997; Batek et al. 1999).

Caveats and Shortcomings

Although land survey data have contributed richly to our understanding of presettlement landscape patterns and vegetation composition, these data are not without fault (Bourdo 1956; Maines et al. 2001; Schulte and Mladenoff 2001; Whitney and DeCant 2001; Wang and Larsen 2006). Although errors and other problems have called into question the utility of PLS data for vegetation reconstruction, it has been determined that such problems represent a small fraction of the total surveys (Bourdo 1956; Hutchison 1988). The shortcomings of PLS data can be classified into two major categories—systematic and taxonomic.

At the root of the systematic shortfalls is the fact that land survey data were not collected for ecological analysis. Land surveys are intended to facilitate the orderly transfer and disposal of property. Nevertheless, the application of land survey data is often questioned because the data were not gathered from a randomly generated sample, which violates the assumptions of many statistical tests. An attendant criticism is that vegetation data was not collected within quarter sections, thus leaving a large gap in the data (Hutchison 1988). Thus, researchers must be cognizant of the spatial resolution of land survey data (Wang and Larsen 2006). In the case of the PLS surveys, measurements were made every quarter to half of a mile. The interval between sampling points is sufficient to mask vegetation patterns in relation to environmental gradients (Delcourt and Delcourt 1977). Therefore, PLS data should be used in regional scale analyses, not at scales less than one mile (Schulte and Mladenoff 2001).

Although land survey data provide quantitative data for woody plant species, no comparable data was recorded for herbaceous species (Brothers 1991). For this reason, land survey data is of greatest utility in forest ecosystems. However, surveyors did designate herbaceous vegetation in qualitative terms, such as wet prairie, dry prairie, barrens, and marsh (Sears 1926a; Finley and Potzger 1951; Anderson 1970). Surveyor bias in witness tree selection has also been demonstrated. One form of bias was the selection of trees exceeding a given diameter, or those known to be long lived or of little economic value. In Pennsylvania, surveyors selected gum trees (*Nyssa* species) as witness trees because of their low market value (Lutz 1930).

Taxonomic shortfalls are related to the surveyors' ability to accurately identify the tree species encountered. In the notes, surveyors typically recorded trees by common name, and, since common names may be regional or have fallen out of usage, this can present a problem when attempting to attribute the correct Latin binomial. Although some surveyors had formal botanical training, most did not (Delcourt and Delcourt 1996). A misidentification is obvious when a species is recorded beyond its range (Mladenoff et al. 2002). For example, in central Oklahoma, surveyors reported the presence of pin oak, water oak, and red oak, which only occur in the eastern portion of the state (Shutler and Hoagland 2004). In addition, trees were often identified to the genus level only. Although three species of elm occur in the Arbuckle Mountains region of Oklahoma (*Ulmus alata, U. americana, and U. rubra*), surveyors list them simply as "elm" (Shutler 2000; Shutler and Hoagland 2004). Related to this issue is the challenge of deciphering the handwritten script of the surveyors.

Research Applications

Despite these drawbacks, land survey data have been extensively utilized for the analysis of past distribution patterns and vegetation composition. H. A. Gleason made the earliest use of PLS data in an examination of persistent forest groves on the prairies of Illinois. After consulting PLS plats, Gleason (1912; 1913) was able to demonstrate that forest groves were afforded protection against fire by wetland features. Since that time, there have been numerous studies of presettlement vegetation at a variety of scales, including township (Bugess 1964), watershed (Fassett 1944; Kapp 1978), county (e.g.: Anderson and Anderson 1975; Ellarson 1949; Schafale and Harcombe 1983; Shutler and Hoagland 2004), region (e.g.: Lutz 1930; Bromely 1935; Mladenoff and Howell 1980; Loeb 1987; Cogbill 2000; Anderson and Baker 2006; Peacock et al. 2008), and state (e.g.: Curtis 1956; Veatch 1959; Schroeder 1981). The majority of presettlement vegetation studies have focused on the Midwest, with the greatest number of publications in Wisconsin (Table 2.1).

Following Gleason (1912; 1913), the most extensive use of PLS data was made by Sears (1925; 1926a; 1926b). In his studies, Sears mapped the historical extent of forest and grassland vegetation and analyzed the relationship between the physical environment and vegetation distribution. Sears' maps of Ohio, appeared in two publications, "virgin" forest (1925) and grasslands (1926a). Three research themes emerge from Sears work which characterize all subsequent analyses of land survey data—mapping the distribution and analysis of plant/environment relations, change in the distribution and abundance of individual species, and detection of change in landcover/vegetation types.

Vegetation Mapping and Environmental Relations

The physical environment is a key determinant in the composition and structure of plant communities. Maps depicting spatial distribution of vegetation are often accompanied by tables of structural measures such as basal area, stem density, and a cumulative measure of importance (see Lutz 1930; Kenoyer 1933; Cottam 1949; Finley and Potzger 1951; Plummer 1975; Delcourt 1976; Ebinger 1987; Leitner and Jackson 1981; Ebinger 1987; Nelson 1997; Batek et al. 1999; Bragg 2003). These indices may be calculated from the distance and diameter data recorded by PLS surveyors.

The use of land survey data in the analysis of vegetation/environment relations is based upon the assumption that these data portray the distribution of vegetation prior to extensive human disturbance. Sears analyzed the role of environment in the distribution of vegetation, particularly the influence of geomorphology and soils in the distribution of grasslands and forests. Using PLS data and contemporary geology maps, he was able to correlate the occurrence of forests with glacial moraines (1925) and prairies with glacial outwash plains (1926a). This approach, with increasing levels of statistical sophistication, has been employed in many later studies. For example, Jones and Patton (1966) analyzed the role of edaphic factors in the distribution of Black Belt prairie in Alabama and determined that the occurrence of alkaline clay soils corresponded with grasslands. Rankin and Davis (1971) supported these conclusions by demonstrating that low tree density and grasslands were correlated with upland and alkaline soils in the Blackland prairie.

A variety of statistical techniques have been used to determine the relationship between presettlement forest distribution and environmental factors. Shanks (1953) used the Coles Index to analyze the association of various tree species with soil type and topography and found that American beech (*Fagus grandfolia*) was the dominant presettlement forest tree, but in areas of broken topography sugar maple (*Acer* *saccharum*) was the canopy dominant. Crankshaw et al. (1965) used multiple regression to analyze the response of tree species to environmental conditions. They reported that sugar maple had a preference for upland silt loam soils, black ash (*Fraxinus nigra*) for alluvial silty clays and poorly drained silty clay terraces, and shingle oak (*Quercus imbricaria*) preferred soils with a high sand content.

Whitney and Steiger (1985) conducted a similar analysis, in an investigation of vegetation site relations in the eastern Prairie Peninsula (see Transeau 1935). Like Crankshaw et al. (1965), they assigned each witness tree to topographic, geologic, and drainage categories. They found that topographic position and drainage influenced the distribution of grassland vegetation, bur oak groves, and wetland communities. It should be noted that these analyses use land survey data but the environmental data is derived from modern soil surveys and geologic maps. Thus, it is often assumed that the changes in these factors have not been significant during the intervening years.

Although climate, soils, and geologic substrate play an important role in the organization of biological communities, species composition is often regulated by disturbance. In fact, Stearns (1949) concluded that the significance of windthrows were an underappreciated factor in the ecology mixed hardwood-conifer forests based upon their prevalence in the surveyors records. In order to understand the importance of disturbance, it is necessary to know the intensity and frequency of disturbance events. However, disturbance patterns may very well be obscured by human activities at the time of or prior to the surveys (Sprugel 1991).

Nonetheless, several studies have used land survey data to determine disturbance type and estimate the frequency of fire in forested ecosystems (for example, Lorimer 1977; Canham and Loucks 1984; Grimm 1984; Whitney 1986; Palik and Pregitzer 1992; Habeck 1994; Johnson 1994; Batek et al. 1999; Zhang et al. 2000; MacLean and Cleland 2003). However, there is apparently bias in the surveyors' records for disturbance. For example, Canaham and Loucks (1984) determined that surveyors only recorded blowdowns in excess of 1 hectare (2.47 acres). Also, references to fire are more frequent in the surveyors journals than on the plats (Canaham and Loucks 1984).

Fire and windthrow are common in northern coniferous forests, but the frequency of occurrence has been debated (Lorimer 1977). Previously, it was held that the return interval was shorter than the maximum lifespan of the constituent tree species, but Lorimer (1977) analyzed surveyor data and demonstrated that return intervals were much longer. He also concluded that the fire history of Maine has been obscured by the occurrence of fires related to logging and clearing. Like Gleason (1912), Grimm (1984) used PLS data to demonstrate the role of rivers as natural fire breaks in Minnesota.

Zhang et al. (1999) used PLS data to estimate an average of 13 fires and 17 windthrow events annually during the mid-1800s in the coniferous forests in Michigan. They also noted a correlation between topography and disturbance type. Fire was most frequent on south aspects and higher elevations and windthrows were correlated with slope position and westerly aspects. In Maine, most windthrows were restricted to lowland coniferous forests, particularly those occurring in swamps and on shallow rocky soil (Lorimer 1977). Therefore, they concluded that the spatial pattern of disturbance represented a shifting mosaic, in which the entire landscape was affected by fire every 480 years and by windthrow every 541 years. Long, narrow windthrows on plats have been attributed to tornadoes (Canham and Loucks 1984).

Distribution and Abundance of Individual Species

Change in the distribution and abundance of a species have profound biogeographic implications. For example, increasing abundance of woody plants in grasslands can lead to a decline in species richness and productivity (Archer 1995). Since surveyors recorded the species of trees encountered, land survey data can provide a reference point in time. Ross (1950) reviewed PLS records for Indiana in a study of the distribution of Virginia pine (*Pinus virginiana*). She found only four individual trees from two Indiana counties, even though the present distribution includes 29 counties. The increased abundance of Virginia Pine was attributed to planting by humans and its aggressive ability to colonize old-fields (Ross 1950). Abrams (2001) reviewed studies using land survey data to determine the distribution and abundance of white pine (*Pinus strobus*) in presettlement forests. White pine is a species of economic importance and, based upon land survey records, its abundance was apparently exaggerated in early written accounts (Lutz 1930; Abrams 2001). Of the 17 case studies reviewed by Abrams, 13 demonstrated substantial decline whereas four showed only modest gains in white pine abundance (Abrams 2001).

Ebinger (1986) and Shotola et al. (1992) compared PLS data with contemporary data sources to determine whether sugar maples (*Acer saccharum*) had increased in abundance at the expense of oaks since the time of settlement. Both studies concluded that sugar maple was indeed increasing in abundance, a shift in composition with ecosystem level implications since acorns are a major food source for wildlife species.

In the early 20th century, the American chestnut (*Castanea dentata*) was driven to the brink of extinction by chestnut blight. As a result, American chestnut was eliminated as a canopy dominant. Land survey data have allowed researchers to characterize the composition of pre-blight forests and compare their composition with modern forest stands (Abrams and Ruffner 1995; Abrams and McCay 1996). There has also been a decline in white oak (*Quercus alba*), beech (*Fagus grandifolia*) and hemlock (*Tsuga canadensis*) (Abrams and Ruffner 1995). However, chestnut oak (*Quercus prinus*), red oak (*Quercus borealis*), and red maple (*Acer rubrum*) have increased in abundance. Not only was American chestnut a victim of blight, it was harvested for timber and to produce charcoal local for local iron industries (Abrams and Ruffner 1995).

American Indian Land Practices

American Indian land use practices had a profound influence on vegetation composition. Although anthropologists have used land surveys to locate American Indian villages, few studies have examined the relationship between these settlements and forest types (Jones and Kapp 1972; Dorney 1981; Dorney and Dorney 1981). Dorney (1981) noted that most Potawatomi villages were located in sugar maple-basswood-oak forest, Waukesha on oak savannas, and Winnebago in oak forests and savannas. Since the villages occurred in both fire tolerant and fire prone vegetation types, he concluded that there was no relationship between village locations and vegetation type. Dorney and Dorney (1989) used PLS data to explain anomalous patterns of species distribution and vegetation structures, such as the presence of fire tolerant vegetation in a region of predominately fire intolerant vegetation. In this case, the location of Potawatomi and Winnebago villages was correlated with the occurrence of oak savannas.

Change Detection

Evaluating the degree of human impact requires multiple observations through time. Land survey data can serve as a baseline for comparison with later data sources (Mladenoff and Howell 1980; Fralish et al. 1991; Smith et al. 1993; DeWeese et al 2007; Surrette et al. 2008). In addition, quantifying the change in spatial extent of land cover types requires the use of ancillary data sources such as forest inventory data, subsequent map products, and aerial photography. Fassett's (1944) study of the Brule River Basin in Wisconsin represents one of the earliest analyses of land cover change using PLS data. Fassett mapped 12 vegetation types as well as agricultural land from PLS plats. He also used PLS data to map the distribution of six important forest trees, including white pine. These maps were then compared with the map generated from the 1932 Wisconsin Land Economic Survey. The results show a pattern of increasing fragmentation of vegetation due to settlement and land clearing for agriculture.

John Curtis (1956) used PLS data to analyze the effects of human settlement on mid-latitude forests and grasslands. Maps derived from 1831 PLS plats for Cadiz Township, Green County, Wisconsin, provided a baseline for comparison with land cover maps from Shriner and Copeland (1904), the Wisconsin Land Economic Survey of 1932, and aerial photography for the year 1950. Shriner and Copeland (1904) addressed the affect of deforestation on streamflow. In 1831, 5.8 percent of all streams were classified as intermittent. However, in 1950, 83.2 percent were so classified. Curtis (1956) calculated that forests occupied 29 percent of Cadiz township in 1831, but only 3.6 percent in 1950 with a 36 percent decrease in perennially flowing springs. Curtis also noted the increasingly linear boundaries between land cover types as opposed to the organic form of boundaries in the early nineteenth century.

Since the publication of these landmark studies, comparisons of repeat aerial photography and survey data are more common (for example, Paterson 1978; Bahre and Shelton 1993; White and Mladenoff 1994; Cole and Taylor 1995; Leahy and Pregitzer 2003). Since aerial photographs are taken perpendicular to the surface of the earth, they are appropriate for planimetric measurement and analysis, much like survey plats. Moreover, it is possible to select truly random sites for analysis with aerial photographs due to their contiguous cover (Bahre 1991; Bahre and Shelton 1993). Limitations to this approach include age of available photographs (first vertical aerial photographs date back only to the mid-1930s) and the poor resolution of many of the early aerial photographs (Bahre 1991).

Burgess (1964) analyzed the change in the extent of land cover types in Helendale Township, Richland County, North Dakota. PLS data for the year 1871 was compared with aerial photography from 1962. Results of this analysis showed the obliteration of tall grass prairie and a significant reduction in forest, savanna, and wetlands in favor of agricultural land. Compositional changes revealed a pronounced decline in the abundance of bur oak (*Quercus macrocarpa*), but an increase of American basswood (*Tilia americana*).

Several studies have compared land survey data with later sources to ascertain change in species composition (e.g. Stearns 1949; Greller 1972; Janke et al. 1978; Palik and Pregitzer 1992; Nelson et al. 1994; Van Deelen et al. 1996; Silbernagel et al.

1997; Cowell 1998; Dyer 2001). Such studies analyze the change in species composition by comparing forest stand metrics such as basal area and stem density. There is also interest in comparing environment relationships to determine whether tree species have different site preferences in modern forests than in presettlement forests. For example, Cowell (1998) compared the composition of secondary growth forests with PLS data from Georgia. He mapped the location of witness trees and attributed them to various physical factors. These data were then compared with quadrat data collected from second growth stands. Although he found little change in the taxa present, there has been change in their abundance. For example, pine species (*Pinus spp.*) were dominant in presettlement forests and immature secondary stands, but not in mature post-settlement stands.

Conclusion

The major schools of nature-society research in contemporary American geography have grappled with the issues of the social causes, contexts, and consequences of environmental transformation (Meyer and Turner 1997), while much of contemporary biogeography has been concerned with ecological changes in the landscape mosaic over time. As natural vegetation cover is lost due to anthropogenic activity, conservation in highly fragmented environments will require innovative approaches (Schwartz 1997). Effective vegetation management, though, must be predicated on an understanding of how present vegetation patterns relate to past human activities. In the absence of long-term ecological experiments, information on past land use and the historical structure and composition of vegetation is essential (Veblen and Lorenz 1991). Land surveys supply a quantitative glimpse into the past, one devoid of the subjectivity common in written accounts. Maps and compositional data derived from land survey records have proven to be an effective baseline from which subsequent changes can be gauged. These records fill a critical gap in quantitative data available for the time prior to and immediately following European settlement and have been used to characterize the vegetation at the time of the survey, analyze plant/environment relationships, and assess the role of disturbance in structuring vegetation.

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Table 2.1. Published accounts by state in which Public Land Survey data are employed for the reconstruction and interpretation of presettlement vegetation. Papers listed in the citation column may be either reconstructions of vegetation at the regional, county, or state level. In addition, several of the cited studies analyze ecological processes and vegetation-environment relationships.

State	Citations
Alabama	Jones and Patton 1966; Rankin and Davis 1971; Shankman and Wills 1995; Predmore et al.
Arkansas	Bragg 2003
California	Fritschle 2008
Florida	Delcourt and Delcourt 1977
Georgia	Plummer 1975; Cowell 1995, 1998
Illinois	Gleason 1912, 1913; Myers and Wright 1948; Kilburn 1959; Anderson 1970; Anderson and Anderson 1975; King and Johnson 1977; Kaminski and Jackson 1978; Rodgers and Anderson 1979; Leitner and Jackson 1981; Ebinger 1986, 1987; Thomas and Anderson 1990; Anderson 1991; Fralish et al. 1991; Shotola et al 1992; Nelson et al. 1994; Brugam and Patterson 1996; Nelson and Sparks 1998; Swigart and Anderson 2000
Indiana	Potzger and Potzger 1950; Rohr and Potzger 1950; Ross 1950; Blewett and Potzger 1951; Finley and Potzger 1951; Potzger et al. 1956; Crankshaw et al. 1965; Lindsey et al. 1965; Lindsey 1972; Cole and Taylor 1995; Barr et. al 2002
Louisiana	Delcourt and Delcourt 1974; Delcourt 1976; DeWeese et al. 2007
Maine	Lorimer 1977
Michigan	Kenoyer 1929, 1933, 1939; Hushen et al. 1966; Jones and Kapp 1972; Janke et al. 1978; Kapp 1978; Paterson 1978; Brewer et al. 1984; Whitney 1986; Dodge 1987; Palik and Pregitzer 1992; Barrett et al. 1995; Delcourt and Delcourt 1996; Schaetzl and Brown 1996; Van Deelen et al. 1996; Dodge 1997; Silbernagel et al. 1997a, 1997b; Brown 1998; Zhang et al. 2000; Leahy and Pregitzer 2003; MacLean and Cleland 2003
Minnesota	Marschner 1930; Grimm 1984; Dyer and Baird 1997; Friedman et al. 2001; Wang and Larsen 2006
Mississippi	Peacock et al. 2008; Surrette et al. 2008
Missouri	Holwell and Kucera 1956; Steyermark 1959; Wuenscher and Valiunas 1967, Nelson 1997; Batek et al. 1999; He et al. 2007
Montana	Habeck 1994
Nebraska	Rothenberger 1989; Johnson 1994
New Jersey	Ehrenfeld 1982

New York	Gordon 1940; McIntosh 1962; Greller 1972; Seischab 1990; Marks and Gardescu 1992; Seischab 1992. Smith et al. 1993
North Dakota	Burgess 1964
Ohio	Sears 1925, 1926a, 1926b; Shanks 1953; Beatley 1959; Ogden 1965; Gordon 1966, 1969; Whitney and Somerlot 1985; Whitney and Steiger 1985; Dyer 2001
Oklahoma	Shutler and Hoagland 2004
Oregon	McAllister 2008
Pennsylvania	Lutz 1930; Abrams and Nowacki 1992; Black and Abrams 2001
Texas	Schafale and Harcombe 1983
Utah	Christensen and Johnson 1964
Vermont	Siccama 1971
Washington	Towle 1982; Wright and Agee 2004
West Virginia	Abrams and McCay 1996
Wisconsin	Trewartha 1940; Fassett 1944; Thomson and Fassett 1945; Cottam 1949; Ellarson 1949; Stearns 1949; Curtis 1956, 1959; Goder 1956; Ward 1956; Neuenschwander 1957; Stroessner and Habeck 1966; Barnes 1974; Finley 1976; Kline and Cottam 1979; Mladenoff and Howell 1980; Dorney 1981; Liegel 1982; Canham and Loucks 1984; Dorney and Dorney 1989; Mladenoff et al. 1993; White and Mladenoff 1994; Barnes 1997; Radeloff et al. 1998; He et al. 2000; Manies and Mladenoff 2000; Maines et al. 2001; Mladenoff et al. 2002; Bollinger et al. 2003; Rhemtulla et al. 2007
Wyoming	Anderson and Baker 2006

CHAPTER 3:

A LANDSCAPE IN TRANSITION: THE HISTORIC VEGETATION OF THE ARBUCKLE MOUNTAINS, OKLAHOMA, 1870 TO 1898

Abstract

The western cross timbers are a spatially heterogeneous region consisting of a mosaic of forest, woodland, savanna, and prairie vegetation types. During much of the 20th century, fire suppression and certain land use practices have resulted in the increase of woody vegetation at the expense of grasslands in the region and may have contributed to an increase in the density of overstory dominant *Quercus* spp. Additionally, widespread habitat fragmentation has been documented in the area in the time since European settlement. In this study, we compare two historical datasets, from the 1870s and 1890s, respectively, to quantify changes in landscape structure and woody plant assemblages corresponding to rapid demographic changes occurring within the cross timbers of the Arbuckle Mountains, Oklahoma, U.S.A During this ~27 year period, forest/woodlands decreased in areal extent by approximately 21,948 ha, while both forest/woodland and grasslands became increasingly fragmented as large scale agriculture became ubiquitous in the region. Differences in stand composition are also documented, though it is uncertain whether these changes relate to taxonomic uncertainties in the historical datasets or actual changes in community dominance. Analyses of changes in density between the two survey periods indicate that the cross timbers of the Arbuckle Mountains were denser immediately prior to European settlement than in the period proceeding settlement, while data from both survey

periods tend to confirm that the contemporary cross timbers are denser than historic times.

KEYWORDS Public Land Survey System; Cross Timbers; Arbuckle Mountains; Historical Vegetation Reconstruction

Introduction

The current biogeographic patterns in a given area are not only the product of contemporary environmental factors, such as climate, substrate, and topography, but historical factors as well, including anthropogenic disturbance regimes (Hermy 1996; Motzkin et al. 1996; Motzkin et al. 1999; Batek et al. 1999; Dupouey et al. 2002). In the time since European settlement, much of the native temperate forests and grasslands of North America have been modified as a result of intensive human activity (e.g. Curtis 1956; Foreman 1998). In particular, timber harvesting and land conversion for agriculture, ranching, and other land use practices have contributed to increased fragmentation of native ecosystems (Lord and Norton 1990; Saunders et al. 1991; Foreman 1998). Additionally, suppression of native fire regimes and other land use practices has resulted in the increase of woody vegetation at the expense of temperate grasslands (Archer 1995; Engle et al. 1997) and the closing of canopies in woodlands and forests at the expense of understory species (Engle et al. 2006; Nowacki and Abrams 2008).

These anthropogenic processes can have profound ecological consequences. For instance, fragmentation (i.e. the reduction of a habitat, ecosystem, or land cover type to a collection of smaller, often discontinuous patches (Foreman 1998)) can alter microclimatic conditions within and surrounding remnant patches (Saunders et al.

1991). Similarly, fire suppression can result in more mesophytic conditions in erstwhile pyrogenic habitats (Nowacki and Abrams 2008). In both instances, the result is often a difference in species assemblages than in pre-disturbed habitats.

To better understand the influences of these and other anthropogenic disturbances on ecosystem structure, researchers are increasingly using historical data to create baselines from which subsequent changes in vegetation can be measured (e.g. Bahre 1991; Maines and Mladenoff 2000; Bahre and Hutchinson 2001; Fritschle 2008). Among the datasets researchers frequently utilize are the survey records of the Public Land Survey System.

The Public Land Survey (PLS) records of the US General Land Office (GLO) represent one of the few quantitative datasets of pre- and early-European settlement vegetation in much of the United States. Despite the inherent limitations of the PLS records (Bourdo 1956; Schulte and Mladenoff 2001; Whitney and DeCant 2001), the notes, witness tree records, and plat maps of the PLS surveys have richly contributed to our understanding of past ecological conditions and have been useful in evaluating the degree of human modification to the landscape (e.g. Fassett 1944; Curtis 1956; Mladenoff and Howell 1980; Smith et al. 1993; Zhang et al. 2000; Dyer 2001).

Public Land Survey records contain two types of data that are useful for the analysis of historic vegetation. As surveyors partitioned the land into a grid of 93.24 km^2 (36-mi^2) townships and further subdivided each township into 2.59 km^2 (1 mi^2) sections, surveyors documented prominent features, such as the location of barrens, prairies, scrublands, and forests; natural disturbances, such as windfalls and erosion; and, in some instances, evidence of recent fires (Hutchison 1988; Whitney and DeCant

2001). Upon returning from the field, these data were compiled into a series of township-wide plats from the areas surveyed.

Surveyors also recorded quantitative information related to “witness” (or “bearing”) trees encountered along the survey lines. These data were recorded at the intersection of section lines, where surveyors noted the nearest tree in each of the adjoining sections, recording its identification and diameter at breast height (DBH), compass direction and distance from the corner section. Surveyors recorded the same information at each quarter section point, but only for the nearest trees the adjoining sections (Stewart 1935; Hutchison 1988). As a result, each corner section could have up to four witness trees and each quarter section a maximum of two trees.

The present-day state of Oklahoma, USA is unique in that the General Land Office conducted two separate surveys in a portion of the state during a relatively short time span (Hoagland 2006). Beginning in the early 1870s, the U.S. federal government surveyed all lands of the Chickasaw Nation in what was then Indian Territory (Figure 3.1; Commissioner of Indian Affairs 1875; Gibson 1981). In 1895, the United States Congress appropriated $200,000 for the survey of all tribal lands in Indian territory, including those lands that had been previously surveyed in the 1870s (Gibson 1981; Carter 1999).

Part of the resurveyed area includes a portion of the state that is characterized by a mosaic of forest, woodland, and grassland vegetation known collectively as the cross timbers (Hoagland et al. 1999). During the past century, a combination of land use practices and fire suppression is believed to have contributed to increased woody plant abundance in former grasslands in the region (Hoagland and Johnson 2001) and may have led to increases in woody plant densities in woodlands and forests (Rice and Penfound 1959; Johnson and Risser 1975; Engle et al. 2006). Moreover, there is evidence of widespread habitat fragmentation in the area resulting from various land use practices (Hoagland and Johnson 2001; Shutler and Hoagland 2004).

The period between the two surveys is marked by rapid demographic changes in the surveyed areas as the Post Bellum period brought rail lines, rapidly expanding towns, and new agricultural-based economies (Gibson 1981; Rundstrom 2007). As such, these PLS survey records may provide valuable insight into the degree of ecological transformation, if any, that correspond to this period of demographic shift. For instances, do we find differences in land cover as depicted on the PLS plats from the two survey periods and, if so, are these differences reflected in the recorded witness tree records from the two surveys? Additionally, determination of changes in woody plant densities between the two survey periods may provide insight into how well the hypothesis of mesophication (Nowacki and Abrams 2008) applies on the western fringe of the eastern deciduous forest.

The goal of this study is, therefore, to evaluate the biological consequences of historic habitat fragmentation utilizing PLS survey data. Specifically, we quantify landscape structure and associated woody plant assemblages at two discrete points in time, one corresponding to pre-European settlement, the other following European settlement. Our analyses involve the quantification of habitat fragmentation; analysis of changes in the distribution and composition of woody plant species; and comparisons of structural differences of arborescent habitats between the two survey periods.

Methods

Study Area

The Arbuckle Mountains cover an area of approximately 215,000 ha in south-central Oklahoma (Figure 3.2). The Arbuckle Mountains, topographically a low plateau, rise a few hundred feet above the surrounding prairie, sloping from an elevation of 411 meters (1,350 feet) in the west to 229 meters (750 feet) in the east (Dale 1956; Hutcheson 1965). The Arbuckle Mountains consist of areas of considerable faulting and folding, resulting in many unusual structural features. The geologic history of the region has led to the exposure of thick late Cambrian to middle Mississippian limestone sediment and late Mississippian and Pennsylvanian sediment (Suneson 1997). The surface geology is characterized mostly by outcrops of carbonate rocks (Ham 1969), though granitic outcrops surrounded by limestones, conglomerates, sandstones, shales, cherts, and other types of rocks are prevalent (Dale 1956; Suneson 1997).

The Arbuckle Mountains can be further subdivided into two distinct physiographic provinces, the Timbered Hills and the Arbuckle Plains (see Figure 3.2). The Timbered Hills are the most topographically distinct feature of the Arbuckle Mountains, rising to a height of about 122 meters (400 feet) above their base and located on a large truncated anticline spanning 388 km^2 (150 square miles). The Timbered Hills are composed of pre-Cambrian porphyritic rock and, like much of the Arbuckles, are extensively eroded and contain many shallow ravines, rounded hills, and flat tablelands (Dale 1956; Hutcheson 1965). The Arbuckle Plains are a fluvikarstic landscape characterized by a gently rolling topography upon intensely faulted limestone beds (Fairchild *et al*. 1990), interspersed with granitic outcrops.

The study area is located in the Subtropical Humid (Cf) climate zone, which is characterized by long, hot summers and short, mild winters (Trewartha 1980). Summer temperatures average 28º C, while winter temperatures average 3º C. Mean annual precipitation is 98 cm, with much of it occurring in April, May, and June (Oklahoma Climatological Survey 2008). November, December, and January are the driest months, though drought conditions as reflected by the vegetation typically occur in July and August (Dale 1956).

The Arbuckle Mountains lies within the cross timbers, a region characterized by a mosaic of forest, woodland, and prairie vegetation. The forest and woodland vegetation of the cross timbers is dominated by two species of woody plants, *Quercus stellata* and *Q. marilandica*, while the grassland communities are dominated by *Andropogon gerardii*, *Panicum virgatum*, *Schizachyrium scoparium*, and *Sorhastrum nutans* (Hoagland et al. 1999). However, reduction of native fire regimes during the past century has resulted in the increase of woody plants at the expense of grassland (Archer 1995; Engle et al. 1997; Hoagland and Johnson 2001) and is believed to have led to the increase canopy cover of dominant overstory *Quercus* spp. (Engle et al. 2006).

Data Analysis

We obtained microfiche copies of transcribed surveyor notes and digital (scanned) township plats for the study area from the Oklahoma Department of Libraries. Forty-two townships encompass the Arbuckle Mountains (Figure 3.3), two of which occur outside of the Chickasaw Nation boundary and, therefore, were not surveyed in the 1870s. The forty remaining townships were first surveyed between the years of 1870 and 1872, with the majority of the surveys (35) occurring in 1871. The entire 1870s survey of the study area spanned 1.25 years (November 1870 to February 1872). Each of the forty townships was resurveyed from November 1897 through December 1898, with most of the surveys (30) conducted throughout 1898. Overall, there was an average of 26.6 years (26 years, 7 months) between the original survey and resurvey (Table 3.1).

We georeferenced each scanned image using a digital township, range, and section dataset for the study area obtained from the Bureau of Land Management's Land Survey Information System (LSIS). We then digitized relevant features from each PLS plat, including land cover types, transportation networks, and man-made structures, into a series of seamless GIS layers. The resulting land cover layers consisted of features delineated by surveyors as forest/woodland, grassland, cultivated areas, and wetlands. The transportation network layers included features identified as wagon roads, cattle trails, other trails, and railroads. The man-made structures layers consisted of any point features that surveyors marked as anthropogenic in origin, such as various buildings, mines, and gins.

In order to quantify change in land cover between the two survey dates, we calculated several landscape indices that influence species composition and distributions and serve as proxies of the degree of habitat fragmentation (Rempel 2008). Metrics calculated for each survey period include class area (measure of total area occupied by a particular land cover type, serves as measure of overall landscape composition and heterogeneity; ca = Σa_i); number of patches (measure of individual occurrences of a given land cover type, serves as a proxy for the degree of subdivisions or fragmentation of a landscape; np = n_i); and mean patch size (average area occupied by each land cover type, related to np-the more patches of a particular class, the smaller the average size of each patch, indicating the amount of fragmentation; mps = ca/np).

We also identified and quantified areas of change by combining each time stamped GIS layer into a single composite layer using a GIS overlay operation (Langram and Chrisman 1988). The resulting composite layer consists of a series of unique condition features, each of which were attributed with both their 1870s and 1890 land cover types. We then used a series of queries to identify and quantify areas that had a either the same land cover type in the 1870s and 1890s or different land cover types in the 1870s and 1890s.

We used the witness tree records to database all recorded corner section and quarter section tree information. Recorded data included common name of the tree species, to which we attempted to apply the appropriate nomenclature, estimated diameter at breast height, and compass bearing and distance from the corner or quarter section point. We determined the x,y coordinates of the intersections of section lines and each quarter section points using the digital township, range, and section layer from the LSIS. The x,y coordinates for each point from which trees were recorded were then joined to the tree data. We used these data to plot the location of each recorded individual using the following formula:

$$X_2 = X_1 + \text{distance} * \cos(\text{angle}), \tag{1}$$

$$Y_2 = Y_1 + \text{distance} * \sin(\text{angle})$$

Where X_2 and Y_2 are the newly derived X and Y coordinates, respectively; X_1 and Y_1 are the starting X and Y coordinates (intersection of section lines and quarter section points), respectively; distance is the recorded distance converted from links (survey notes) to meters; and angle is compass bearing converted to radians ((degree*Π)/180). For all calculations, we used Albers Conical Equal Area coordinates.

To examine relationships between plotted distributions of an individual taxon and environmental variables, we intersected plotted witness tree records from both survey periods with a digital 1:250,000 USGS surficial geology layer (Cederstrand 1996) and a moisture availability index layer (Pallardy 1995; Batek et al. 1999). The moisture availability index (MI) layer was created by combining a slope and an aspect layer generated from a 1/3 arc second (approximately 10 m) National Elevation Dataset (USGS 2008) into a composite layer. In order to do this, we reclassified the aspect layer into eight 45° classes based on the midpoint azimuths (i.e. 0°/360°, 45°, 90°, 135°, 180°, 225°, 270°, and 315°) and reclassified the slope layer into five classes: 0 (< 1%), 1 (1-2.15%), 2 (2.16-4.64%), 3 (4.65-10%), and 4 (> 10%). The two layers were then combined using the following formula:

$$\mathrm{MI} = (\cos(\mathrm{Aspect} - 45) * \text{slope class}) \quad (2)$$

The resulting layer has values ranging from -4 (very xeric) to +4 (very mesic; Batek et al. 1999).

We estimated the spatial association between selected tree species and environmental variables by calculating positive (W^+) and negative (W^-) weights for each tree species and each class in the environmental layers using methods described by Bonham-Carter et al. 1989 and Bonham-Carter and Agterberg 1999. W^+ and W^- are estimated for each class of an evidential layer using the following formulae (Bonham-Carter (1994)):

$$W_i^+ = \log_e \frac{P\{B_i | D\}}{P\{B_i | \overline{D}\}} \tag{3}$$

$$W_i^- = \log_e \frac{P\{\overline{B}_i | D\}}{P\{\overline{B}_i | \overline{D}\}} \tag{4}$$

Where $P\{B_i | D\}$ is the probability of class *i* of layer *B* given tree species *D*, which is equal to $N\{B_i \cap D\} / N\{D\}$. Similarly, $P\{B_i | \overline{D}\}$ is the probability of class *i* of layer *B* given the absence of tree species *D* or $N\{B_i \cap \overline{D}\} / N\{\overline{D}\}$; $P\{\overline{B}_i | D\}$ is the probability of class *i* of layer *B* being absence given the presence of tree species *D* or $N\{\overline{B}_i \cap D\} / N\{D\}$; and $P\{\overline{B}_i | \overline{D}\}$ is the probability of class *i* of layer *B* being absence given the absence of tree species *D* or $N\{\overline{B}_i \cap \overline{D}\} / N\{\overline{D}\}$.

If the spatial association is greater than would be expected by chance, W^+ is positive and W^- is negative. If the spatial association is less than would be expected by chance, W^+ is negative and W^- is positive. A value nearing zero indicates randomness (Kemp et al. 1999; Raines et al. 2000). The larger the difference between the positive and negative weights (W^+- W^-), known as the contrast (*C*), the greater the spatial association (Bonham-Carter et al. 1989).

We tested the null hypothesis of no differences in species composition in different environmental units (i.e. on different geological formation or moisture classes) between the two survey periods using the contrast (*C*) and a multi-response permutation procedure (MRPP; Biondini et al. 1985). MRPP tests for significance differences between two or more sampling units by comparing mean within group distances of *a priori* groups to within group mean distances of randomly assigned groups (Mielke

1991). A low P-value (<0.05) indicates differences between groups are greater than expected from the random sampling. Differences between the spatial associations served as an indication that other factors, such as anthropogenic activities, may be influencing the distribution of individual taxon.

In order to determine the structure of woody vegetation, we calculated basal area (πr^2), relative dominance (basal area individual taxon/basal area all taxa), relative density (number of individuals of a taxon/number of all individuals all taxa), and importance value (IV); average of relative density and relative dominance) for each taxon for each surveyed period. Additionally, in order to determine whether there have been changes in tree density in the study area, we calculated mean distance from each survey point to recorded trees (Batek et al. 1999), as well as density at each survey point using the point-centered quarter method (Cottam and Curtis 1956). All of the above measurements excluded areas in which no witness trees were recorded.

In order to determine whether there was a significant difference between average distance to recorded trees, calculated density, and basal area at each survey point for each survey period, we evaluated the calculated values from each survey period using the Mann-Whitney U test (Wilcoxon rank sum test). We selected the Mann-Whitney U test because the data are non-Gaussian: The Mann-Whitney U test is the non-parametric alternative to the two-sample t test used to determine whether the medians of two independent distributions are different (Venables et al. 2008).

We also used calculated stem density values from each monument point and kriging to create continuous density surfaces for each survey period. We first measured the spatial autocorrelation of the sample points using a semivariogram.

Because of the spatial stationarity of the data, we interpolated the density data using ordinary kriging using a spherical semiovariogram model. The interpolated surfaces were used to characterize the differences in dominant arborescent community types, which we classified following Anderson and Anderson 1975 and Nelson et al. 1998: savanna/woodland (0.5-47 trees/ha); open forest (47-96 tree/ha); and closed forest (>96 trees/ha). Areas in which no trees were recorded were considered open grassland.

Results

Landscape Change and Fragmentation

During the period comprising the 1870s PLS, surveyors depicted the landscape of the Arbuckle Mountains as primarily a mosaic of forest/woodland and grassland vegetation with little evidence of human modifications in the form of agriculture or other land use practices (Figure 3.4). Grasslands were the dominant land cover type, covering approximately 113,114 ha of the study area (54%), while the forest/woodland cover type covered approximately 96,271 ha (46%). Cultivated lands, consisting of gardens, orchards, and farmed lands, covered only a fraction of total land area (approximately 178 ha), of which 160 ha occurred in the Arbuckle Plains (Figure 3.5).

Based on survey records, the study area was sparsely populated in the 1870s as reflected by the low number of man-made structures in the area. Surveyors noted a total of 30 different man-made structures, consisting primarily of residences (Table 3.2). This is further reflected in the transportation networks the surveyors recorded (Table 3.3; Figure 3.6). There were a total of 263 km of road and trail networks documented throughout the study area.

Patch analysis results of the 1870s data showed a relatively patchy landscape compromised of 219 grassland patches, 126 woodland patches, 44 agriculture plots, and 3 small areas delineated as wetlands (Figure 3.7). The average grassland patch size was 517 ha, while the average forest/woodland patch was approximately 764 ha. Median patch size of grasslands was 11.03 ha, with patches ranging in size from 0.005 ha to 47,465.6 ha. Median patch size of forest/woodlands was 10.32 ha, with patches ranging in size from < 0.001 ha to 50,839.9 ha in size. Overall, cultivated areas were rather small, averaging 4 ha, with the largest agriculture plot at approximately 23 ha (Figure 3.8).

By the 1890s, the landscape had undergone rapid change, characterized by an increase in habitat fragmentation as a result of forest/woodland clearance, a dramatic increase in cultivated areas (Figure 3.9) and the built environment. Specifically, the forest/woodland cover class decreased in total area to approximately 74,323 ha (35% of the total landscape), while areas mapped as grasslands slightly increased to 119,034 ha (57% of the landscape; see Figure 3.5). However, these figures may be misleading because a portion of these so-called grasslands were grazed by livestock (Doran 1976; Gibson 1981). Cultivated areas showed the greatest change between the two survey years, increasing to approximately 16,214 ha (8% of the total landscape) in 537 agriculture plots, thereby averaging approximately 30 ha per agriculture field. Additionally, there were 821 man-made structures in the area and the total linear distance of transportation networks increased to 1,703 km (Table 3.3; Figure 3.6).

These changes in the landscape structure are further reflected in the overall patchiness of the landscape (Figure 3.7). Both forest/woodland and grassland patches increased in number (to 213 and 271, respectively), while the mean patch size of each (349 ha and 439 ha, respectively) decreased. Grassland patch sizes ranged from < 0.001 ha to 62,009.6 ha with a median patch size of 2.35 ha. Forest/woodland patches ranged in size from 0.00018 ha to 32,763.3 ha with a median patch size of 10.32 ha. Overall, the increase in the number of patches of each cover type and the corresponding decrease in patch size is indicative of a trend towards greater fragmentation of the landscape (Figure 3.8).

As Figure 3.10 illustrates, the greatest landscape change occurred in the form of forest/woodland conversion to grasslands (25,159 ha). However, there were also 11,017 ha of grasslands that changed to forest/woodland between the two survey periods. Moreover, both forest/woodland and grasslands areas (7,900 and 8,248 ha, respectively) were cleared for cultivation, while a 116 ha of cultivated lands in the 1870s was mapped as either forest/woodland or grasslands in the 1890s.

Land cover conversion between the two surveys occurred throughout the Arbuckle Mountains, not any one subregion. During the 1870s, evidence of land conversion in the form of agriculture was limited primarily to the Blue River and its tributaries in the Arbuckle Plains physiographic region, mostly on soils of limestone or shale origin. Agriculture in the Timbered Hills physiographic province was limited to the Washita River basin (Figure 3.2). By the 1890s, agriculture had spread to most bottomlands in the Arbuckle Mountains, including areas of granitic parent material. Prominent areas that underwent relatively little land conversion between the two surveys, though, include several large prairie patches on Ordovician-aged limestones in the Timbered Hills and on Precambrian-aged granites Arbuckle Plains. Additionally, upland forested areas on soils from a variety of parent materials and lower elevation forested areas on rocky soils of granitic, rhyolitic, and limestone origin remained fairly consistent between the two surveys.

Species Composition and Vegetation Structure

Surveyors recorded a total of 2,578 individual trees representing 28 different taxa in the 1870s (Figure 3.11; Table 3.4). *Quercus stellata* had the highest frequency with 1,234 individuals. Other commonly reported taxa included *Q. velutina* with 529 reported individuals; *Ulmus* spp. with 328 reported individuals; and *Carya texana* with 118 recorded individuals.

In the 1890s, a total of 2,980 individual trees representing 25 different taxa were recorded (Figure 3.12; Table 3.4). *Quercus stellata* was once again the most abundant species with 1,242 recorded individuals. *Ulmus* spp, *Q. marlandica*, *Q. falcata*, and *Carya illinoinensis* were also commonly reported, with 502, 346, 200, and 132 individuals, respectively.

Overall, there was a total of 30 different species recorded during the two surveys (Table 3.4). Surveyors documented five species in the 1870s that were not recorded in the 1890s: *Malus ioensis*, *Cercis canadensis*, *Prunus* spp., *Crataegus* spp., and *Morus rubra*. In addition to the aforementioned species, four species had a higher frequency in the 1870s than the 1890s: *Q. velutina*; *Populus deltoides*; *C. texana*; and *Q. alba*.

Surveyors recorded two species, *Q. nigra* and *Sapindus saponaria* var. *drummondii* in the 1890s that were not reported in the 1870s, while 13 additional species had a higher frequency in the 1890s than the 1870s: *Fraxinus* spp.; *Juglans nigra*; *Q. marilandica*; *Maclura pomifera*; *Q. macrocarpa*; *Sideroxylon lanuginosum*;

Ulmus spp.; *Celtis laevigata*; *Juniperus* spp.; *Carya illinoinensis*; *Diospyros virginiana*; *Q. palustris*; *Q. falcata*; *Q. stellata*; and *Quercus* spp. (identified only as "oak" in the survey notes).

The dominant species (see Table 3.4) were distributed throughout the study area and on a variety of parent materials and moisture index classes. Ordovician limestone and Precambrian granite are the predominate geological units in the study area and, as a result, most important taxa were found in relatively high numbers on either or both of these units. However, based on weights (Table 3.5), the spatial associations between each taxon and geological units varied. Results of the MRPP, though, did not indicate any distributional shifts of the most important taxa between the two surveys related either to parent material (T = 1.266, P = 0.92) or moisture classes (T = 1.102, P = 0.869).

In the 1870s, surveyors recorded trees from a total of 1,088 corner or quarter section points. Trees averaged a DBH of 27.91 cm (10.99 in) and a distance of 16.07 m from the survey points. The average density in areas in which trees were recorded was 148.55 stems/ha. By contrast, in the 1890s, surveyors recorded trees from a total of 1,261 points. Trees averaged a DBH of 27.48 cm and an average distance of 21.161 m from each point. Average density in areas in which trees were recorded was 78.99 stems/ha. Based on the results of the Mann-Whitney U test, we rejected the null hypotheses that there was no change between the two survey periods in bearing tree distances (P < 0.001; Figure 3.12) and stem densities (P < 0.001). However, we were unable to reject the null hypothesis that the average diameter between the two survey periods varied significantly (P = 0.365).

Interpolated density values resulted in approximately 42,500 ha of the 96,271 ha mapped as forest/woodland in the 1870s being classified as closed forest (Figure 3.13). Additionally, approximately 25,980 ha were classified as open forest and 27,300 as savanna/woodlands. The remainder was classified as non-forested. By the 1890s, only approximately 8,723 ha of the 73,314 ha mapped as forest/woodland was classified as closed forest. Area calculated to be open forest was approximately 27,122 ha, while savanna/woodland covered an area of approximately 38,919 ha.

Discussion

Land Use Change and Fragmentation

In the late 1830s, the U.S. federal government began the process of removing the Chickasaw tribe from Mississippi and Alabama to a portion of southeastern Oklahoma (see Figure 3.1). Prior to removal, Chickasaw rolls showed a population of approximately 5,000 to 6,000 individuals, of which federal officials enrolled approximately 4,000 for emigration to Indian Territory. The vast majority of Chickasaw arrived in present-day Oklahoma by 1839, though small trickles continued to emigrate to the area through 1850 (Gibson 1981).

At the time of their arrival in present-day Oklahoma, bands of Kickapoo and Shawnee Indians had established villages in the Washita Valley, located slightly north of the Arbuckle Mountains, while Kiowa and Comanche roamed unimpeded on the western margins of the Chickasaw's new lands (see Figure 3.1). As a result of the dangers poised by these hostile tribes, the Chickasaw remained on the eastern fringes of their territory, settling in five camps located in the Choctaw District and, therefore, outside of the Arbuckle Mountains. Settlement within their own district didn't occur until the early 1850s with the establishment of Fort Arbuckle, in current-day Murray County (Gibson 1981).

This piecemeal movement into the Arbuckle Mountains is reflected in the 1870s survey. Few man-made structures existed throughout the 215,000 ha area and agriculture was limited primarily along rivers and streams in small plots likely used for subsistence purposes (Gibson 1981). Nonetheless, the Chickasaw maintained large herds of domesticated animals prior to removal (Morris 1947; Doran 1976). Upon arrival to their new lands, the Chickasaw continued ranching and even expanded this enterprise due to opportunities presented by the extensive prairies in their new home (Gibson 1981). Indeed, an enumeration in the Chickasaw Nation in the 1850s counted 14,788 domestic animals (Doran 1976).

Other anthropogenic modifications to the environment, such as intentionally set fires in prairies, have been documented in the area (Stewart 2002). Early traveler accounts of the area (see Dyksterhuis 1948 for a review) reference frequent fires throughout the cross timbers. As Irving (1983) wrote of the cross timbers, "[t]he fires made on the prairies by the Indian hunters, had frequently penetrated these forests, sweeping in light transient flames along the dry grass, scorching and calcining the lower twigs and branches of the trees, and leaving them black and hard…."

PLS data have been used to document land use patterns (e.g. DeWeese et al. 2007), natural disturbances (e.g. Schulte et al. 2005), and fire frequency (e.g. Lorimer 1977; Zhang et al. 2000). The 1870s surveyor notes, though, are limited in their description of specific land use practices, such as ranching, within the Arbuckle Mountains (though surveyors did map approximately 32 km of cattle trails in the area during the 1870s survey). Additionally, unlike PLS data for other states (Lorimer 1977; Zhang et al. 2000), the notes for the Arbuckle Mountains do not contain any mention of recent fire. Nonetheless, the ecological implications of increased ranching and/or fire abatement are many. Both ranching and fire suppression have been shown to be a critical factor in the increase of some woody species (Briggs et al. 2002) and fire suppression is believed to be a driving factor in the increased densification of wooded and forested areas (Dyksterhuis 1948; Dyksterhuis 1957; Rice and Penfound 1959; Engle et al. 2006; Nowacki and Abrams 2008).

In the period following the U.S. Civil War, the Chickasaw Nation saw rapid growth as rail lines bisecting the Chickasaw Nation were built. By the 1890s, eight new towns, each with populations in excess of 1,000, sprouted up along the railroad lines in the Chickasaw Nation. By 1900, an estimated 150,000 whites, some legally, others illegally, were living in the Chickasaw Nation (Gibson 1981).

Accompanying this rapid demographic shift was an intensification of land use practices, primarily in the expansion of large scale agriculture. In 1886, the superintendent of the Five Civilized Tribes reported that agriculture in the Chickasaw Nation was increasing geometrically, having already doubled in the last five years (Owen 1886). Additionally, ranching intensity continued to increase and new pressures on the land, primarily in the realm of natural resource extraction (oil and coal) were introduced (Gibson 1981).

The intensified land use practices between the two surveys are reflected in overall changes in the landscape structure (see Figures 3.6 and 3.7). Increases in the number of patches of both the grassland and forest/woodland categories, coupled with decreases in the average size of said patches, is indicative a trend towards greater habitat fragmentation. Additionally, the construction of transportation networks (e.g. railroads and cattle trails) and various structures represent further fragmentation of landscape. However, these changes are not reflected in the land cover maps because surveyors represented such features as lines and points, respectively, and the survey notes for the Arbuckle Mountains do not contain any areal measurements for these features.

The structure of a landscape, i.e. the size, shape, numbers, kinds, and configurations, of landscape elements (habitat patches) influences species richness within the landscape (Forman 1998; Heegaard et al. 2007). By extension, changes to landscape structure through fragmentation effects species assemblages within remnant and disturbance patches (Forman 1998; Hill and Curran 2003). The size, shape, and degree of isolation of these patches, in particular, influence the species composition of the patches (Hill and Curran 2003). Additionally, these patches are often further influenced by alterations in the physical environment, such as changes in hydrological regimes and/or radiation fluxes (Saunders et al. 1991), which are themselves a product of fragmentation. The result is often markedly different species composition within these patches than that of the pre-fragmented ecosystem.

Species Composition and Structure

Contemporary vegetation studies of the Arbuckle mountains (e.g. Hopkins 1941; Dale 1956; Rice and Penfound 1959; Hutcheson 1965; Johnson and Risser 1975) have shown that woodland communities vary considerably with soil type and moisture availability, with *Q. stellata* and *Q. marilandica* as co-dominants in dry upland areas of granitic parent material. *Carya texana* is another important upland woodland species in the cross timbers, typically found in drier potions of the *Quercus*-*Carya* forest types. Important bottomland species include *Q. muhlenbergii, Celtis laevigata, C. laevigata* var. *reticulate, Platanus occidentalis, Ulmus americana, U. rubra, Carya illinoensi, Juglans nigra, Salix nigra,* and *Populus deltoides* (Dale 1956; Rice and Penfound 1959; Kennedy 1973). Moreover, the suppression of fire since European settlement has resulted in a dramatic increase of *Juniperus virginiana* and *J. asheii* in the Arbuckles region (Hoagland et al. 1999).

By and large, the woody species assemblages from the two survey periods tend to correspond to 20th century vegetation studies in the region (e.g. Dale 1956; Rice and Pendfound 1959). However, some peculiarities exist. For instance, studies have determined that *Q. stellata,* and *Q. marilandica* are the most important woody species in the region, accounting for 90% of the canopy cover and 50% of basal area of the cross timbers (e.g. Rice and Penfound 1959; Johnson and Risser 1975; Hoagland and Johnson 2001). During the 1870s' survey, though, the second most commonly reported *Quercus* species (behind *Q. stellata*) was *Q. velutina* (529 occurrences), which the surveyors identified as "black oak". *Quercus marilandica*, identified as "blackjack" by the surveyors, was only recorded six times (compared to 315 in the 1890s; see table 3.4 for a comparison of values between the 1870, 1890s, and Rice and Penfound (1959) surveys).

Though *Q. velutina* has been documented in the region (Dale 1956; Rice and Penfound 1959: Hutcheson 1965), it reaches its western extent in central Oklahoma (Little 2000) and, with the exceptions of Shutler and Hoagland (2004) and Hutcheson

(1965), has not been frequently reported in the Arbuckle Mountains. Hoagland and Johnson (2001) didn't record any instances of *Q. velutina* within the Chickasaw National Recreation Area (located in the Arbuckle Plains physiographic province) and the Oklahoma Vascular Plants Database (Hoagland et al. 2008) only contains 21 records for *Q. velutina* within the six counties in which the Arbuckle Mountains occur. Additionally, Rice and Penfound's summary data (Hoagland and Hough 2008) only list 33 instance of *Q. velutina* occurring with the six counties in which the Arbuckle Mountains occur.

There are several possibilities for the seemingly anomalous *Q. velutina* records in the 1870s survey. In the field notes, surveyors recorded trees by common name (Fagin and Hoagland 2002) and surveyors rarely had formal botanical training (Delcourt and Delcourt 1996). Misidentification and use of regional and/or out-dated common names presents a unique challenge in attributing the correct Latin nomenclature in vegetation reconstructions from PLS data. Surveyors, for instance, may have used the term "black oak" as a common name for *Q. marilandica* rather than *Q. velutina*. This is unlikely, though. Surveyors reported the six *Q. marilandica* individuals from four different townships. In all instances, the surveyors also reported *Q. velutina* from these townships and, in one instance, three of the six reported *Q. marilandica* occurred from a section corner from which *Q.velutina* was also reported.

Several *Quercus* species with which surveyors may have confounded *Q. velutina* are conspicuously absent from the field notes. For example, *Q. buckleyi* is common in uplands of the Arbuckle Mountains, while *Q. shumardii* is found in both bottomlands and mesic uplands (Little 1996). Both of these species, as well as *Q.*

velutina, are members of the subgenus *Erythrobalanus*, an economically important group that includes several other of species that occur in the Arbuckles, as well, including *Q. marilandica*. It is possible that surveyors lumped members of *Erythrobalanus* into a single group, intentionally or due to lack of training.

A third possibility is that the *Q. velutina* identification is correct. Hutcheson's (1965) study of the vegetation of the Timbered Hills found that *Q. velutina* was the most abundant woody species on north-facing slopes of limestone origin and of secondary importance on south-facing slopes. Similarly, Shutler and Hoagland's (2004) study of the historic vegetation of Carter County, found that *Q. velutina* was historically the second most important woody species (behind *Q. stellata*) in their study area. However, this study also used PLS data and is, therefore, subject to the same caveats vis-à-vis *Q. velutina*. The apparent variations in the abundance of *Q. velutina* in the Arbuckle Mountains may be on account of the species' commercial value (Burns and Honkala 1990)--the seemingly precipitous decline in abundance of the species in the region might be attributable to selective harvesting (see, for instance, Francaviglia 2000). Additionally, the habitat fragmentation that occurred during the period between the two survey periods may account for the reduced abundance of this species.

The values from the 1890s survey for *Q. stellata*, *Q. marilandica*, and *Q. velutina*, are more inline with several previous studies (see tables 3.1 and 3.4). Nonetheless, in the 1890s, surveyors recorded three *Quercus* spp. in addition to *Q. marilandica* and *Q. velutina* that are members of the *Erythrobalanus* subgenus, *Q. falcata* (184), *Q. palustis* (27), and *Q. nigra* (5), none of which have been subsequently documented in the Arbuckle Mountains. Surveyors also recorded 164 instances of

Quercus only to the genus level. There are several *Quercus* spp. that occur in the Arbuckle Mountains, though in addition to the aforementioned species (Dale 1956), including *Q. macrocarpa*. *Q, muhlenbergii*, and *Q. sinuata* var. *breviloba*. When these various *Quercus* spp. recorded by surveyors are taken in sum, the total (510) is comparable to the number of occurrences of "black oak" from the 1870s (529).

One conspicuous difference between the historical and contemporary composition of the arborescent communities of the Arbuckle Mountains pertains to *Juniperus* spp. During the past fifty years, *Juniperus* spp. have increased in abundance throughout Oklahoma, primarily due to fire suppression and other land use practices (Rice and Penfound 1959; Johnson and Risser 1975; Snook 1985; Engle et al. 1997). Two species of *Juniperus*, *J. virginiana* and *J. ashei*, occur within the Arbuckle Mountains. Historically, *J. ashei* was restricted to rocky outcrops and dissected upland soils of limestone origin (Hart and Price 1990). *Juniperus virginiana*, though, is found in numerous habitats throughout the region (Lawson 1985). However, young *J. virginiana* are intolerant to fire and it was less abundant in Oklahoma prior to widespread fire suppression (Snook 1985).

Witness tree records from both the 1870s and 1890s seem to confirm a limited distribution of *Juniperus* spp. in the area prior to and immediately following European settlement, with only 11 individuals total recorded during the two surveys. Bias in witness tree selection (see below) may account for surveyors overlooking *Juniperus* spp. in some instances. However, this alone cannot account for the relatively low frequency of *Juniperus* spp during both surveyors. The *Juniperus virginiana-Schizachyrium scoparium* woodland association (Hoagland and Johnson 2001), for instance, is now a major vegetation type in parts of the Arbuckle Mountains. Additionally, many former grasslands in the Arbuckle Mountains are today dominated by a single woody species, either *J. viriginiana* or *J. ashei.*

Aside from the above differences, the composition of the woodland and forests of the Arbuckle Mountains in the 1870s and 1890s, respectively, are roughly analogous to more contemporary studies of the region. Due to taxonomic uncertainties, we are unable to definitively ascertain whether rapid land conversion in the area between the two survey periods resulted in compositional differences in the arborescent communities of the Arbuckle Mountains. The differences in reported *Q. velutina* and *Q. marilandica* from the two surveys is the most striking difference between the two surveys, especially when compared to the contemporary composition of the upland forests of the Arbuckle Mountains. Additionally, the infrequency of *Juniperus* spp. records seem to confirm prior assessments (e.g. Rice and Penfound 1959; Johnson and Risser 1975; Snook 1985; Engle et al. 1997; Hoagland and Johnson 2001) of limited distribution prior to widespread fire suppression and other land use practices.

While there are limited compositional differences between the two survey periods, the historical structure of these forests is of particular note. It has long been posited that the arborescent communities of the cross timbers, in general, were less dense in historical times (e.g. Dyksterhuis 1957; Rice and Penfound 1959; Engle et al. 2006). According to this hypothesis, prior to widespread European settlement, much of the contemporary forests of the cross timbers was woodland and savanna. Fire suppression and other land use practices, such as grazing, have contributed to an increase in density of dominant overstory *Quercus* species (Engle et al. 2006).

Rice and Penfound's (1959) study of the upland forests of Oklahoma represents one of the few quantitative studies of the post-settlement structure of the forests in the Arbuckle Mountains region. Their summary data (Hoagland and Hough 2008) indicate that, at the time of their analyses, the average density of the upland forests in the counties encompassing the Arbuckle Mountains was 216.68 trees/ha. We found that historically density values varied throughout the arborescent communities in the Arbuckle Mountains. During the 1870s, the average density of all points from which trees were recorded was 148.55 trees/ha. By the 1890s, the average density had decreased to 78.99 trees/ha, which likely corresponds to the decrease in forest/woodland cover during the period between the two surveys.

While it appears that PLS data confirm the hypothesis of historically less dense cross timbers within the Arbuckle Mountains, surveyor bias in witness tree selection can affect these estimates. Though surveyors were instructed to record the bearing, distance, and diameter to the nearest tree in each adjacent section, witness tree selected was often influenced by tree size, conspicuousness in a stand, longevity, or economic value (Lutz 1930; Bourdo 1956; Grimm 1984; Nelson 1997). The point-centered quarter method to determine tree density assumes unbiased tree selection (Cottam and Curtis 1956). As a result, PLS data may actually underestimate historical tree densities because selected witness trees were not necessarily the closest individual to each survey point.

Assuming similar biases from each survey period, the data provide density indices useful for comparing the two surveys (Grimm 1984). The decrease in density between the 1870s and 1890s is not surprising given the documented land clearance that occurred during this period. This raises interesting questions about the basis of long-held assumptions of less-dense savannas and woodlands in the cross timbers prior to European settlement. While experiments (e.g. Johnson and Risser 1975; Engle et al 2006) indicate that fire is an important maintenance factor in cross timber savannas, most accounts of the savanna-like nature of the cross timbers in the region are based on early settler accounts (Dyksterhuis 1948; Rice and Penfond 1959). These claims, then, may be based on evidence after substantial change in the landscape occurred.

Earlier, qualitative accounts of the region present divergent views. Gregg (1975) wrote of a virtually impenetrable, thickly matted undergrowth in the cross timbers, while Irving (1983) characterized his journey through the cross timbers as a struggle "through forests of cast iron." Conversely, Marcy (1981) stated that the trees of the cross timbers stood at such intervals "that wagons can without difficulty pass between them in any direction." Based on our values from the 1870s survey, both the divergent accounts may be correct. While there certainly were large areas of savanna and open forest in the cross timbers of the Arbuckle Mountains, there also was significant areas of closed canopy forest.

Conclusion

The decades immediately following the Chickasaw's arrival in the Arbuckle Mountains region are characterized by a landscape in transition. Widespread habitat fragmentation for agriculture and other commercial enterprises (e.g. timber harvesting) resulted in the reduction of both the areal extent and overall density of forest and woodland vegetation. Despite lack of evidence that these changes had an immediate impact on the overall composition of the woody taxa in the region, they nonetheless provide important insights into the pre-European ecology of the cross timbers of the Arbuckle Mountains. The PLS data indicate a shift in importance of *Q. velutina* and *Q. marilandica* in the period proceeding European settlement in the Arbuckle Mountains; confirm less dense arborescent communities in historic times; and show an extremely low abundance of *Juniperus* spp. compared to the present. Despite several inherit limitations of PLS data, the repeat survey datasets proved to be a valuable tool to ascertain the biological implications of early habitat fragmentation and an effective means to evaluate long-held beliefs about the historical structure of these arborescent communities.

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Table 3.1. Month and year of the Public Land Surveys of the Arbuckle Mountains, 1870s and 1890s.

1870s				1890s			
MONTH	YEAR	DEPUTY SURVEYOR	TOWNSHIP	MONTH	YEAR	DEPUTY SURVEYOR	SPAN (YRS)
Sep.	1871	Ehud Noble Darling	1N4E	Nov.	1897	Frank E. Lewis	26.17
Aug.	1871	Ehud Noble Darling	1N5E	Feb.	1898	Fred Watts Jr	26.50
Oct.	1871	Ehud Noble Darling	1N6E	Feb.	1898	J. P. Thayer	26.33
Oct.	1871	Ehud Noble Darling	1N7E	Dec.	1898	Fred Watts Jr	27.17
Dec.	1870	Ehud Noble Darling	1S1E	Dec.	1897	J. C. Wilkinson	27.00
Dec.	1870	Theodore H. Barrett	1S1W	Jun.	1898	Wm O. Beall	27.50
Feb.	1871	Ehud Noble Darling	1S2E	Dec.	1897	Oscar Jones	26.83
Feb.	1872	Theodore H. Barrett	1S2W	May	1898	Frank F. Sweet	26.25
Sep.	1871	Ehud Noble Darling	1S3E	Feb.	1898	J. C. Wilkinson	26.42
Jun.	1871	Ehud Noble Darling	1S4E	Feb.	1898	Oscar Jones	26.67
Jun.	1871	Ehud Noble Darling	1S5E	Jan.	1898	Thr Johnson	26.58
Sep.	1871	Ehud Noble Darling	1S6E	Jan.	1898	J. W. Riley	26.33
Sep.	1871	Ehud Noble Darling	1S7E	Feb.	1898	J. W. Riley	26.42
Sep.	1871	Ehud Noble Darling	1S8E	Feb.	1898	J. W. Riley	26.42
Oct.	1871	Ehud Noble Darling	2N4E	Dec.	1897	Frank E. Lewis	26.17
Aug.	1871	Ehud Noble Darling	2N5E	Feb.	1898	Fred Watts Jr	26.50
Oct.	1871	Ehud Noble Darling	2N6E	Feb.	1898	J. P. Thayer	26.33
Oct.	1871	Ehud Noble Darling	2N7E	Dec.	1897	Fred Watts Jr	26.17
Nov.	1870	Ehud Noble Darling	2S1E	Dec.	1897	Frank E. Lewis	27.08
Nov.	1870	Theodore H. Barrett	2S1W	Jun.	1898	Geo W. Hooper	27.58
Jan.	1871	Ehud Noble Darling	2S2E	Dec.	1897	Frank E. Lewis	26.92
Jan.	1871	Theodore H. Barrett	2S2W	Jun.	1898	J. E. Beavers	27.42
Sep.	1871	Ehud Noble Darling	2S3E	Jan.	1898	George A. Purington	26.33
Jun.	1871	Ehud Noble Darling	2S4E	Jan.	1898	Frank E. Lewis	26.58
Jul.	1871	Ehud Noble Darling	2S5E	Jan.	1898	Fred Watts Jr	26.50
Sep.	1871	Ehud Noble Darling	2S6E	Jan.	1898	J. P. Thayer	26.33
Sep.	1871	Ehud Noble Darling	2S7E	Feb.	1898	Thr Johnson	26.42
Sep.	1871	Ehud Noble Darling	2S8E	Feb.	1898	J. W. Riley	26.42
Sep.	1871	Ehud Noble Darling	3N5E	Jan.	1898	Fred Watts Jr	26.33
Oct.	1871	Ehud Noble Darling	3N6E	Feb.	1898	J. P. Thayer	26.33
Jan.	1871	Ehud Noble Darling	3S2E	Dec.	1897	Oscar Jones	26.92
Jul.	1871	Ehud Noble Darling	3S3E	Jan.	1898	J. C. Wilkinson	26.50
May	1871	Ehud Noble Darling	3S4E	Jan.	1898	Oscar Jones	26.67
Jul.	1871	Ehud Noble Darling	3S5E	Jan.	1898	Thr Johnson	26.50
Aug.	1871	Ehud Noble Darling	3S6E	Jan.	1898	J. W. Riley	26.42
Aug.	1871	Ehud Noble Darling	3S7E	Feb.	1898	Thr Johnson	26.50
Aug.	1871	Ehud Noble Darling	3S8E	Feb.	1898	J. W. Riley	26.50
May	1871	Ehud Noble Darling	4S4E	Jan.	1898	Oscar Jones	26.67
Apr.	1871	Ehud Noble Darling	4S5E	Dec.	1897	Thr Johnson	26.67
Jun.	1871	Ehud Noble Darling	4S6E	Dec.	1897	J. W. Rile	26.50

Table 3.2. Comparison of 1870s and 1890s structures from PLS plats.

Structure Type	1870s	1890s
Residents	24	787
Store	2	2
Post Office	1	7
Mill	1	1
Capital	1	0
Blacksmith	1	1
School House	0	11
Church	0	2
Cemetery	0	2
Mine	0	1
Tank	0	2
Triangulation Signal	0	1
Gin	0	3
Sawmill	0	1
Total	30	821

Table 3.3. Comparison of 1870s and 1890s transportation networks from PLS plats.

Transportation	1871	1897
Wagon Road	202.64	1,703.23
Trail	28.55	0
Cattle Trail	31.80	0
Railroad	0	63.66
Total Length (KM)	**262.99**	**1,766.89**

Taxon	1870s # Trees	1870s Rel. Dom.	1870s Rel. Den.	1870s I.V.	1890s # Trees	1890s Rel. Dom.	1890s Rel. Den.	1890s I.V.
Quercus stellata	1234	46.368	47.867	47.117	1242	40.331	41.678	41.005
Quercus velutina	529	15.442	20.520	17.981	73	2.509	2.450	2.479
Ulmus spp.	328	29.296	12.723	21.009	474	21.174	15.906	18.540
Carya texana	118	0.982	4.577	2.779	69	0.568	2.315	1.441
Quercus alba	81	1.701	3.142	2.422	57	0.739	1.913	1.326
Carya illinoinensis	56	1.231	2.172	1.702	123	5.459	4.128	4.793
Fraxinus spp.	45	0.983	1.746	1.364	69	1.324	2.315	1.820
Quercus falcata	37	0.607	1.435	1.021	184	5.713	6.174	5.944
Celtis laevigata	24	0.416	0.931	0.673	58	1.261	1.946	1.603
Juglans nigra	23	0.493	0.892	0.693	42	2.236	1.409	1.822
Quercus palustris	22	0.209	0.853	0.531	27	0.448	0.906	0.677
Populus deltoides	19	0.744	0.737	0.740	6	0.200	0.201	0.201
Quercus macrocarpa	18	0.658	0.698	0.678	19	0.567	0.638	0.602
Quercus marilandica	6	0.386	0.233	0.309	315	12.541	10.570	11.556
Platanus occidentalis	6	0.042	0.233	0.138	6	0.287	0.201	0.244
Diospyros virginiana	5	0.262	0.194	0.228	17	0.388	0.570	0.479
Juniperus spp.	4	0.055	0.155	0.105	7	0.204	0.235	0.219
Cercis canadensis	4	0.003	0.155	0.079	-	-	-	-
Morus rubra	3	0.028	0.116	0.072	-	-	-	-
Quercus spp.	3	0.014	0.116	0.065	164	3.600	5.503	4.552
Maclura pomifera	3	0.018	0.116	0.067	11	0.351	0.369	0.360
Sideroxylon lanuginosum	2	0.022	0.078	0.050	7	0.024	0.235	0.129
Prunus spp.	2	0.004	0.078	0.041	-	-	-	-
Acer negundo	2	0.024	0.078	0.051	2	0.023	0.067	0.045
Malus ioensis	1	0.001	0.039	0.020	-	-	-	-
Gymnocladus dioicus	1	0.004	0.039	0.022	1	0.004	0.034	0.019
Salix spp.	1	0.001	0.039	0.020	1	0.001	0.034	0.017
Crataegus spp.	1	0.010	0.039	0.024	-	-	-	-
Quercus nigra	-	-	-	-	5	0.046	0.168	0.107
Sapindus saponaria	-	-	-	-	1	0.002	0.034	0.018

Table 3.4. Comparison of frequency (# trees), relative dominance (Rel. Dom.), relative density (Rel. Den.) and importance value (I.V.) for all recorded taxon, 1870s and 1890s.

	Quercus stellata		*Quercus marilandica*		*Quercus velutina*		*Carya texana*		*Carya illinoinensis*		*Juniperus* spp.	
Geology	**1870s**	**1890s**	**1870s**	**1890s**	**1870s**	**1890s**	**1870s**	**1890s**	**1870s**	**1890s**	**1870s**	**1890s**
PA	0.0397	-0.7548	-	-1.6003	-0.6882	1.1058	0.5663	-	-	0.8140	-	5.4879
MS	0.4186	0.0633	-	-0.2438	0.307	-0.2587	-0.0628	0.2199	0.7539	1.1175	-	1.5912
D	0.6293	0.5718	-	0.1494	0.8491	1.5099	0.2447	0.3589	-0.0544	0.5579	3.7769	-
O	-1.1604	-1.2023	-	-0.1996	-0.4715	-0.2357	-0.2285	-0.0586	1.0782	0.1345	-	-0.9147
CL	-0.2159	-0.4784	-0.6179	-1.1111	-1.8548	-1.2336	-	0.5209	-	-0.3658	-	-
CR	-0.5317	0.6068	-	-0.7854	0.3509	-	-	-	-	-	-	-
P	-	-	-	-	-	-	1.7326	-	-	-	-	-
PAS	0.3761	-	-	-	-	-	-	-	-	-	-	-
PG	1.1721	1.3198	-	0.642	0.4281	-1.8886	0.4307	-0.0795	-2.357	-1.5062	-	-
PS	0.5919	0.8921	1.7584	-0.7405	0.2921	1.2755	-0.4447	-	-	-	1.7584	-
Moisture Index												
-4 (Xeric)	0.2169	0.0248	-	-1.1798	-0.2776	0.3607	-0.8801	0.4071	0.6157	-	-	-
-3	-0.4484	-0.1503	-	-1.2739	0.1172	0.2758	0.0483	-0.8329	-0.6318	-	-	-
-2	0.1138	0.0455	-	-0.0509	0.1300	0.5185	-0.2675	0.3887	0.1705	-0.4956	0.7468	1.8959
-1	-0.1051	-0.0997	-0.6865	-0.0533	-0.1662	-0.6692	-0.1289	-0.0848	-0.4808	-0.2683	0.9707	-
0	-0.0059	-0.3210	0.0958	0.2024	-0.1149	-0.6954	0.9250	-0.4738	0.7206	0.3686	-	-
1	0.0094	0.1132	0.0789	0.3134	0.1370	0.6273	-0.1607	-0.0738	0.3986	0.6870	0.6081	-
2	0.1922	0.2204	1.2073	0.1429	0.0376	-0.2183	-0.6480	0.0959	-0.7287	0.1757	-	0.2481
3	-0.0276	0.2874	1.4563	-0.5471	-0.0436	-0.5652	0.2408	0.6784	-0.3150	-0.3972	-	-
4 (Mesophytic)	-0.3643	0.0785	-	-0.7441	0.2819	0.8496	-1.3800	-0.8260	-	-0.7057	-	2.9734

Table 3.5. Contrast values from calculated weights for surficial geology and the moisture availability index. (PA=Pennsylvania Shale/Limestone; MS=Mississippian Shale/Limestone; D=Devonian Shale/Limestone; O=Ordovician Limestone; CL=Cambrian Limestone; CR=Cambrian Rhyolite; P=Permian Sandstone; PAS=Pennsylvanian Sandstone; PG=Precambrian Granite; and CS=Cretaceous Sandstone.).

Figure 3.1. The Chickasaw Nation, 1855-present.

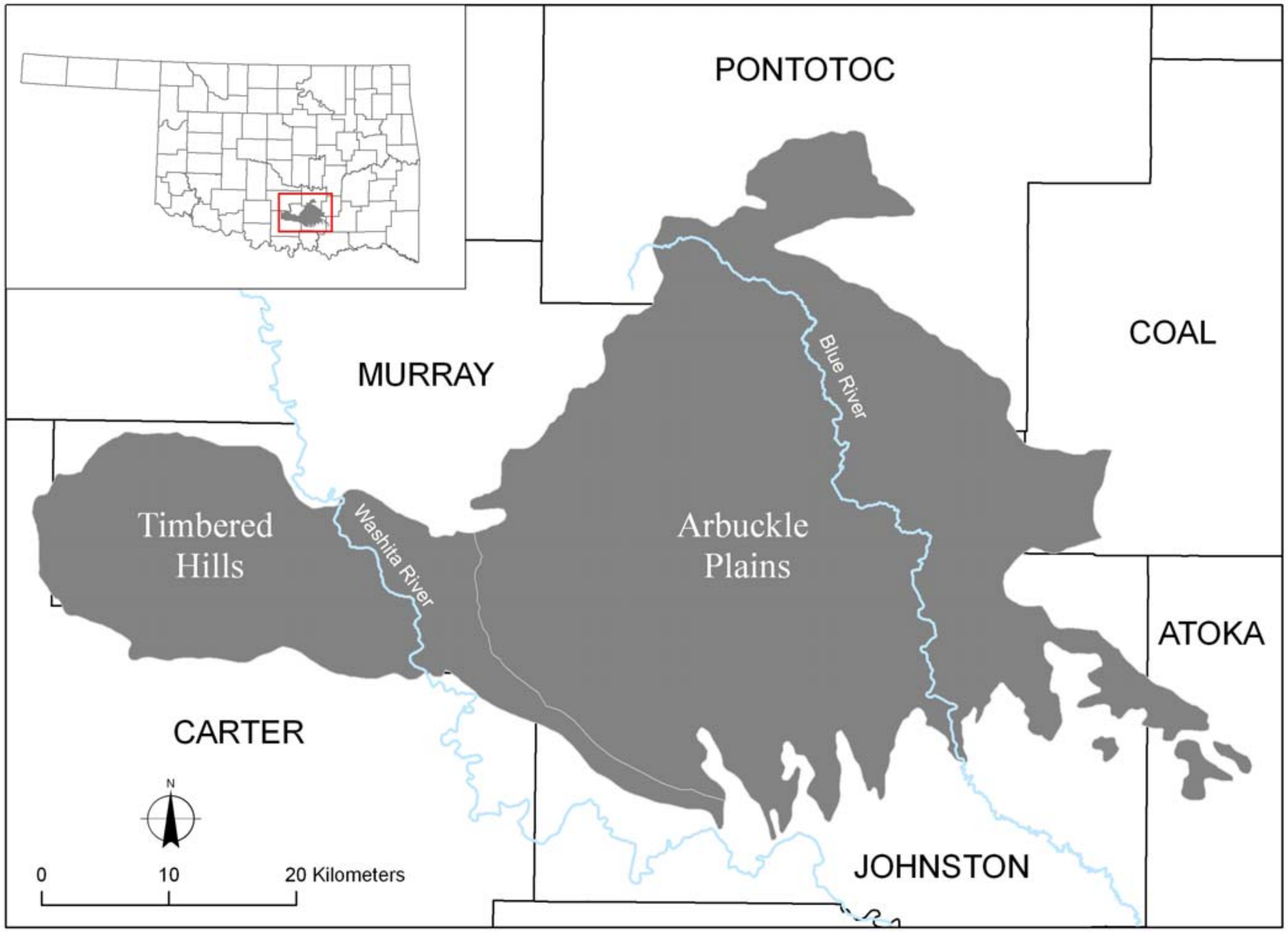


Figure 3.2. Study area location in south-central Oklahoma.

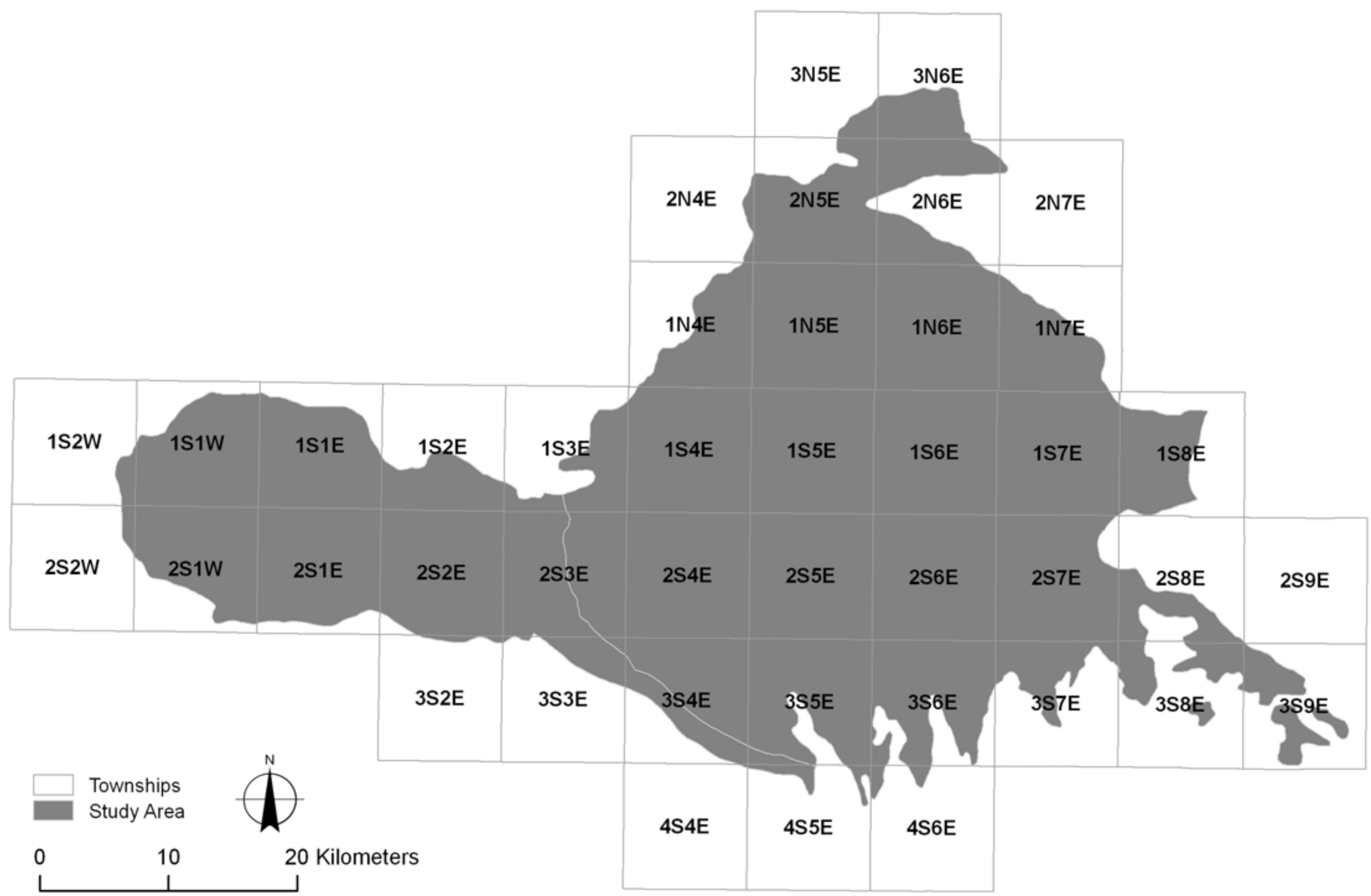


Figure 3.3. The forty-two townships encompassing the Arbuckle Mountains.

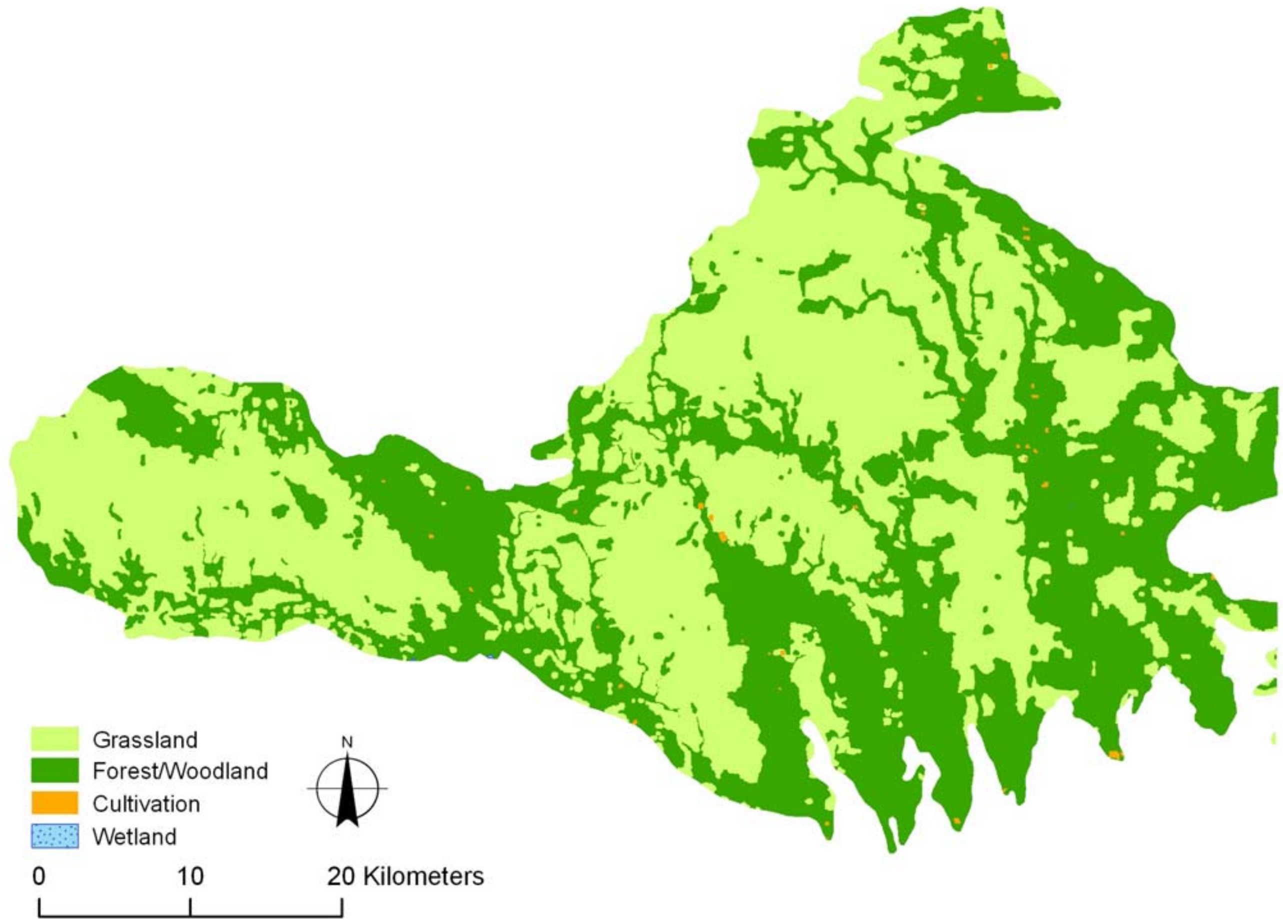


Figure 3.4. 1870s land cover as depicted on the PLS plats.

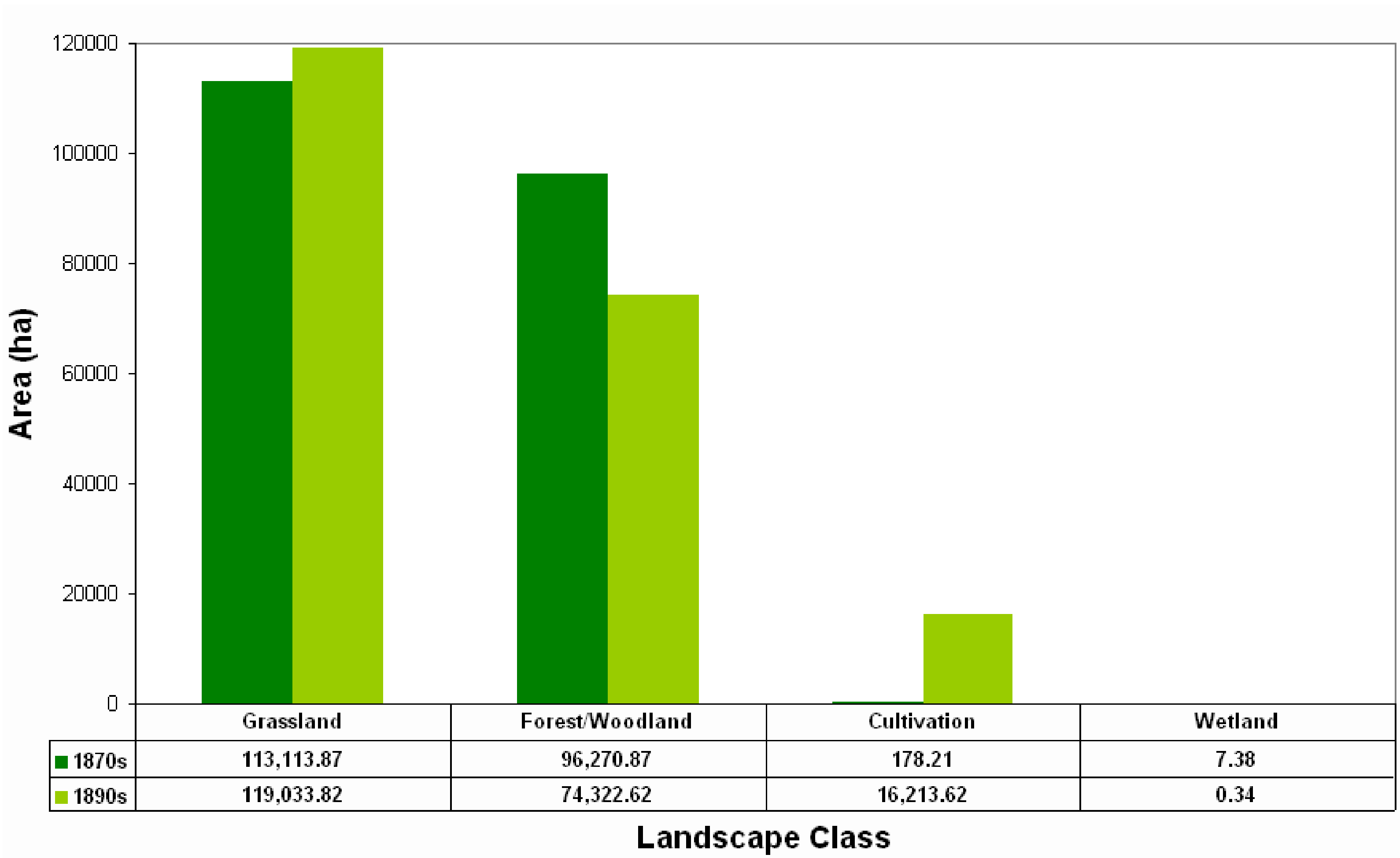


Figure 3.5. Comparison of calculated landscape area for each land cover class, 1870s and 1890s.

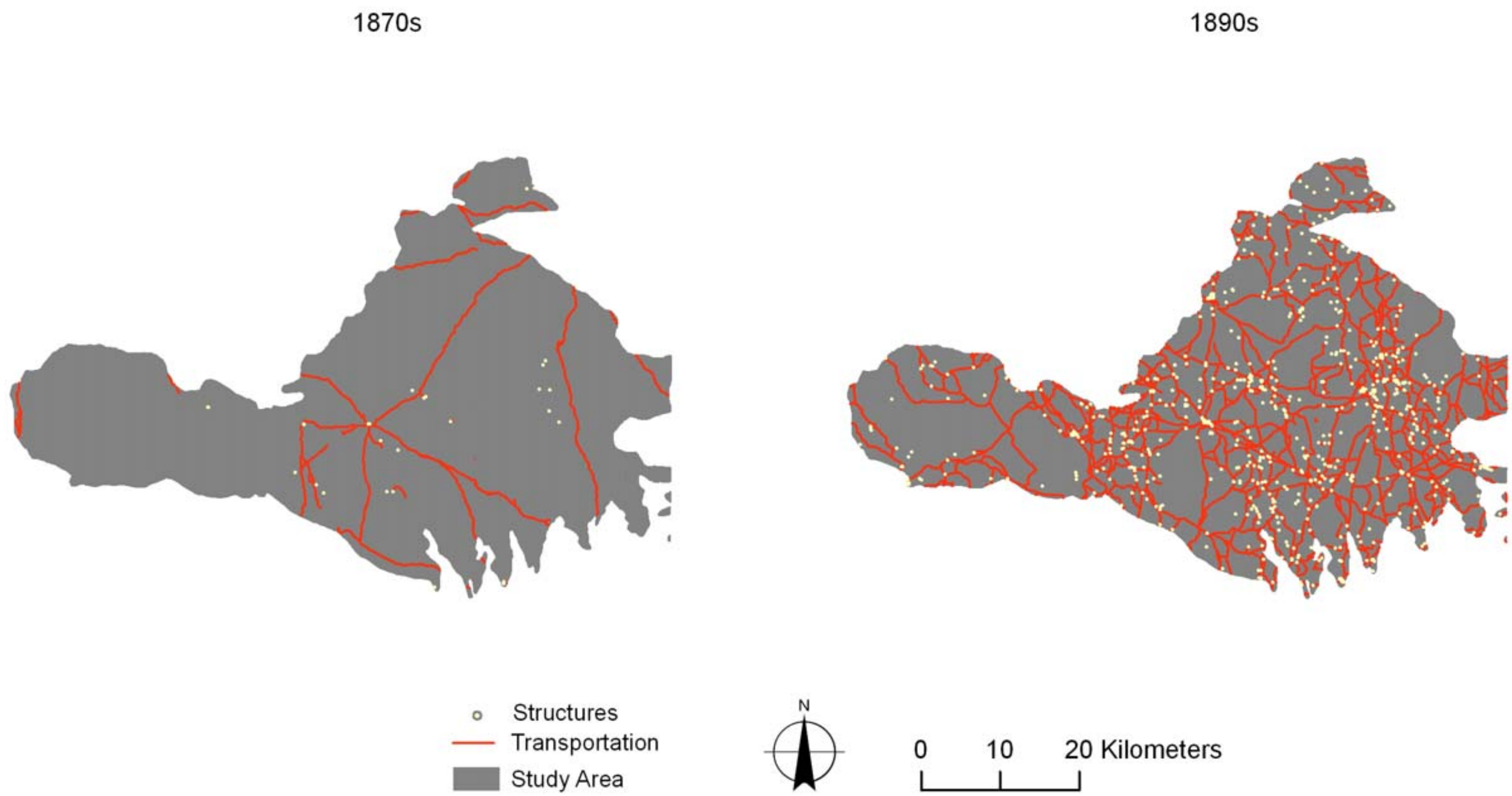


Figure 3.6. Structures and transportation networks in the Arbuckle Mountains, 1870s and 1890s

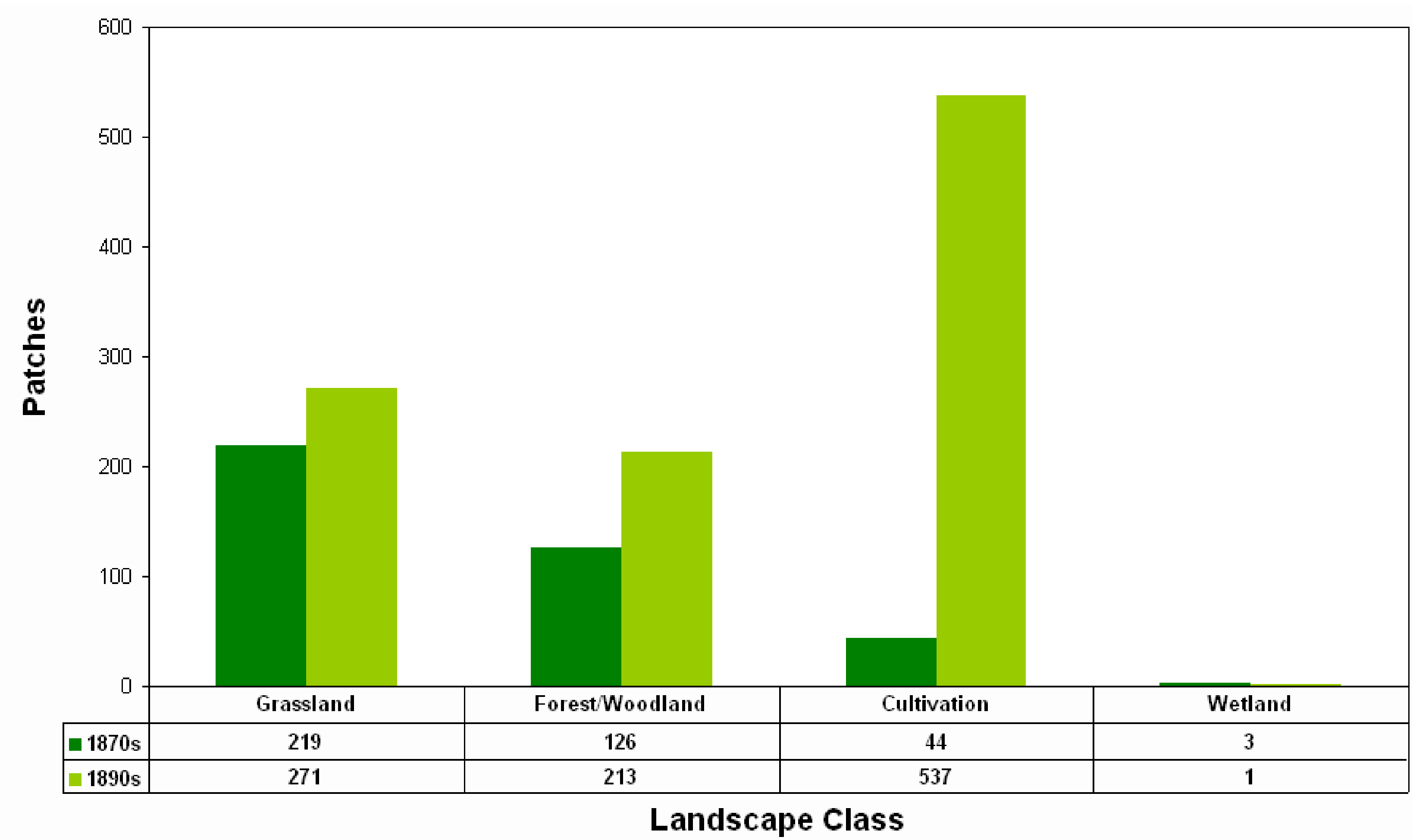


Figure 3.7. Comparison of calculated number of patches for each land cover class, 1870s and 1890s.

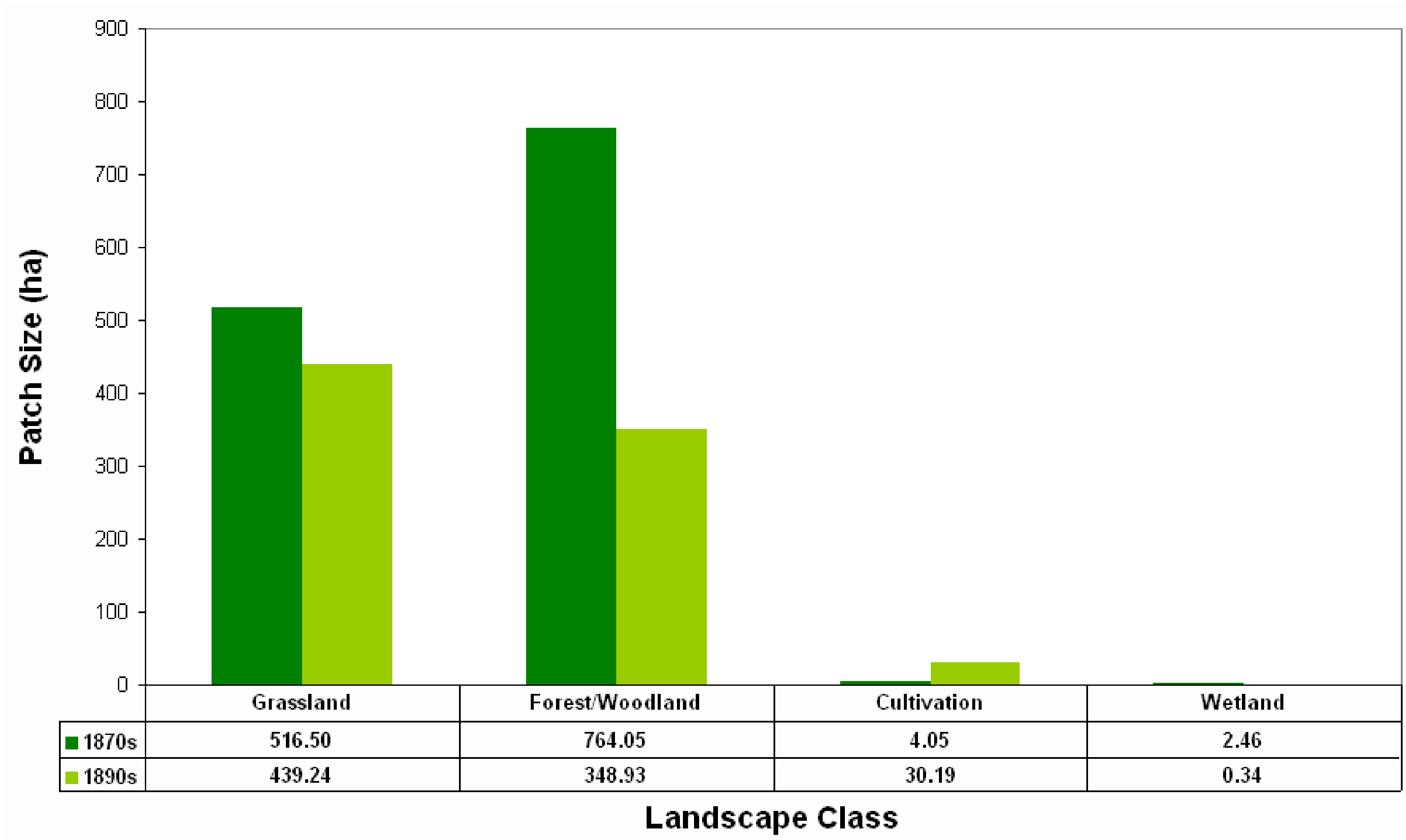


Figure 3.8. Comparison of mean patch size for each land cover class, 1870s and 1890s.

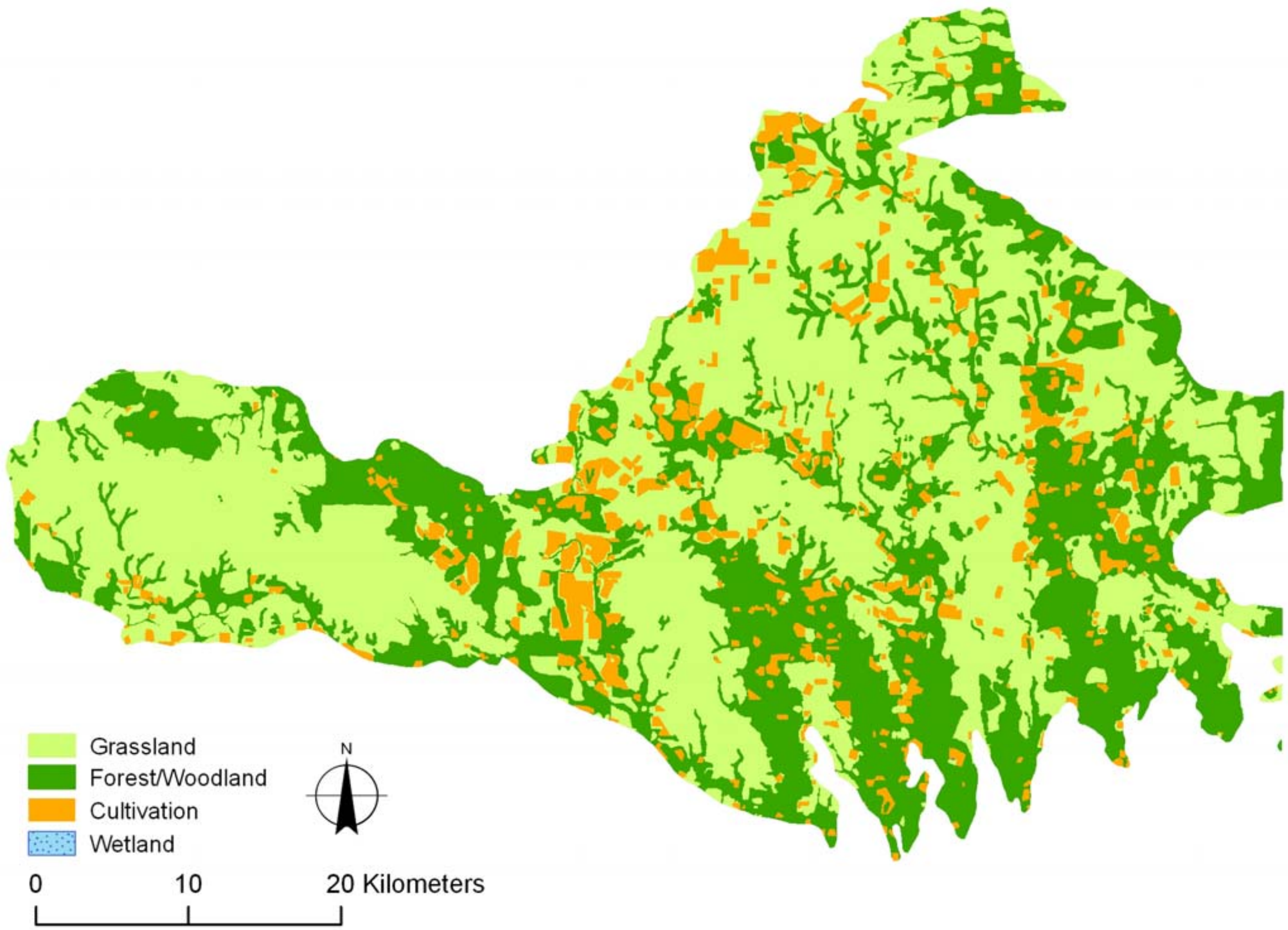
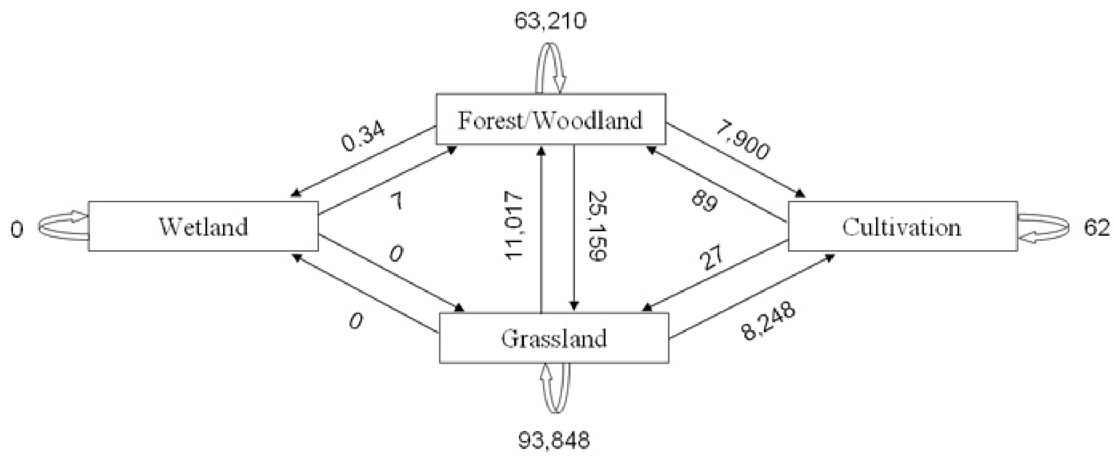


Figure 3.9. 1890s land cover as depicted on the PLS plats.

Figure 3.10. Trajectories of change: arrows indicate the direction of change from one land cover class to another between the two survey periods. All values listed are hectares. For instance, between the 1870s and 1890s surveys, 25,159 ha of forest/woodland was converted to grassland and 8,248 ha of grassland was converted to cultivation.



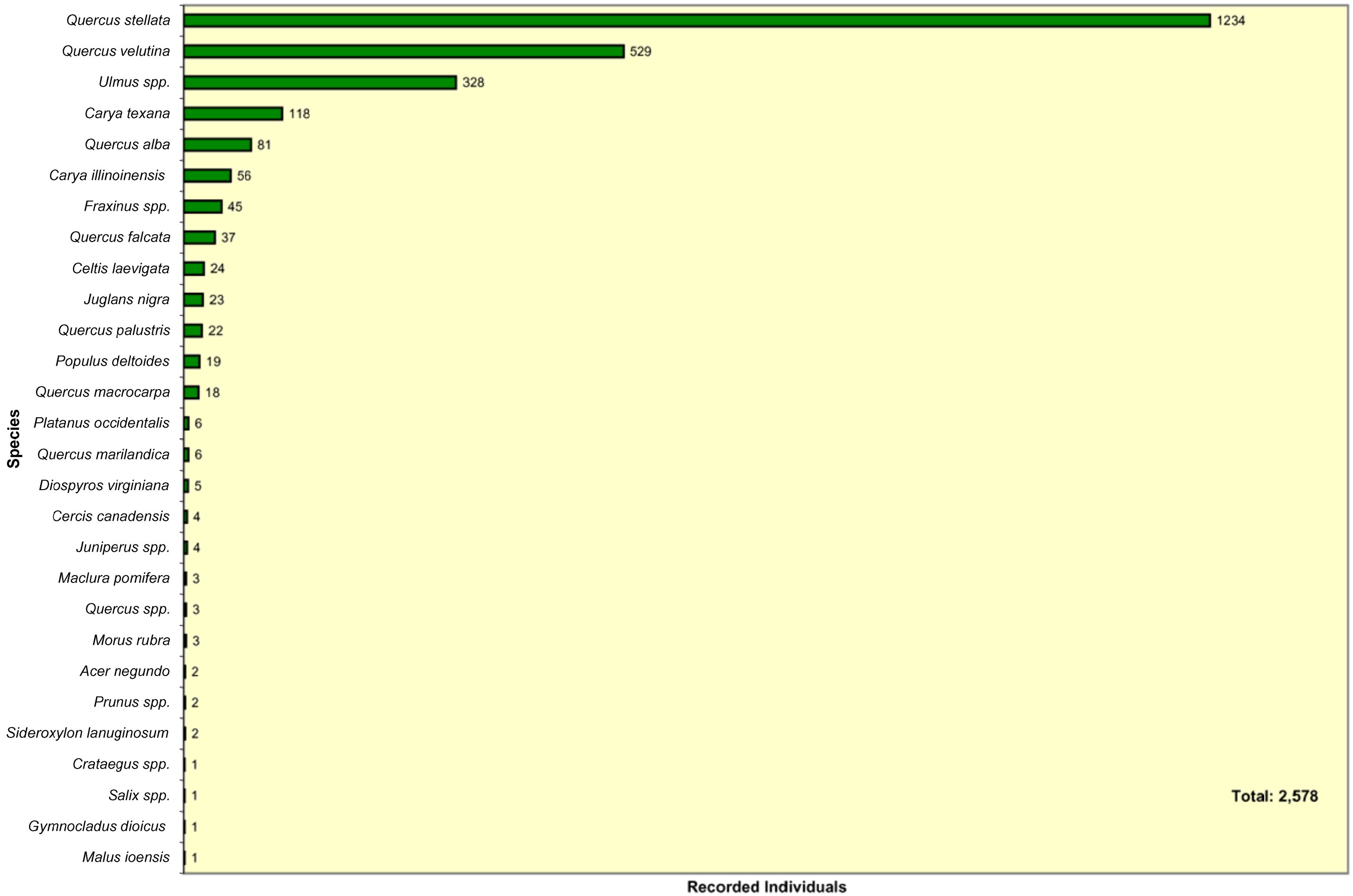


Figure 3.11. Frequency distribution of individual taxon, 1870s.

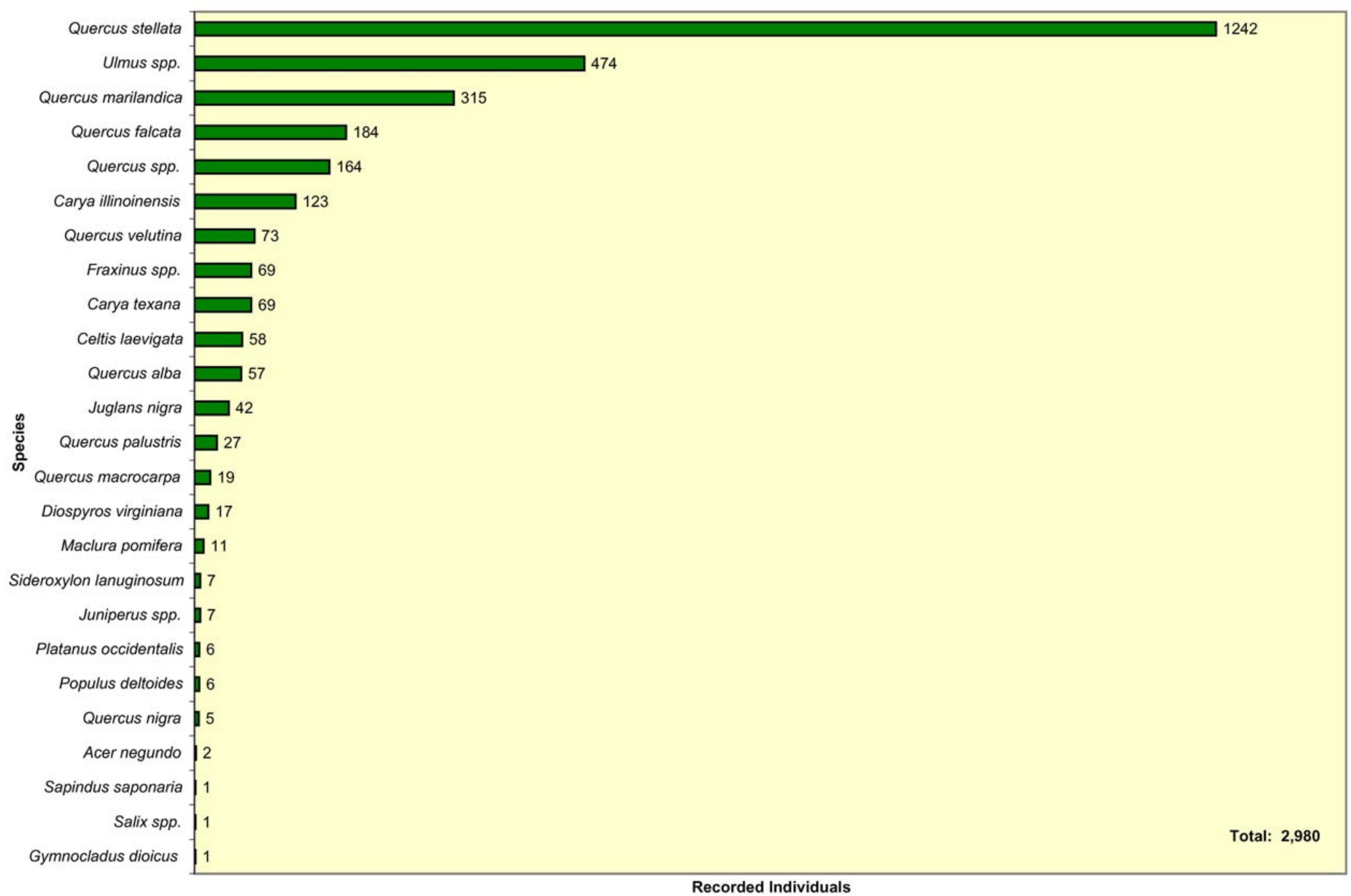


Figure 3.12. Frequency distribution of individual taxon, 1890s.

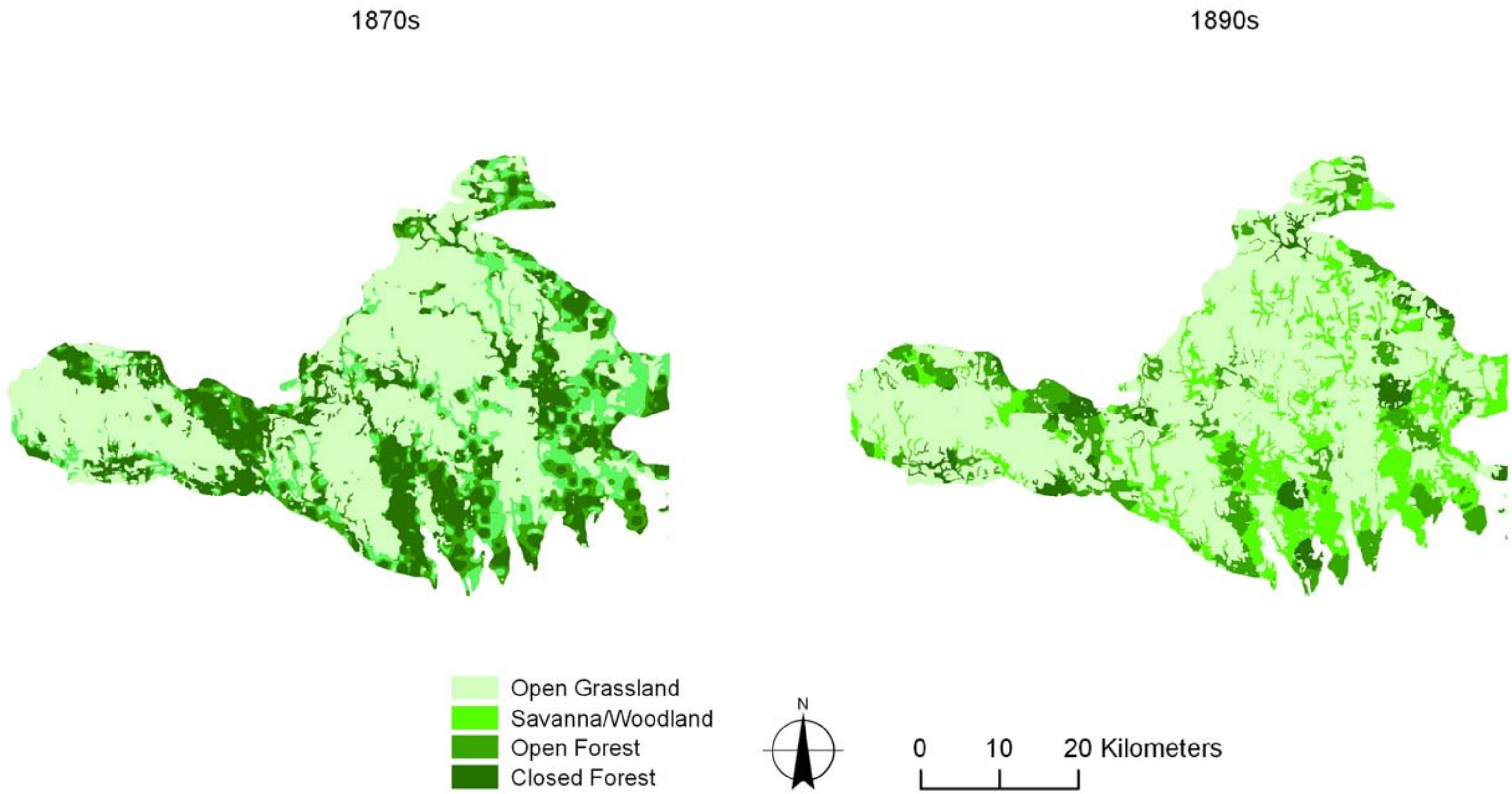


Figure 3.13. Comparison of interpolated density values, 1870s and 1890s.

CHAPTER 4:

PREDICTIVE PROBABILISTIC MAPPING OF PUBLIC LAND SURVEY SYSTEM WITNESS TREE DATA USING WEIGHTS-OF-EVIDENCE MODELING

Aim The purpose of this study was to test the efficacy of using weights-of-evidence (WofE) to estimate the probable historical distribution of select woody plant taxa based on discrete occurrence data and a series of environmental covariates.

Location The Arbuckle Mountains in south-central Oklahoma

Methods We utilize weights-of-evidence, a discrete multivariate method based on a log-linear form of Bayes' Rule, to estimate the probable historical distribution of six important woody plant taxa of the cross timbers of south-central Oklahoma. The models use known spatial associations between discrete witness tree data from the Public Land Survey System (PLS) and six environmental covariates to generate continuous posterior probability distribution maps.

Results We successfully created statistically-valid posterior probability distribution maps for *Quercus stellata, Q. marilandica*, *Q. velutina*, *Carya texana, C. illinoinensis*, and *Juniperus* spp. Each posterior probability map was classified into four predictive categories, high probability, moderate probability, low probability, and high uncertainity, thereby enabling better estimations of the historical distribution of individual taxon from coarse-resolution PLS data. Model validation indicated that the WofE method adequately estimated the posterior probabilities of *Q. stellata, Q. marilandica, C. texana,* and *Juniperus* spp., but underpredicted posterior probabilities for *C. illinoinensis* and *Q. velutina*.

Main conclusions Past attempts to convert discrete PLS witness tree data into continuous distributions have primarily utilized various interpolation techniques that fail to consider the numerous environmental covariates that can influence the distribution of individual tree species. The weights-of-evidence method belongs to a growing body of methods that has been used to successfully predict species distributions from point occurrence data based on known spatial associations with environmental variables. This research indicates that WofE can be used to produce statistically valid maps of the historic distribution of woody plant taxa from PLS data.

Keywords Public Land Survey System, witness trees, weights-of-evidence, Arbuckle Mountains, cross timbers, presettlement forest, historical vegetation reconstruction, Oklahoma

Introduction

The structure and composition of North American forests at the time of European settlement have received considerable attention in recent years (e.g. Manies *et al*. 2001; Wang 2005; DeWeese *et al.* 2007). Since past disturbance regimes have been shown to effect the current composition of an ecosystem (Dupouey 2002), these historical vegetation reconstructions typically serve as baselines from which subsequent changes in ecosystems can be evaluated (Bahre 1991; Fralish *et al.* 1991; Fritschle 2008); provide insight into the contemporary composition of landscapes (Dupouey et al. 2002); and are valuable tools in restoration ecology (Radeloff et al. 2000). A number of resources are available to researchers interested in historical vegetation reconstructions, among them the records of the Public Land Survey System (PLS); Fagin & Hoagland 2002; Wang 2007).

Public Land Survey data provide one of the few quantitative datasets of pre-and early-European settlement vegetation for the western United States (Schulte & Mladenoff 2001; Whitney & DeCant 2001). As surveyors partitioned the land into 93.24 km^2 (36-mi^2) townships and further subdivided each township into 2.59 km^2 (1 mi^2) sections, they created township plats on which they mapped land cover types and locations of prominent physical and man-made features (Hutchinson 1988). Surveyors also recorded quantitative information related to so-called witness trees encountered along the survey lines. At the intersection of section lines and at each quarter section point (0.8 km along a section line), surveys noted the nearest tree in each of the adjoining sections, recording its identification and diameter at breast height (DBH), as well as the compass direction and distance from the corner or quarter section point.

Public Land Survey records have been used to evaluate vegetation dynamics (Bahre 1991; DeWeese *et al*. 2007), composition and structure of historical forest and woodland communities (Anderson and Anderson 1975), species-environment interactions (Cowell 1995; Mladenoff *et al*. 2002), and distribution and abundance of individual species (Abrams 2001; Wang & Larsen 2006). Per the latter, quantifying the areal extent of select woody species from PLS records has proven difficult due to the coarse sampling structure--tree data were only collected along section lines at 0.8 km (0.5 mi.) intervals. Additionally, bias in tree selection has been demonstrated, with tree size, longevity, and/or economic value often influencing witness tree selection (Lutz

1930; Bourdo 1956). As a result of these biases, insufficient data often exists to estimate the areal extent of select species.

Nonetheless, several attempts have been made to convert discrete PLS point data into continuous data using kriging and other interpolation methods (e.g. Brown 1998; Batek *et al.* 1999; He *et al.* 2000; Wang & Larsen 2006; Wang 2007). While these methods may adequately represent the spatial patterns of individual species over large areas (Wang & Larsen 2006), these methods typically fail to consider the numerous covariates, such as edaphic conditions or topographic position, which can influence the distribution of individual species at finer scales. Instead these models treat witness tree data as numeric values (typically 1 for present, 0 for absent) that can be interpolated without consideration of underlying ecological processes (He *et al.* 2007).

A more statistically rigorous method calls for combing species/environment relationships to estimate the areal extent of individual species from point data (Hooten *et al.* 2003; He *et al.* 2007). One such method that shows potential is weights-of-evidence (WofE). Weights-of-evidence is a discrete, data-driven multivariate method originally developed for the purpose of medical diagnosis (Bonham-Carter *et al.* 1989), but later adapted for spatial predictions (Agterberg *et al.* 1993). Weights-of-evidence uses a log-linear form of Bayes' rule to measure the spatial association between maps of independent variables and dependent variable point data (Bonham-Carter *et al.* 1989; Bonham-Carter & Agterberg 1999).

Weights-of-evidence has been used extensively to identify probable areas of undiscovered mineral resources (e.g. Bonahm-Carter *et al.* 1988; Porwal *et al.* 2003); to predict possible locations of archeological sites (e.g. Diggs & Brunswig 2006; Holmes

2007); for delineating high landslide risk (e.g. Neuhäuser & Terhorst 2007; Bui *et al.* 2008); and for estimating groundwater vulnerability to contaminants (e.g. Arthur *et al.* 2007; Masetti *et al.* 2007). However, despite its potential, its use in ecological studies has been limited to habitat quality assessment (Romero-Calcerrada & Luque 2006; Kindall & Van Manen 2007); inferring breeding success in bird (MacNally 2007); and mapping probabilities of wildfires (Dickson *et al*. 2006; Romero- Calcerrada *et al*. 2008). We know of no applications of WofE in predictive studies of the historical distribution of individual woody plant species, though He *et al*. (2007) used a similar approach with a hierarchical Bayesian method.

The objective of this study is to test the efficacy of WofE modeling to estimate the potential pre- and early-European distribution of select woody plant taxa from discrete PLS witness tree data. Specifically, we analyzed recorded occurrences of six important woody plant taxa (*Quercus stellata, Q. marilandica, Q. velutina, Carya texana, C. illinoinensis*, and *Juniperus spp.*) with six environmental covariates (soils, geological substrate, elevation, slope, aspect, and historical land cover) to calculate the posterior probability of their historical occurrence in the Arbuckle Mountains, Oklahoma. These estimates can then be used as a baseline from which subsequent changes in woody plant distributions can be gauged and to ascertain whether past land use practices and other anthropogenic disturbance regimes have influenced the distribution of individual taxon (Dupouey *et al.* 2002). Within the Arbuckle Mountains, this is of particular interest due to increases in abundance and dominance of *Juniperus* spp. at the expense of native grasslands and other woodland communities during the past century (Rice & Penfound 1959; Johnson & Risser 1975; Engle *et al.* 1997).

Methods

Study Area

The Arbuckle Mountains in south-central Oklahoma are a spatially heterogeneous region covering an area of approximately 215,000 ha (Figure 4.1). The Arbuckle Mountains are a topographically low plateau, rising a few hundred meters above the surrounding prairie, sloping from an elevation of 411 meters (1,350 feet) in the west to 229 meters (750 feet) in the east (Dale 1956; Hutcheson 1965). Structurally, the Arbuckle Mountains consist of extensive faulting and folding which has exposed late Cambrian to middle Mississippian limestone and late Mississippian and Pennsylvanian sedimentary rocks (Suneson 1997). The surface geology is characterized mostly by outcrops of carbonate rocks (Ham 1969), though one also finds granitic outcrops surrounded by limestones, conglomerates, sandstones, shales, cherts, and other types of rocks (Dale 1956; Suneson 1997).

The Arbuckle Mountains can be further subdivided into two distinct physiographic provinces, the Timbered Hills and the Arbuckle Plains. The Timbered Hills are the most topographically distinct feature of the Arbuckle Mountains, rising to a height of about 122 meters (400 feet) above their base and located on a large truncated anticline spanning 388 km^2 (150 square miles). The Timbered Hills are composed of pre-Cambrian porphyritic rock are extensively eroded into many shallow ravines, rounded hills, and flat tablelands (Dale 1956; Hutcheson 1965). The Arbuckle Plains are a fluvial-karstic landscape, underlain by the major aquifer and characterized by a gently rolling topography upon intensely faulted limestone beds (Fairchild *et al.* 1990).

The study area is located in the Subtropical Humid (Cf) climate zone, which is characterized by long, hot summers and short, mild winters (Trewartha 1980). Summer temperatures average 28º C, while winter temperatures average 3º C. Mean annual precipitation is 98 cm, with much of it occurring in April, May, and June (Oklahoma Climatological Survey 2007). November, December, and January are the driest months, though drought conditions typically occur in July and August (Dale 1956).

The Arbuckles lay within a region of vegetation known as the cross timbers, a mosaic of forest, woodland, and prairie vegetation types (Hoagland *et al.* 1999). The woodland communities of the Arbuckle Mountains vary considerably with soil type and moisture availability, with *Quercus stellata* and *Q. marilandica* as the most important species on dry, upland soils. *Carya texana* and *Q. buckleyi* are important secondary species in mesic to xeric upland sites, respectively. Important bottomland species include *Q. muehlenbergii, Celtis laevigata* var. *laevigata, C. laevigata* var. *reticulata, Platanus occidentalis, Ulmus americana, U. rubra, Carya illinoensis, Juglans nigra, Salix nigra,* and *Populus deltoides* (Rice & Penfound 1959; Hoagland & Johnson 2001).

Data Sources

Weights-of-evidence modeling proceeds in phases: development of a spatial database, extracting predictive evidence for the phenomena under investigation, calculating weights for each predictive map (evidential layer), combining the weights from each evidential layer to predict occurrence potential, and model evaluation (Kemp *et al.* 1999; Raines *et al.* 2000). The spatial database includes the identification of sites (each represented by a single *x,y* coordinate pair) in which the spatial phenomenon under investigation is known to have occurred (the dependent variable). In this study, the points are historical woody plant occurrences. The series of independent variables used for the prediction of other occurrences of the phenomena under investigation is also defined. In WofE modeling, the predictor variables typically take the form of GIS layers consisting of two or more classes (Bonham-Carter & Agterberg 1999).

For the dependent variable, we used PLS witness tree data. The General Land Office (GLO) conducted two surveys in the study area. The first lasted from 1870 to 1872, the second from 1897 to 1898. Based on prior analysis of these data (Fagin and Hoagland forthcoming), we determined that *Quercus stellata, Q. marilandica*, *Q. velutina*. *Carya texana,* and *C. illinoinensis* were among the most important woody taxa in the study area (Table 4.1). These witness tree records were used as the occurrence data in our WofE models. Additionally, during the past century, *Juniperus* spp. have increased in abundance and dominance throughout Oklahoma, primarily due to fire suppression and other land use practices (Rice & Penfound 1959; Johnson & Risser 1975; Engle *et al.* 1997). Because of increased importance in the study area since historic times, we also incorporated *Juniperus* spp. occurrences into our models.

We identified six environmental layers to use as our predictor variables. Two criteria went into the selection of the independent variables: factors known to influence the distribution of the selected taxa within the study area and data availability at both the spatial and temporal scale under investigation: Data selected included those features believed to adequately represent the spatial heterogeneity of the study area, while maintaining relative consistency from the time of surveys and the time the data were actually acquired. The covariates selected were substrate (parent material), soil type, elevation, slope, aspect, and historical land cover (Table 4.2).

Substrate data were extracted from a preexisting 1:250,000 scale digital dataset of surficial geology for the Arbuckle-Simpson Aquifer (Cederstrand 1996). General soil association data were obtained from the 1:250,000 U.S. General Soil Map (STATSGO2) Database (USDA NRCS 2007). The terrain data (elevation, slope, and aspect) were derived from the National Elevation Dataset (NED) 1 arc second (approximately 30 m) digital elevation model (USGS 2008). Elevation data were reclassified into 25 m elevation classes, while slope and aspect were combined into a single composite layer after Pallardy (1995) and Batek *et al.* (1999) to create a moisture availability index layer. Land cover data were obtained from a map consisting of digitized PLS plats (Fagin & Hoagland forthcoming). All data layers were converted to 1 arc second integer rasters. After initial weights for each layer were calculated (see below), each layer was generalized to increase model robustness (Bonham-Carter & Agterberg 1999).

Calculating Weights

The weights-of-evidence method is based on a log-linear form of Bayes' Theorem, with an assumption of conditional independence of the evidential layers (Bonham-Carter & Agterberg 1999; Raines *et al.* 2000). The weights-of-evidence method involves the following calculations (Bonham-Carter *et al.* 1989): 1. Estimation of the prior probability of the occurrence under investigation; 2. Calculation of positive (W^+) and negative (W^-) weights for each class in each evidential layer; and 3. Calculation of the posterior probability for each unique overlap condition of combinations of evidential layers.

The prior probability ($P\{D\}$) of an occurrence, that is, the probability of an occurrence under equal conditions, is calculated as $N(D)/N(T)$, where $N(D)$ is the number of unit cells in the study area with known occurrences of a selected taxon and $N(T)$ is the total number of unit cells within a study area. According to Bayes' Theorem, the conditional (posterior) probability that D will occur given class i of predictor variable B (i.e. $P\{D|B_i\}$) can be calculated from the prior probability as:

$$P\{D|B_i\} = P\{D\}\frac{P\{B_i|D\}}{P\{B_i\}} \tag{1}$$

Similarly, the posterior probability of an occurrence given the absence of an indicator can be stated as:

$$P\{D|\overline{B}_i\} = P\{D\}\frac{P\{\overline{B}_i|D\}}{P\{\overline{B}_i\}} \tag{2}$$

In the weights-of-evidence method, two weights, W^+ and W^-, are estimated for each class of an evidential layer (for derivation of weights, see Bonham-Carter (1994)):

$$W_i^+ = \log_e \frac{P\{B_i|D\}}{P\{B_i|\overline{D}\}} \tag{3}$$

$$W_i^- = \log_e \frac{P\{\overline{B}_i|D\}}{P\{\overline{B}_i|\overline{D}\}} \tag{4}$$

The weights represent a measure of spatial association between occurrences and classes of an evidential layer. If the spatial association is greater than would be expected by chance, W^+ is positive and W^- is negative. If the spatial association is less than would be expected by chance, W^+ is negative and W^- is positive. A value nearing zero indicates randomness (Kemp *et al.* 1999; Raines *et al.* 2000). The difference between W^+ and W^- is known as the contrast C. Thus $C = W^+ - W^-$. The larger the value of C is, the greater the spatial association (Bonham-Carter *et al.* 1989). The studentized value of C (C_s) is C divided by its standard deviation and provides a measure of confidence (Bonham-Carter 1994).

There are three possible approaches for calculating weights. Categorical weights are calculated for each class in an evidential layer. Ascending by pattern areas and descending by pattern areas are used for proximity analysis of ordered data. In ascending by pattern area, weights are calculated from the lowest to highest classes, while in descending by pattern area, weights are calculated from the highest to lowest classes. The evidential layers we used were all categorical, though.

Generalizing Evidential Layers

All evidential layers used in our model consisted of more than two classes. While WofE was originally designed for use with binary evidential layers, the use of multi-class data is often necessary to adequately represent the spatial heterogeneity of an area (Porwal *et al.* 2001). Nonetheless, layers with too many classes can reduce the robustness of the model, especially where there is limited occurrence data, and it is therefore advantageous to generalize each layer to just a few classes. The selection of threshold values for generalization is typically determined by the spatial association between the occurrences and the predictor variable. As such, thresholds that maximize C or C_s are typically deemed best (Bonham-Carter *et al.* 1988; Kemp *et al.* 1999). A C_s value greater than 1.96 indicates that the hypothesis that $C = 0$ can be rejected at $\alpha = 0.05$ (Bonham-Carter *et al.* 1989). We used the following values of C_s shown to maximize C_s (Romero-Calcerrada & Luque 2006; Romero-Calcerrada *et al.* 2008) as thresholds for generalization: W_1: $C_s < 1.96$; W_2: $1.96 \leq C_s < 3$; W_3: $3 \leq C_s < 4$; W_4: $4 \leq C_s < 5$; and W_5: $C_s \leq 5$.

Combining Weights

The posterior probability (P_k) is estimated by summing the weights from each evidential layer and the $\log_e$ prior probability (Raines *et al.* 2000; Carranza 2004):

$$p_k = e\sum_{j=1}^{m} W_j^k + \log_e P\{D\} \tag{5}$$

Additionally, a layer representing total confidence ($P_k/\sigma_{\text{Total}}$) is generated. A final predictive map is created by dividing P_k by the prior probability and classifying the output into four predictive categories (Romero-Calcerrada & Luque 2006):

1. High probability: $P_k/P\{D\} > 5$ and $P_k/\sigma_{\text{Total}} > 1.5$
2. Moderate probability: $5 > P_k/P\{D\} > 1$ and $P_k/\sigma_{\text{Total}} > 1.5$
3. Low probability: $1 > P_k/P\{D\}$ and $P_k/\sigma_{\text{Total}} > 1.5$
4. High uncertainity: $P_k/\sigma_{\text{Total}} < 1.5$

We created six predictive maps, one for each taxon under investigation.

Test of Conditional Independence

Weights-of-evidence assumes that the predictor variables are conditionally independent (CI) from each other with regard to the dependent variable *D* (Bonham-Carter *et al.* 1989; Kemp *et al.* 1999; Raines *et al.* 2000). Violation of this assumption can result in under- or over-estimation of weights (Kemp *et al.* 1999). Though CI is almost always violated to some degree, it is still necessary to test the amount of violation and to determine whether this violation distorts the results (Bonham-Carter 1994). If significant violation is found, one or more evidential layers that show a strong correlation to one another should be removed from the final model. We calculated overall conditional independence using two methods. A conditional independence ratio (CI) and the Agterberg-Cheng (omnibus) test of conditional independence (Agterberg & Cheng 2002).

The conditional independence ratio is a calculation of the ratio of the number of known occurrences, $N\{D\}$ to the number of predicted occurrences, $N\{D_{pred}\}$, where $N\{D_{pred}\}$ is estimated by summing the product of the area in unit cells, $N\{A\}$ and the posterior probability of each unique condition cell, P_k (Bonham-Carter 1994):

$$N\{D_{pred}\} = \sum_{k=1}^{m} P_k N\{A\} \tag{6}$$

A conditional independence ratio < 0.85 may indicate a violation of conditional independence (Bonham-Carter 1994).

The Agterberg-Cheng test (Agterberg & Cheng 2002) is a one-tailed test of the null hypothesis that $N\{D_{pred}\} = N\{D\}$ and is tested as the difference between $N\{D_{pred}\}$ and $N\{D\}$ divided by the standard deviation of $N\{D_{pred}\}$:

$$CI = \frac{N\{D_{pred}\} - N\{D\}}{s(N\{D_{pred}\})} \tag{7}$$

Probability values greater than 0.95 indicate the hypothesis of CI should be rejected. However, any values > 0.5 indicate some degree of conditional independence (Agterberg & Cheng 2002).

Model Validation

We used the split-sample approach in which the number of occurrences is divided into two randomly generated sets, a model building set and a validation set, to evaluate each of the models (Carranza & Hale 2002; Romero-Calcerrada & Luque 2006; Neuhäuser & Terhorst 2007). Each model set is combined with the probability map to determine the overall predictivity of the model. A conservative estimate of the usefulness of a predictive map is if it correctly identifies at least 70% of the occurrences that were used to build the model and at least 50% of the occurrences used to validate the model (Carranza & Hale 2000). However, in cases with a small number of occurrences (< 20; Agterberg & Cheng 2002; Carranza 2004), such an approach is impractical because each set would be too small of generate robust results (Carranza 2004). An independent set of validation data is therefore necessary. However, since we are working with historical data, no other independent dataset was available. Instead, in those cases, we used overall predictivity of the model building set and the calculated total uncertainty (posterior probability/σ_{total}) as a test for the robustness of the model. High posterior probability/σ_{total} ratio values indicate low uncertainty, while lower values indicate higher uncertainty (Kemp *et al.* 1999). Calculations of uncertainty are explained in Bonham-Carter *et al.* (1988).

Model Runs

We ran six models, one for each taxon under investigation. Due to variability in data availability and/or quality for each taxon, parameters for each model varied. For *Quercus stellata*, *Carya texana*, and *Carya illinoinensis*, we used PLS witness tree data from the 1870s surveys. However, there was a limited number of *Q. marilandica* occurrences in the 1870s survey (see Table 4.1) and we, therefore, used the 1890s PLS occurrence data. Additionally, *Q. velutina* occurrence data from the 1870s are higher than subsequent surveys of the region, but consistent with data from the 1890s (e.g.

Dale 1956; Rice & Penfound 1959: Hutcheson 1965). Thus we used the 1890s PLS point data for *Q. velutina*. Lastly, despite the dramatic increase in abundance during the past century, the *Juniperus* spp. records from both the 1870s and 1890s were too small to create an effective model, so it was necessary to combine the 1870s and 1890s *Juniperus* spp. occurrence data into a single dataset. All six models used the same evidential layers.

Each dataset with a sufficient number of occurrence points was randomly split into two sets; one for model building, the other for validation. The model building set consisted of 65% of the witness tree records for each taxon and the validation set consisted of 35% of the records. The two exceptions were for *Q. stellata* and *Juniperus* spp. In the case of the former, we thinned the witness tree records to just 20% of all occurrences because there were ample records. In the case of the latter, the volume of occurrence data were insufficient to split the dataset into model building and validation datasets.

Results

A total of 619 occurrence points representing six different taxa were combined with the evidential layers to produce six posterior probability maps of occurrence, one for each taxon under investigation. The weights of evidence results for the six models are summarized in Figures 4.2 and 4.3. These results indicate that the effectiveness of using the WofE method with PLS data varied by taxon, with the models accurately predicting between 41.67 to 91.43% of the model building points and between 37.04 to 87.87% of the validation set. The models accurately predicted the distributions of *Q. stellata*, *Q. marilandica*, *C. texana*, and *Juniperus* spp. However, the models underpredicted the distributions of *Q. velutina* and *C. illinoinensis*. The following results are presented by taxon.

Quercus stellata

Quercus stellata was found on a wide variety of geologic, edaphic, moisture, and elevation, classes (Table 4.3). *Q. stellata* showed the greatest spatial association to Precambrian-aged granitic formations, though it also occurred on Cambrian-aged limestones, and Ordovician, Devonian, and Mississippian-aged shales. Additionally, *Q. stellata* showed a high spatial association with well-drained, upland sites and was limited primarily to areas delineated as closed forest and/or woodland on the 1870 land cover map.

Based on the C_s values (Table 4.3), the geological layer was reclassified to 3 classes, the soils layer and elevation layers to 4 classes each, and the moisture availability index and historical land cover layers to binary classes. The combination of the five reclassified evidential layers resulted in 907 unique conditions, with posterior probability values ranging from < 0.001 to 0.602, a range that reflects very low probability (likely open grasslands) to high probability (likely closed forest). The resulting probabilistic map for *Q. stellata* (Figure 4.2a) contained 72,068.31 ha (~34.46% of the total probabilistic map output) classified as high probability of occurrence and 34,817.49 ha (~16.6% of the total probabilistic map output) classified as medium probability of occurrence. Additionally, 86,972.94 ha (~41.58%) of the output map were classified as low probability, while 15,293.7 ha (~7.3%) had high uncertainty, so no prediction was possible.

The overall conditional independence of *Q. stellata* and the evidential layers was 15.9%. The conditional independence ratio was 0.89 and the probability that the model is not conditionally independent based on the Agterberg-Cheng (omnibus) test was 92.1%. Per the former, any value below 1 may indicate some conditional dependence (Bonham-Carter 1994), while any value greater than 95% on the latter indicate the hypothesis of conditional independence should be rejected (Agterberg & Cheng 2002). Our results indicate that the hypothesis of conditional independence should not be rejected.

Of the 245 occurrences in the model building set, 176 (71.84%) fell within high probability zones, 48 (19.59%) fell within moderate probability zones, 19 (7.76%) fell with low probability zones, and 2 (0.82%) fell within areas with high uncertainty. Of the 989 points in the validation dataset, 696 (70.37%) fell within high probability zones, 173 (17.49%) occurred within moderate probability zones, 108 (10.92%) fell with low probability zones, and 12 (1.21%) fell within areas with high uncertainty (Table 4.4a). Based on these results, the predictions of the *Q. stellata* model are deemed valid.

Quercus marilandica

Occurrences for this species were primarily on dry, rocky, upland sites on granite, limestone, shale, and sandstone. Though individual *Q. marilandica* occurrences were primarily in areas delineated by surveyors as closed forest and woodlands (49%), a number of occurrences were also recorded from areas mapped at grassland/savanna (46%) and from areas demarcated as cultivation (5 %; Table 4.5).

All of the evidential layers were reclassified to binary classes with the exception of the surficial geology layer, which was reclassified to ternary classes (see Table 4.4).

The combination of the reclassified evidential layers resulted in 607 unique conditions, with posterior probability values ranging from 0.0003 to 0.792. The resulting probabilistic map for *Q. marilandica* (Figure 4.2b) contained 70,604.28 ha (~33.77% of the total probabilistic map output) classified as high probability of occurrence, 64,178.55 ha (~30.70%) classified as medium probability of occurrence, and 52,372.35 ha (~25.05%) classified as low probability. Approximately, 21,896.01 ha (~10.47%) of the output probabilistic map had high uncertainty, so no prediction was possible.

The overall conditional independence of *Q. marilandica* and the evidential layers was 29.1%. The Conditional Independence Ratio was 0.94, indicating some degree of conditional independence between two or more of the datasets. However, Bonham-Carter (1994) notes that predicted numbers are almost always higher than observed values in WofE and this is usually a concern when expected values are 15% higher than observed values (i.e. CI ratio < 0.85). The omnibus test of CI also indicated that there was some degree of conditional independence in this model. The probability that the model is not conditionally independent was 85.5%. However, since this value was below 95%, the hypothesis of conditional independence was not rejected (Agterberg & Cheng 2002).

The model for *Q. marilandica* only performed moderately well (Table 4.4b). A total of 160 (78.05%) of the model building occurrences occurred in areas estimated to be high or medium probability of occurrence. Of these, though, only 99 (48.29%) occurred on areas of high probability, while 61 (29.76%) occurred on areas of moderate probability. Additionally, 41 (20%) occurrences occurred on areas estimated to be low probability. The validation set saw similar results. A total 83 (75.45%) of the validation points occurred on areas estimated to be moderate to high probability. Of these, 46 (41.82%) were found on areas of high probability, while 37 (33.64%) were found on areas of moderate probability.

Quercus velutina

Recorded instances of *Q. velutina* indicate that this species was far more limited in its distribution compared to either *Q. stellata* or *Q. marilandica* (Table 4.6). Individuals occurred most frequently on moderately well-drained, karstic soils and also found primarily at higher elevations on somewhat xeric to mesic sites. Moreover, almost 40% of the individuals in the model building set were located in areas surveyors delineated as open prairie/savanna.

All of the evidential layers were reclassified to binary classes with the exception of the surficial geology layer, which was reclassified to ternary classes (see Table 4.6). The combination of the reclassified evidential layers resulted in 185 unique conditions, with posterior probability values ranging from 0.00035 to 0.970. The resulting probabilistic map for *Q. velutina* (Figure 4.2c) contained 13,677.48 ha (~6.52% of the total probabilistic map output) classified as high probability of occurrence, 11,150 ha (~5.33%) classified as medium probability of occurrence, and 112,641.11 ha (~58.67%) classified as low probability. Approximately, 61,852.59 ha (~29.49%) of the output probabilistic map had high uncertainty, so no prediction was possible.

The overall conditional independence of *Q. velutina* and the evidential layers was 41.6%. The Conditional Independence Ratio was 0.90, indicating some degree of conditional independence between two or more of the datasets. The omnibus test of CI also indicated that there was some degree of conditional independence in this model. However, it was not above the threshold to reject the hypothesis of conditional independence. The probability that the model is not conditionally independent was 79.2%.

The model underpredicted *Q. velutina* occurrences (Table 4.4c). Only 25 (54.35%) of the model building points occurred in areas estimated to be high or medium probability of occurrence. Of these, though, only 19 (41.30%) occurred on areas of high probability, while 6 (13.04%) occurred on areas of moderate probability. However, 17 (36.96%) points in the model building set occurred on areas estimated to be low probability. The validation set saw similar results. Only 10 (37.03%) of the validation points occurred on areas estimated to be moderate to high probability.

Carya texana

Carya texana showed the greatest spatial association to well-drained soils on Pennsylvanian-aged limestone, shale, and sandstone. Most individuals were found at mid-elevations (710-1,030 m) and occurred most frequently in areas mapped by surveyors as closed forest and woodland. Several individuals, though, occurred in areas delineated as open grassland/savanna by surveyors (Table 4.7).

All of the evidential layers were reclassified to ternary classes with the exception of the moisture availability index layer, which was reclassified to binary classes (see Table 4.7). The combination of the reclassified evidential layers resulted in 204 unique conditions, with posterior probability values ranging from 0.0001 to 0.99. The resulting probabilistic map for *C. texana* (Figure 4.2d) contained 24,736.05 ha (~11.82% of the total probabilistic map output) classified as high probability of occurrence, 33,105.51 ha (~15.82%) classified as medium probability of occurrence, and 123,765.84 ha (~59.17%) classified as low probability. Approximately, 27,545 ha (~13.17%) of the output probabilistic map had high uncertainty, so no prediction was possible.

The overall conditional independence of *C. texana* and the evidential layers was 20.7%. The Conditional Independence Ratio indicated some degree of conditional independence at 0.86. The omnibus test of CI value of 89.7 was not above the threshold to reject the hypothesis of conditional independence.

The model for *C. texana* performed moderately well (Table 4.4d). A total of 58 (76.32%) of the model building points occurred in areas estimated to be high or medium probability of occurrence. Of these, 41 (53.95%) occurred on areas of high probability, while 17 (22.37%) occurred on areas of moderate probability. Additionally, 14 (18.42%) occurrences occurred on areas estimated to be low probability. The validation set saw lower results. A total 25 (59.52%) of the validation points occurred on areas estimated to be moderate to high probability and 16 (38.10%) occurred on areas estimated to be low probability.

Carya illinoinensis

Carya illinoinensis occurred primarily on moderately well-drained and well drained soils derived from Ordovician-aged limestone. Individuals were found on a variety of topographic classes, but showed the greatest spatial association to flat surfaces. Additionally, approximately 36% of individuals in the model building set were located in areas surveyors delineated as open prairie/savanna (Table 4.8).

All of the evidential layers were reclassified to ternary classes with the exception of the moisture availability index and land cover layers, which were reclassified to binary classes (see Table 4.8). The combination of the reclassified evidential layers resulted in 105 unique conditions, with posterior probability values ranging from 0.00186 to 0.958. The resulting probabilistic map for *C. illinoinensis* (Figure 4.2e) contained 9,070 ha (~4.34% of the total probabilistic map output) classified as high probability of occurrence, 14,973 ha (~7.14%) classified as medium probability of occurrence, and 181,937 ha (~87%) classified as low probability. Approximately, 3,207 ha (~1.5%) of the output probabilistic map had high uncertainty, so no prediction was possible.

The overall conditional independence of *C. illinoinensis* and the evidential layers was 51.3%. The Conditional Independence Ratio was 0.91, while the omnibus test of CI was 74.4%. Based on these values, we were not able to reject the hypothesis of conditional independence.

The model for *C. illinoinensis* performed poorly (Table 4.4e). A total of 8 (22.22%) of the model building points occurred in areas estimated to be high or medium probability of occurrence, while an additional 8 points (22.22%) occurred on areas with uncertainty too high to make a prediction. Moreover, 20 (55.56%) occurrences occurred on areas estimated to be low probability. The validation set results were slightly better with a total 7 (35%) of the validation points occurring on areas estimated to be moderate to high probability, 10 (50%) occurring on areas estimated to be low probability, and 3 (15%) on areas with high uncertainty.

Juniperus spp.

Juniperus spp. had a very limited distribution, with the majority of individuals found on Ordovician or Mississippian shale and limestone, though two individuals were found on Precambrian granite. The *Juniperus* spp. individuals were found at elevations between 710-1,110 m, primarily on moderate to steep south facing slopes. The *Juniperus* spp. individuals were also found in both forest/woodland and grassland/savanna areas (Table 4.9).

Because overall C_s values were low, we adjusted our confidence level from 1.96 to 1.5. As a result, the geology evidential layer was reclassified to four classes, while the remaining evidential classes except land cover were reclassified to binary classes. Despite adjusting the confidence level, the C_s values in the land cover class were still too low and this layer was therefore excluded from further analysis (Table 4.9). The combination of the remaining evidential layers resulted in 84 unique conditions with posterior probability values ranging from 0.0001 to 0.945. The resulting probabilistic map for *Juniperus* spp. (Figure 4.2f) contained 11,817.18 ha (~5.5% of the total probabilistic map output) classified as high probability of occurrence, 10,982.52 ha (~5.13%) classified as medium probability of occurrence, and 167,126 ha (~78%) classified as low probability. Approximately, 24,055 ha (~11.24%) of the output probabilistic map had high uncertainty, so no prediction was possible.

The overall conditional independence of the *Juniperus spp.* and the evidential layers was 53.1%. The Conditional Independence Ratio indicated some degree of conditional independence at 1.16. The omnibus test of CI value of 26.6 was not above the threshold to reject the hypothesis of conditional independence.

Of the 11 occurrences in the model building setting, 9 (81.82%) fell within high probability zones, 1 (9.09%) fell within moderate probability zones, 1 (9.09%) fell with low probability zones, and 0 (0%) fell within areas with high uncertainty. Due to the small number of occurrences, it wasn't feasible to divide the *Juniperus* spp. into separate model building and validation sets (Carranza 2004). The results of the model building set, though, indicate that the model performed well (Table 4.4f).

Discussion and Conclusions

Quantitative studies of the historical vegetation of the cross timbers are limited (e.g. Shutler 2001; Shutler & Hoagland 2004). Nonetheless, many believe that the arborescent communities of the region were less widespread prior to European settlement (e.g. Rice & Penfound 1959; Engle *et al.* 2006). According to this theory, fire suppression and other land use practices, such as grazing, have contributed to increases in dominant overstory *Quercus* species (Engle *et al.* 2006). Moreover, there is sufficient evidence that, in the period since widespread European settlement, *Juniperus* spp. have encroached in former grasslands and woodlands throughout the region, resulting in the conversion of the former to woodlands and the latter to closed canopy forest (Rice & Penfound 1959; Johnson & Risser 1975; Engle *et al.* 1997; Hoagland & Johnson 2001).

Because these changes often proceed at rates that exceed the availability of quantitative data, estimating changes in woody plant distribution since historic times is problematic (Briggs *et al.* 2002). Moreover, the few quantitative historical datasets available typically have resolutions too coarse for ecological analysis (Delcourt & Delcourt 1996; Manies & Mladenoff 2000; He *et al.* 2000). For instance, Manies &

Mladenoff (2000) found that, while the coarse resolution sampling of the PLS data could accurately estimate the relative forest composition of the landscape and the order of dominance of different vegetation types, estimates of area occupied by each vegetation type were unreliable. The results of this study, though, indicate that weights-of-evidence is an effective tool to overcome some of these limitations of historical data.

Weights-of-evidence belongs to a growing body of research techniques that can be used to predict species distribution from point occurrence data (see Guisan & Zimmermann 2000; Elith *et al.*2006 for reviews of similar methods). Weights-of-evidence has been used successfully by geoscientists (e.g Bonahm-Carter *et al.* 1988; Porwal *et al.* 2003), archeologists (e.g. Diggs & Brunswig 2006; Holmes 2007), geomorphologists (e.g. Neuhäuser & Terhorst 2007; Bui *et al.* 2008), hydrologists (e.g. Arthur *et al.* 2007; Masetti *et al.* 2007), and ecologists (Romero-Calcerada & Luque 2006; MacNally 2007). Our results indicate that WofE can also be used to create statistically significant maps of the historic distribution of woody plant taxa from PLS data.

Several caveats for the use of weights-of-evidence (or similar modeling techniques (see for instance He *et al.* 2007)) with PLS data must be stated, though. Weights-of-evidence utilizes a series of evidential layers to predict the posterior probability of occurrence of the phenomenon under investigation. An underlying assumption in the use of such layers in predictive mapping of historical data is that contemporary datasets adequately represent historical environmental conditions. In our models, this assumption limited our selection of evidential layers primarily to abiotic variables that are assumed to relatively consistent since the time of the PLS survey and the time these data were acquired. However, even this assumption is not entirely correct. Dupouey *et al.* 2002, for instance, have demonstrated that intensive human modifications to landscapes can cause irreversible damage to soils over a relatively short time span; which, in turn, can impact the biodiversity of an area. Additional anthropogenic modifications to the landscape, such as the construction of artificial lakes, can change landscape characteristics from historic times.

The inability to incorporate additional evidential layers that may otherwise help improve predictions is another drawback in modeling historical data. For example, climatic variables, such as mean annual precipitation and temperature, length of growing season, and temperature extremes may influence the distribution of certain organisms and these variables have been used successfully in similar distributional models that utilized current occurrence data (e.g. Elith *et al.* 2006). Such historic datasets were unavailable, though. However, this likely did not adversely influence the results of this study, because climate variables are relatively uniform across the Arbuckle Mountains (Oklahoma Climatological Survey 2007) and any microclimatic variables may be reflected in the topographic-related evidential layers (i.e. slope, aspect, and elevation).

Other abiotic variables that may have improved the modeling of several of the taxa are fire frequency and/or intensity. Again, these data were either unavailable at the spatial and temporal scales required for our models or not available at all. Nonetheless, fire restricts the distribution of *Juniperus* spp. (e.g. Rice & Penfound 1959; Johnson & Risser 1975; Engle *et al.* 1997; Hoagland & Johnson 2001). Additionally, fire suppression since widespread European settlement is believed to have led to increases in canopy cover of dominant *Quercus* spp. (Engle *et al.* 2006).

Reqirements of conditional independence of the datasets can also be problematic with the limited availability of adequate evidential layers. Weights-of-evidence assumes that the predictor variables are conditionally independent from each other with regard to the dependent variable (Bonham-Carter *et al.* 1989; Kemp *et al.* 1999; Raines *et al.* 2000). Violation of this assumption can result in under- or over-estimation of weights (Kemp *et al.* 1999). When significant conditional dependence occurs, evidential layers showing conditional dependence should be rejected from the analysis (Bonham-Carter 1994) or combined into a single composite layer (Agterberg & Cheng 2002), as we did with the slope and aspect layers. However, with limited evidential layers, removing and/or combing layers may compromise the overall model. In such instances, other modeling approaches might be considered, such as weighted logistic regression (Agterberg *et al.* 1993).

Other potential limitations to use of weights-of-evidence with PLS data are the occurrence data themselves. Wang (2005) and Wang and Larsen (2006), for instance, cite limitations in positional accuracy in witness tree data. Modeling species/environment relationships requires a high degree of positional accuracy. However, selection of an appropriate cell size of evidential layers can help minimize issues with positional precision and accuracy, assuming the witness tree data in the PLS surveys are correct.

Public Land Survey data are also constrained by taxonomic uncertainty. In a number of instances, surveyors recorded certain taxa to genus level (Shutler &

Hoagland 2004). For instance, surveyors listed only "cedar," but two species of *Juniperus* occur in the Arbuckle Mountains; *J. virginiana* and *J. ashei*. Conversely, the weights-of-evidence method may actually aid in classifying such individuals to finer taxonomic levels. Historically, *J. ashei* was restricted to rocky outcrops and dissected upland soils of limestone origin (Hart and Price 1990; Diamond and True 2008). *Juniperus virginiana*, though, is found in numerous habitats throughout the region, but is primarily found in valleys in the Arbuckle Mountains (Little 2000). Based on our overlay analysis, 9 of the 11 recorded *Juniperus* individuals occurred on areas dominated by limestone and shale, while two occurred on granitic material at lower elevations (see Table 4.9). By calculating the spatial associations with various environmental layers and identifying spatial relationships, it may be feasible to identify these congeners to the specific level (see Mladenoff *et al.* 2002 for a similar approach using logistic regression). In our case, it is likely that the nine individuals found on karstic areas are *J. ashei*, while the two individuals found on granitic parent materials are *J. virginiana*.

Despite these inherent limitations, we believe that the weights-of-evidence method has proven to be an effective method to produce probablistic distributions of individual species from discrete PLSdata. Within the last decade, there has been an increase in the use of PLS data in ecological analysis (see Fagin & Hoagland 2002; Wang 2005). As use of these data become more common place, the need to map these data to finer resolutions increases. In the case of the cross timbers, these probabilistic maps will enable better estimates of the degree and direction of increases in woody plant abundance since historic times.

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Taxon	1870s # Trees	1870s Rel. Dom.	1870s Rel. Den.	1870s I.V.	1890s # Trees	1890s Rel. Dom.	1890s Rel. Den.	1890s I.V.
Quercus stellata	1234	46.368	47.867	47.117	1242	40.331	41.678	41.005
Quercus velutina	529	15.442	20.520	17.981	73	2.509	2.450	2.479
Ulmus spp.	328	29.296	12.723	21.009	474	21.174	15.906	18.540
Carya texana	118	0.982	4.577	2.779	69	0.568	2.315	1.441
Quercus alba	81	1.701	3.142	2.422	57	0.739	1.913	1.326
Carya illinoinensis	56	1.231	2.172	1.702	123	5.459	4.128	4.793
Fraxinus spp.	45	0.983	1.746	1.364	69	1.324	2.315	1.820
Quercus falcata	37	0.607	1.435	1.021	184	5.713	6.174	5.944
Celtis laevigata	24	0.416	0.931	0.673	58	1.261	1.946	1.603
Juglans nigra	23	0.493	0.892	0.693	42	2.236	1.409	1.822
Quercus palustris	22	0.209	0.853	0.531	27	0.448	0.906	0.677
Populus deltoides	19	0.744	0.737	0.740	6	0.200	0.201	0.201
Quercus macrocarpa	18	0.658	0.698	0.678	19	0.567	0.638	0.602
Quercus marilandica	6	0.386	0.233	0.309	315	12.541	10.570	11.556
Platanus occidentalis	6	0.042	0.233	0.138	6	0.287	0.201	0.244
Diospyros virginiana	5	0.262	0.194	0.228	17	0.388	0.570	0.479
Juniperus spp.	4	0.055	0.155	0.105	7	0.204	0.235	0.219
Cercis canadensis	4	0.003	0.155	0.079	-	-	-	-
Morus rubra	3	0.028	0.116	0.072	-	-	-	-
Quercus spp.	3	0.014	0.116	0.065	164	3.600	5.503	4.552
Maclura pomifera	3	0.018	0.116	0.067	11	0.351	0.369	0.360
Sideroxylon lanuginosum	2	0.022	0.078	0.050	7	0.024	0.235	0.129
Prunus spp.	2	0.004	0.078	0.041	-	-	-	-
Acer negundo	2	0.024	0.078	0.051	2	0.023	0.067	0.045
Malus ioensis	1	0.001	0.039	0.020	-	-	-	-
Gymnocladus dioicus	1	0.004	0.039	0.022	1	0.004	0.034	0.019
Salix spp.	1	0.001	0.039	0.020	1	0.001	0.034	0.017
Crataegus spp.	1	0.010	0.039	0.024	-	-	-	-
Quercus nigra	-	-	-	-	5	0.046	0.168	0.107
Sapindus saponaria	-	-	-	-	1	0.002	0.034	0.018

Table 4.1. Comparison of frequency (# trees), relative dominance (Rel. Dom.), relative density (Rel. Den.) and importance value (I.V.) for all recorded taxon from PLS data, 1870s and 1890s.

Table 4.2. Evidential layers, data sources, and the approaches to calculate weights.

Covariate (Evidential Layer)	Source Data	Calculated Weight
Surficial Geology	1:250,000 Vector Layer	Categorical Weights
Soil Association	1:250,000 Vector Layer	Categorical Weights
Elevation	1 Arc Second Raster Layer	Categorical Weights
Moisture Availability Index	1 Arc Second Raster Layer	Categorical Weights
Land Cover	Scanned & Digitized PLS Township Plats	Categorical Weights

Table 4.3. Calculated weights, contrast, and studentized contrast (C_s) for *Quercus stellata*. Only classes that met the C_s threshold of > 1.96 shown.

CLASS	GEOLOGICAL FORMATION	W+	W-	CONTRAST	Cs
Md	Mississippian Delware Creek Shale	0.7796	-0.0275	0.8071	2.6614
Dw	Devonian Woodford Shale	1.0191	-0.0762	1.0953	5.2143
Cth	Cambrian Timbered Hills Group	0.9246	-0.0150	0.9397	2.2101
pCt	Precambrian Tishimingo and Troy Granites	0.8458	-0.2733	1.1191	8.2144

CLASS	SOILS CLASS	W+	W-	CONTRAST	Cs
s6316	Shidler-Scullin-Rock outcrop-Lula-Claremore	-0.5853	0.2412	-0.8265	-5.2464
s6314	Normangee-Heiden-Durant	0.4920	-0.0268	0.5188	1.9698
s6328	Hector-Endsaw-Bolivar	1.2221	-0.0087	1.2308	2.0400
s6315	Rock outcrop-Kiti	-0.3858	0.1152	-0.5010	-3.0356
s6310	Durant-Clarita-Chigley	0.6855	-0.0252	0.7108	2.3486
s6309	Garvin-Clarita-Chigley	0.9570	-0.0128	0.9698	2.0845
s6308	Rock outcrop-Chigley-Agan	0.8580	-0.2798	1.1378	8.3716

CLASS	ELEVATION RANGE	W+	W-	CONTRAST	Cs
3	215 - 240	0.6549	-0.0721	0.7270	3.8060
4	240 - 265	0.8200	-0.1668	0.9868	6.4975
5	265 - 290	0.4759	-0.1040	0.5799	3.7246

CLASS	MOISTURE CLASS	W+	W-	CONTRAST	Cs
1	1	0.6675	-0.1755	0.8430	2.5293

CLASS	LAND COVER CLASS	W+	W-	CONTRAST	Cs
1	Forest/Woodland	0.6972	-1.7231	2.4203	11.2109
2	Grassland/Savanna	-1.7214	0.6951	-2.4166	-11.1937

Table 4.4. Validation results from each model run.

Taxon	High Count (%)	Medium Count (%)	Low Count (%)	Uncertain Count (%)	
Q. stellata	176 (71.84)	48 (19.59)	19 (7.76)	2 (0.82)	*Model*
	696 (70.37)	173 (17.49)	108 (10.92)	12 (1.21)	*Validation*
Q. marilandica	99 (48.29)	61 (29.76)	41 (20)	4 (1.95)	*Model*
	46 (41.82)	37 (33.64)	23 (20.91)	4 (3.64)	*Validation*
Q. velutina	19 (41.30)	6 (13.04)	17 (36.96)	1 (2.17)	*Model*
	8 (29.63)	2 (7.41)	15 (55.56)	2 (7.41)	*Validation*
C. texana	40 (52.63)	17 (22.37)	15 (19.74)	4 (5.26)	*Model*
	12 (28.57)	13 (30.95)	16 (38.10)	1 (2.38)	*Validation*
C. illinoinensis	11 (30.56)	4 (11.11)	20 (55.56)	1 (2.78)	*Model*
	6 (30)	4 (20)	10 (50)	0 (0)	*Validation*
Juniperus spp.	9 (81.82)	0 (0)	2 (18.18)	0 (0)	*Model*
	0 (0)	0 (0)	0 (0)	0 (0)	*Validation*

Table 4.5. Calculated weights, contrast, and studentized contrast (C_s) for *Quercus marilandica*. Only classes that met the C_s threshold of > 1.96 shown.

CLASS	GEOLOGICAL FORMATION	W+	W-	CONTRAST	Cs
Dw	Devonian Woodford Shale	0.5939	-0.0349	0.6288	2.2958
Osfv	Ordovician Sylvan Shale, Fenvale Limestone, and Viola Limestone	-0.9168	0.0384	-0.9552	-2.0990
Obm	Ordovician Bromide, Tulip Creek, and McLish Formations	0.4540	-0.0681	0.5221	2.6979
IPm	Pennsylvanian McAlester Formation (Shale)	3.3502	-0.0047	3.3550	2.5738
Owk	Ordovician West Spring Creek	-0.6151	0.0546	-0.6697	-2.2352
pCt	Precambrian Tishimingo and Troy Granites	0.4589	-0.1129	0.5718	3.4540

CLASS	SOIL CLASS	W+	W-	CONTRAST	Cs
s6316	Shidler-Scullin-Rock outcrop-Lula-Claremore	0.2485	-0.1851	0.4336	3.0548
s6315	Rock outcrop-Kiti	-0.7788	0.1890	-0.9678	-4.5788
s6308	Rock outcrop-Chigley-Agan	0.4381	-0.1063	0.5443	3.2664

CLASS	ELEVATION RANGE	W+	W-	CONTRAST	Cs
4	240 - 265	0.3879	-0.0602	0.4481	2.3179
7	315 - 340	0.2821	-0.0748	0.3569	2.1457
9	365 - 390	-2.3622	0.1000	-2.4622	-3.4606

CLASS	MOISTURE CLASS	W+	W-	CONTRAST	Cs
-3	-3	0.7695	-0.0476	0.8171	3.1476

CLASS	LAND COVER CLASS	W+	W-	CONTRAST	Cs
1	Forest/Woodland	0.3334	-0.2410	0.5744	4.0463
2	Grassland/Savanna	-0.2247	0.2372	-0.4619	-3.2449

Table 4.6. Calculated weights, contrast, and studentized contrast (C_s) for *Quercus velutina*. Only classes that met the C_s threshold of > 1.96 shown.

CLASS	GEOLOGICAL FORMATION	W+	W-	CONTRAST	Cs
IPv	Pennsylvanian Vanoss Group (Shale)	4.0785	-0.0216	4.1001	2.6940
Dw	Devonian Woodford Shale	1.6386	-0.1790	1.8176	4.6750
Osfv	Ordovician Sylvan Shale, Fenvale Limestone, and Viola Limestone	1.2251	-0.1585	1.3837	3.6097
IPd	Pennsylvanian Deese Group (Limestone)	2.9192	-0.0208	2.9400	2.4598
pCt	Precambrian Tishimingo and Troy Granites	-1.9961	0.1524	-2.1485	-2.1213
Ka	Cretaceous Antlers Sand	1.7031	-0.0555	1.7586	2.7905

CLASS	SOIL CLASS	W+	W-	CONTRAST	Cs
s6308	Rock outcrop-Chigley-Agan	-1.9960	0.1524	-2.1483	-2.1212
s6279	Yahola-Reinach-McLain-Dale	2.2354	-0.1034	2.3387	4.5358

CLASS	ELEVATION RANGE	W+	W-	CONTRAST	Cs
7	315 - 340	0.5974	-0.1969	0.7943	2.4852

CLASS	MOISTURE CLASS	W+	W-	CONTRAST	Cs
1	1	0.6675	-0.1755	0.8430	2.5293

CLASS	LAND COVER CLASS	W+	W-	CONTRAST	Cs
1	Forest/Woodland	0.3759	-0.2839	0.6597	2.1381
2	Grassland/Savanna	-0.3686	0.3446	-0.7132	-2.2635

Table 4.7. Calculated weights, contrast, and studentized contrast (C_s) for *Carya texana*. Only classes that met the C_s threshold of > 1.96 shown.

CLASS	GEOLOGICAL FORMATION	W+	W-	CONTRAST	Cs
IPh	Pennsylvanian Holdenville Formation (Shale)	2.9291	-0.0125	2.9416	2.4104
Ooj	Ordovician Oil Creek and Joins	1.2433	-0.2128	1.4562	5.3109
Ok	Ordovician Kindblade Formation (Limestone)	0.8301	-0.0642	0.8943	2.3298
Owk	Ordovician West Spring Creek	-1.4275	0.0895	-1.5171	-2.1100
Ocm	Ordovician Cool Creek	-1.3799	0.0838	-1.4637	-2.0355
Pg	Permian Garber Sandstone	2.2296	-0.0118	2.2414	2.0048
IPd	Pennsylvanian Deese Group (Limestone)	2.2988	-0.0119	2.3107	2.0529

CLASS	SOILS CLASS	W+	W-	CONTRAST	Cs
s6316	Shidler-Scullin-Rock outcrop-Lula-Claremore	0.4421	-0.3996	0.8417	3.5758
s6315	Rock outcrop-Kiti	-2.3662	0.3024	-2.6686	-3.7180
s6279	Yahola-Reinach-McLain-Dale	1.8799	-0.0701	1.9500	4.2646

CLASS	ELEVATION RANGE	W+	W-	CONTRAST	Cs
3	215 - 240	0.9090	-0.1162	1.0252	3.2747
6	290 - 315	0.4783	-0.1193	0.5977	2.2162

CLASS	MOISTURE CLASS	W+	W-	CONTRAST	Cs
0	0	1.5575	-0.0655	1.6229	3.6160

CLASS	LAND COVER CLASS	W+	W-	CONTRAST	Cs
1	Forest/Woodland	0.6757	-1.5383	2.2140	6.2024
2	Grassland/Savanna	-1.6550	0.6892	-2.3443	-6.2411
6	Cultivated	3.1850	-0.0127	3.1977	2.4948

Table 4.8. Calculated weights, contrast, and studentized contrast (C_s) for *Carya illinoinensis*. Only classes that met the C_s threshold of > 1.96 shown.

CLASS	GEOLOGICAL FORMATION	W+	W-	CONTRAST	Cs
MsW	Mississippian Sycamore and Weldon Limestones	2.6611	-0.0262	2.6874	2.3816
Osfv	Ordovician Sylvan Shale, Fenvale Limestone, and Viola Limestone	1.3490	-0.1919	1.5409	3.7434
Ooj	Ordovician Oil Creek and Joins	0.7988	-0.1044	0.9032	1.9859

CLASS	SOILS CLASS	W+	W-	CONTRAST	Cs
s6310	Durant-Clarita-Chigley	1.2348	-0.0625	1.2973	2.0944
s6279	Yahola-Reinach-McLain-Dale	2.4852	-0.1379	2.6231	5.0137

CLASS	ELEVATION RANGE	W+	W-	CONTRAST	Cs
3	215 - 240	0.8700	-0.1099	0.9799	2.1522

CLASS	MOISTURE CLASS	W+	W-	CONTRAST	Cs
-1	-1	0.9151	-0.1352	1.0503	2.4488
0	0	2.1538	-0.1333	2.2871	4.4666

CLASS	LAND COVER CLASS	W+	W-	CONTRAST	Cs
1	Forest/Woodland	0.3364	-0.4090	0.7454	2.1309
2	Grassland/Savanna	-0.4073	0.3344	-0.7417	2.1204

Table 4.9. Calculated weights, contrast, and studentized contrast (C_s) for *Juniperus* spp. Only classes that met the C_s threshold of > 1.5 shown.

CLASS	GEOLOGICAL FORMATION	W+	W-	CONTRAST	Cs
IPa	Pennsylvanian Ada Formation (Shale)	3.8004	-0.3123	4.1127	5.6196
Md	Mississippian Delware Creek Shale	2.5275	-0.2964	2.8239	4.0746

CLASS	SOILS CLASS	W+	W-	CONTRAST	Cs
s6315	Rock outcrop-Kiti	1.1038	-1.3882	2.4920	3.1816

CLASS	ELEVATION RANGE	W+	W-	CONTRAST	Cs
4	240 - 265	0.9066	-0.2017	1.1083	1.6286

CLASS	MOISTURE CLASS	W+	W-	CONTRAST	Cs
-2	-2	0.7178	-0.3554	1.0732	1.7659

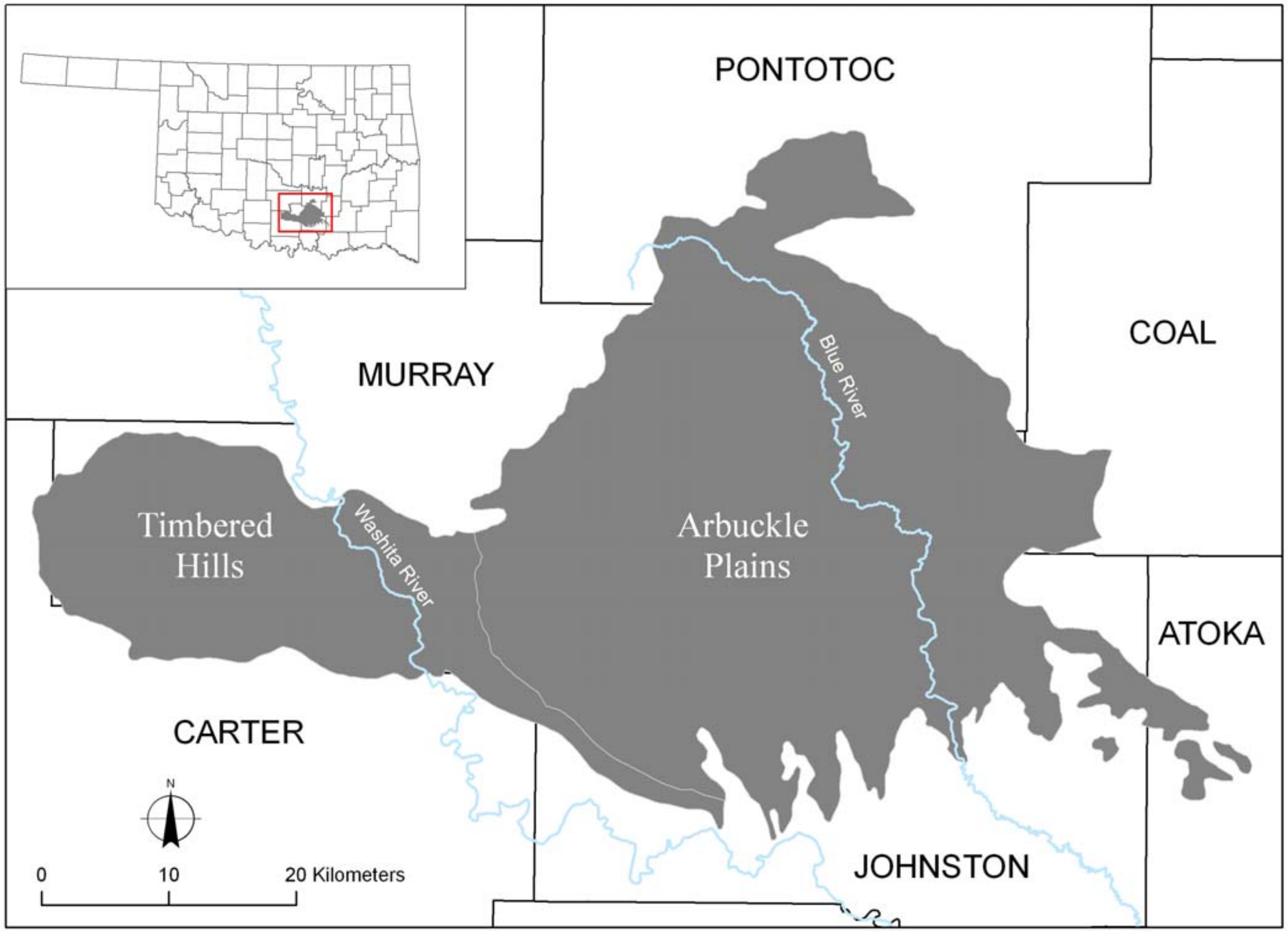


Figure 4.1. Study area location in south-central Oklahoma.

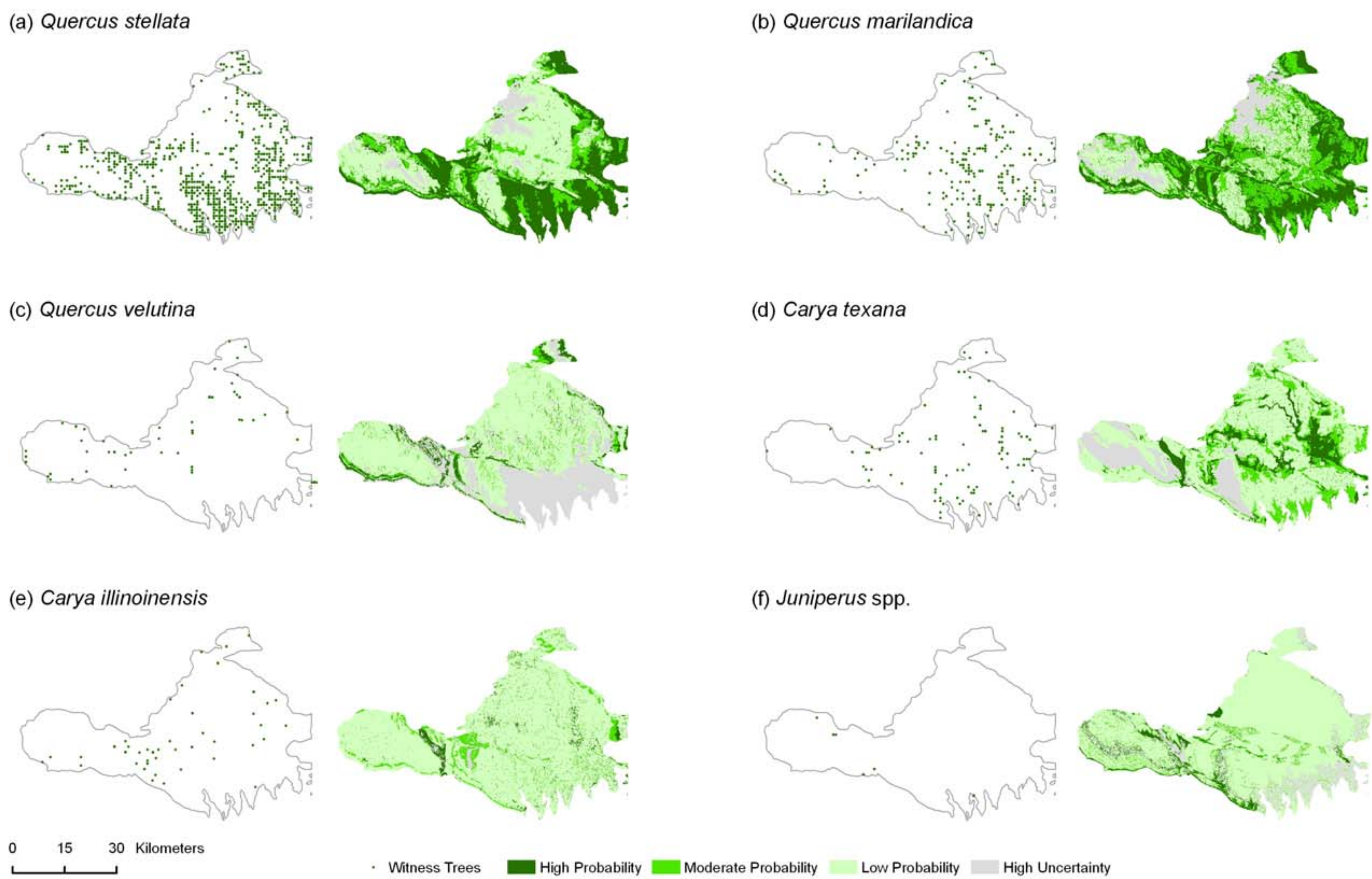
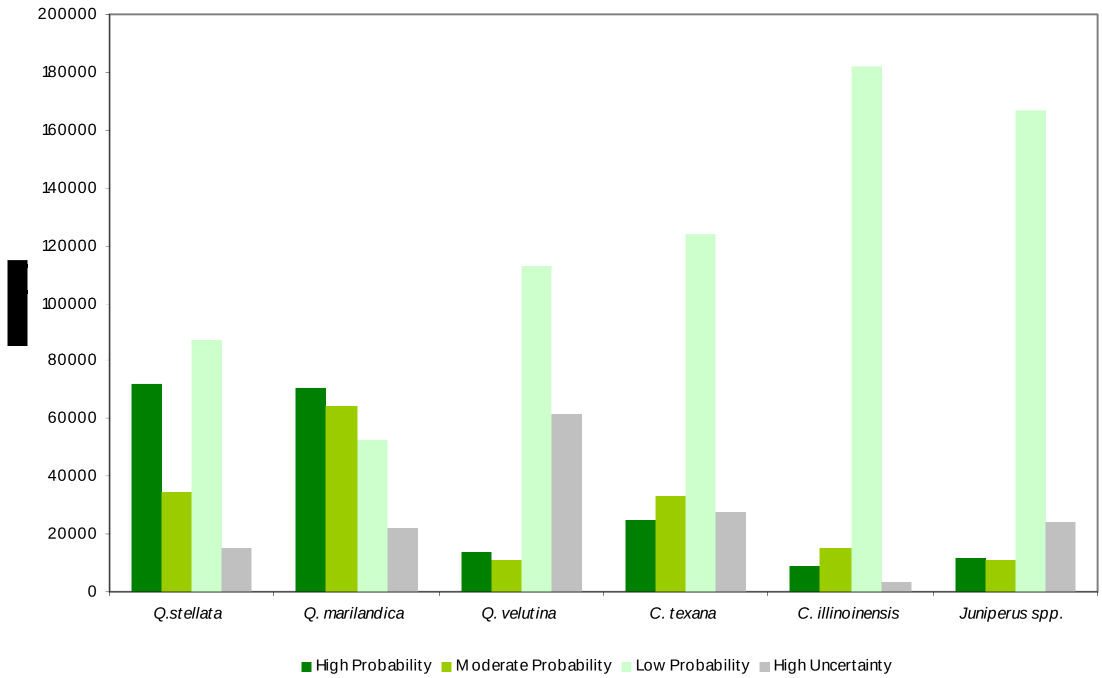


Figure 4.2. Discrete PLS point distributions and continuous probability surfaces for the six taxa.

Figure 4.3. Estimated area of each probabilistic class for the six taxa.



CHAPTER 5:

CONCLUSIONS: TOWARDS A HISTORICAL-ECOLOGICAL SYNTHESIS

"*Nothing endures but change*" Heraclitus of Ephesus

Shifting Mosaics

Few descriptions of a landscape are as evocative or elegant as *mosaic*. Like a canvas consisting of tessellated objects, any given landscape is a patchwork of varying land use and land cover types, a product of interactions between environmental gradients and disturbance regimes. However, unlike a Hellenistic or Byzantine mosaic designed to produce *static* images of cultural or spiritual significance (Cormack 2000), a land mosaic (Forman 1998) is both spatially heterogeneous and temporally variable. A landscape, then, should be thought of as a shifting mosaic.

To apply the Heraclitian axiom that all things are in flux to landscape analysis begs the question of the utility of documentation of such ephemera. To answer this, I will borrow liberally from Wallace (1855). Every landscape element has come into existence coincident both in space and time with other closely allied landscape elements. In other words, the current composition, structure, and function of a landscape are the products of a landscape's antecedents. As one or more landscape elements change, these alterations also affect the characteristics of adjacent elements in the land mosaic.

Here, a landscape element refers specifically to a patch, a relatively homogeneous area that differs from its surroundings (Forman 1998). The principles of island biogeography (MacArthur and Wilson 1967) and landscape ecology (Forman and

Godron 1986) posit that the size, shape, and landscape position of patches, i.e. the landscape structure, influence the assemblages of taxa found within a landscape. For example, the size and distribution of patches in a landscape may be of importance for taxa that require a habitat of a minimum size or of a specific configuration (Turner 1989). Evidence also suggests that patch size is positively correlated to species richness (Darlington 1957; MacArthur and Wilson 1967; Forman 1998), while the number of patches of a particular habitat type may affect the number of subpopulations of a spatially-dispersed population (e.g. Ingegnoli 2002). Additionally species assemblages along a habitat edge, the portion of a patch close to the perimeter, often differ from those of the interior of patches (Laurance et al. 2007).

It follows that changes in the structure of a landscape will result in changes of the function (the interaction between the spatial elements) and composition (number of patch types) of a landscape. These changes, in turn, produce alterations in the abiotic environment of so-called remnant patches. In particular, changes in vegetation structure, due to natural and/or anthropogenic disturbances, can alter fluxes of radiation, wind, and water across a landscape (Saunders et al. 1991). These, in turn, can affect the assemblages of species found within the remnant patches.

To demonstrate, imagine a wildfire that removes understory brush and overstory canopy cover from an erstwhile closed canopy forest. Prior to the disturbance, the amount of solar radiation penetrating the canopy and reaching the understory was likely minimal, thereby limiting herbaceous plants to shade-tolerant species. After the disturbance, newly created forest openings may allow more sunlight to penetrate to the forest floor, enabling more heliophytic (sun-loving) species to colonize the disturbed areas. Conversely, the suppression of fire in formerly pyrogenic (fire-maintained) environments has had the opposite effect (Engle 2006; Nowacki and Abrams 2008)—an increase in shade tolerant species at the expense of heliophytic species.

To further demonstrate, imagine a forest patch cleared for agricultural purposes. Changes in the dominant plant growth forms of a patch, here, from tree-dominated forest or woodlands to herb-dominated row crops, can alter not only radiation fluxes, but also momentum transfer and hydrological cycling across the landscape (Saunders et al. 1991). Changes in wind patterns may result in increased physical damage to remnant vegetation (Grace 1977) and increased evapotranspiration and desiccation (Lovejoy et al. 1986). Changes in growth forms may also alter the amount of rainfall interception and surface- and groundwater flow (Saunders et al. 1991). These changes, in turn, can influence species composition within both the remnant patch, as well as the disturbance patch (Forman 1998).

While change in a land mosaic can occur absent human intervention, humans have become a dominant factor in accelerating land cover change (Turner et al. 1994). Moreover, the nature of an anthropogenic land mosaic is often substantially different from so-called natural land mosaics. For instance, natural processes rarely produce linear boundaries like those associated with transportation networks or industrialized agriculture, in nature. The effects of these land modifications reverberate throughout a land mosaic, not just within the patches directly modified. Isolating the anthropogenic signal is often difficult, but a growing body of evidence suggests that current biogeographic patterns must be assessed not only in the context of contemporary environmental conditions, but anthropogenic historical factors as well (e.g. Motzikin et al. 1999; Dupouey et al. 2002). An integrative historic-ecological approach is, therefore, necessary to properly understand the biogeographic consequences of any shifting mosaic (Bürgi et al. 2009).

Fragmentation

Fragmentation is the process of breaking up of a habitat or ecosystem into smaller patches (Forman 1998). Quammen (1996) used the analogy of a Persian carpet to describe fragmentation: Imagine fine 12' x 18' Persian carpet, Quammen directs the reader. If one were to cut the carpet into 36 2' x 3' pieces, the end result is not 36 fine Persian rugs. Rather, as Quammen notes, "three dozen ragged fragments, each one worthless and commencing to come apart."

Let's now transpose this logic to the fragmentation that is occurring in ecosystems across the globe. The dissecting of habitats into smaller and smaller fragments is the leading cause of so-called "relaxation to equilibrium," "faunal collapse," "ecosystem decay," or any other euphemism one wishes to use to describe the loss of global biodiversity. Of course, habitat fragmentation does not proceed in the orderly manner of cutting a rug into thirty-six equally sized remnants. Rather varying degrees of fragmentation occur throughout a habitat, with the prime areas usually fragmented first. Additionally, while fragmentation may degrade a habitat, calling it "useless" may be a bit hyperbolic. Indeed, some organisms will thrive in under these degraded conditions. The term also begs the question of whose interests may be served or not served by fragmentation.

The contemporary landscape of the Arbuckle Mountains (Figure 5.1) is an example of a fragmented landscape. Once an area characterized by large patches of unbroken forest/woodlands and savannas and grassland (see Figure 3.6), the contemporary Arbuckle Mountains are characterized by discontinuous areas of forest/woodlands and grasslands, interspersed with large-scale agricultural, pastures, residential/industrial areas, and man-made lakes and ponds. In order to understand the ecological and biological consequences of these changes, it is necessary to have knowledge of the anterior period.

As discussed in Chapters 2 and 3, the use of baselines from which subsequent change can be evaluated, i.e. historical vegetation reconstructions, represents the primary method of gauging the degree and consequences of habitat fragmentation. Within the western United States, the records of the Public Land Survey System (PLS) have been used extensively towards this end (see Chapter 2). Yet, certain caveats about the overall effectiveness of these data to evaluate the ecological consequences of fragmentation must be reiterated.

As previously discussed (Chapters 2, 3, and 4), PLS data contain two separate sets of data of interest to researchers conducting historical vegetation reconstructions: plat maps depicting generalized land cover types (Hutchinson 1988) and witness tree data collected at the specified intervals along section lines (Whitney and DeCant 2001). For reconstructing past landscape level vegetation, the plat map data proved invaluable in this research. Additionally, due to the unique nature of the Oklahoma PLS datasets, we have been able to quantify the amount of fragmentation that corresponded to a rapid demographic transition (Chapter 3). However, despite efforts to evaluate the biological consequences of these changes, the PLS witness tree data have limited utility.

First, PLS data lack quantitative data relative to herbaceous taxa (Brothers 1991) and even some smaller stature woody vegetation. Returning to our previous examples of disturbances altering radiation, momentum, and hydrological fluxes, many plant taxa that may be affected by these alterations were not documented by the PLS. Additionally, fragmentation effects not only plant taxa, but animal taxa as well (Andrén 1994). Lastly, as previously discussed (Chapters 2 and 3), witness tree selection was often influenced by tree size, conspicuousness in a stand, longevity, or economic value.

Let's consider this in light of current tracked species within the Arbuckle Mountains. The Oklahoma Natural Heritage Inventory (ONHI) maintains a biodiversity data management system. Of the 34 tracked species found within the Arbuckle Mountains (Table 5.1), only two (*Alnus maritima* and *Quercus sinuata* var. *breviloba*) had the potential to be recorded by surveyors. Both are considered shrubs to small trees and neither were recorded in either of the surveys conducted in the Arbuckle Mountains, perhaps due to their small stature, uncommonness, or a combination thereof.

This is not to imply that only tracked species should be of concern when discussing fragmentation. Nor should this imply that the woody taxa documented in the PLS surveys are not also of interest. However, the period under investigation in Chapter 3 (approximately 27 years) may not be enough to see any direct effects on those primarily ubiquitous taxa that the surveys did document.

Upon fragmentation, remnant patches will often contain more species than the remnant patch can support (Saunders et al. 1991). A species' persistence within a remnant patch is contingent upon both localized extinction rates within patches and movement among patches (i.e. connectivity; Forman 1998). Island biogeography theory (MacArthur and Wilson 1967) predicts that species in isolated patches should have a lower probability of persistence (Turner 1989). However, rates of species relaxation will vary among taxa due to differential dispersal ability, competitive advantage, population dynamics, and numerous other ecological factors (Saunders et al. 1991). This may, in part, explain why we did not see significant differences in species distributions between the 1870s and 1890s (Chapter 3).

We nonetheless see at least one conspicuous difference in the woody taxa between the two survey years, the seemingly precipitous decline in *Quercus velutina* and the increased importance of *Q. marilandica*. Whether this is a product of fragmentation, the result of selective harvesting of the former, or perhaps survey misidentification remains unanswered. Additionally, while the 27-year interval between the two surveys may not be adequate to evaluate the effects of fragmentation on certain woody plant taxa, fragmentation has been on ongoing process within the region (see Figure 5.1). Future research, then (see below), can compare contemporary woody plant assemblages to these historic datasets.

Woody Plant Encroachment

Fragmentation typically implies a decrease in patch area. However, coincident with the loss of area of one land cover type is an increase of area of another (Andrén 1994). An obvious example is land clearance for a particular land use activity, such as agriculture. While such land clearance may result in the reduction in area of grasslands, for instance, it signals the increase of area of another patch type. Though not technically fragmentation in the traditional sense of the word, another process responsible for the increase in one patch type at the expense of another is woody plant encroachment, i.e. the increase of woody plant abundance at the expense of grasslands.

Within the past century and a half, woody plant encroachment has occurred in many parts of the world (Archer 2005; Barnes et al. 2008). These increases in woody plant abundance have been attributed primarily to changes in fire regimes (Archer et al. 1995), livestock grazing (Scholes and Archer 1997), climate variability (Bahre and Shelton 1993; Archer et al. 1995) or a combination thereof (Miller and Rose 1995). The ecological consequences of these changes are numerous and include changes in the structure and function of habitat for various grassland and understory organisms (Horncastle et al. 2005; Engle 2006), decreases in productivity and herbaceous species diversity (Barnes et al. 2008), changes in microclimate (Hibbard et al. 2001), and changes in biogeochemical cycles (Barnes et al. 2008).

Similarly, attempts to quantify increases of woody plant abundance usually proceed from known baselines of woody plant distributions. Aerial photographs represent the first truly quantitative datasets from which areal measurements of woody vegetation can be made. However, evidence suggests that native grasslands can be converted to closed canopy forest in as little as 35 to 40 years (Briggs et al. 2002). The first vertical aerial photographs taken perpendicular to the Earth's surface date back only to the 1930s (Bahre and Shelton 1993), and often cover periods after substantial woody plant encroachment had already occurred (e.g. Bragg and Hulbert 1976; Briggs et al. 2002).

A number of researchers (e.g. Bragg and Hulbert 1976; Bahre and Shelton 1993) have turned to PLS data in attempts to quantify increases in woody plant abundance since pre- and early-European settlement. However, as discussed in Chapter 4, quantification of the areal extent of select woody species from these records has proven difficult due to the coarse sampling structure (0.8 km). Additionally, biases in tree selection often precluded documentation of some of the more pernicious taxa in relationship to woody plant encroachment.

The discrete, data-driven approach known as weights-of-evidence presented in Chapter 4 represents an attempt to overcome some of these seemingly inherent limitations in PLS data. By combining known occurrences of a taxon with covariates that influence the distributions thereof, we are able to better estimate the historical distribution of key taxa. This approach has been demonstrated to be effective in instances when there are a small number of known occurrences (e.g. Carranza 2004), as is often the case with taxon that had limited distributions in historic times. The method has proven to be equally effective at mapping distributions at scales finer than that offered by PLS data, alone.

Within the Arbuckle Mountains, there are two species primarily responsible for woody plant encroachment, *Juniperus virginiana* and *Juniperus ashei*. *Juniperus virginiana* is the most widely distributed coniferous tree in the eastern United States, occurring in every state east of the 100th meridian (Lawson 1985). However, young *J. virginiana* are fire intolerant and the species was uncommon in Oklahoma prior to European settlement (Hoagland et al. 1999). *Juniperus ashei* has a much more restricted distribution, with disjunct populations in Arbuckle Mountains, the Ozarks (eastern Oklahoma, Missouri, and Arkansas), the Edwards Plateau (central Texas), and northeast Mexico (Adams 2008). Within the Arbuckle Mountains, *J. ashei* is found on dry, rocky ridges of limestone origin, while *J. virginiana* is found in more often in valleys (Little 2000).

During the past 50 years, both species have increased their ranges in the Arbuckle Mountain, primarily due to fire suppression and other land use practices (Engle et al. 1997). Though numerous attempts have been made to quantify the degree and direction of the increases in abundance of these species in the Arbuckle Mountains and elsewhere (e.g. Bragg and Hulbert 1976; Briggs et al. 2002), few studies have established baselines from periods preceding widespread fire abatement. The methods discussed in Chapter 4 represent a statistically valid method to estimate individual taxon distributions in historic times and may help provide greater insight into the degree and directions of woody plant encroachment.

Mesophication

Previously, I briefly discussed the role of fire as a disturbance factor that could alter species composition in the understory of forest and woodlands. However, many ecosystems are pyrogenic. In such systems, the suppression of fire represents the disturbance that can lead to altered ecosystem structure and function, such as that caused by the increase of woody plants at the expense of grasslands.

Regular fires help maintain openings in forested ecosystems, allowing enough sunlight to penetrate to support a diversity of understory herbaceous vegetation (Engle et al. 2006). Indeed, prior to widespread European settlement, the forest and woodlands of eastern North America were believed to be less dense than those of the present, primarily due to regular burns. Coincident with these density increases since historic times has been compositional shifts from high diversity, xerophytic, fire tolerant species to low diversity, more mesophytic, fire-sensitive species (Nowacki and Abrams 2008).

Within the past year, a new term, “mesophication,” has entered the ecological lexicon to describe this process (Nowacki and Abrams 2008). While it is uncertain whether the process as described by Nowacki and Abrams (2008) occurs on the western fringes of the Eastern Deciduous Forest, there is evidence that similar processes are occurring. For instance, Johnson and Risser (1975) cite the reduction in frequency and intensity of fires as the disturbance regime responsible for the conversion of most central Oklahoma savannahs to forests during the past century. Similarly, Engle et al. (2006) cite the reduction of fire since European settlement as the primary factor contributing to increases in canopy cover in the cross timbers of overstory *Quercus* spp.

The PLS data from both the 1870s and 1890s confirm lower historic forest densities than more recent studies (Chapter 3). Nonetheless, as previously discussed, these historic data do not contain information on the herbaceous understory affected by these changes. Calculated density measurements and subsequent studies in comparable environments must, therefore, be used to predict such composition. Nonetheless, as discussed in Chapter 3, the density measurements used assume unbiased tree selection (Cottam and Curtis 1956). As a result, PLS data may actually underestimate historical tree densities because selected witness trees were not necessarily the closest individual to each survey point.

Summation

As Forman (1998) wryly notes, the fortuneteller who predicts change is always correct. While it may not be possible to step into the same landscape twice, snapshots from bygone eras provide valuable insight into the contemporary biogeography of a given place. This dissertation has been an exploration of methods to improve our understanding of the past biogeographies, thereby providing a means to better describe the present. Although I have primarily drawn from the resources of the Public Land Surveys, this dissertation is not about PLS data, per se. Rather, the overarching goal has been to develop baselines from which the processes that have shaped the contemporary landscape of a region, such as fragmentation, woody plant encroachment, and mesophication, can be better understood. Since these changes are an ongoing process, the 1870s and 1890s merely represent a starting point from which these change can be gauged. As such, this dissertation represents as much a beginning as it does an end.

This dissertation has also focused on the Arbuckle Mountains. The selection of the Arbuckle Mountains was based on numerous criteria, including that the Arbuckle Mountains are a spatially heterogeneous, ecological important (see Table 5.1) area. Additionally, the Arbuckle Mountains are found within an area surveyed twice by the PLS, thereby enabling repeat analysis of historic vegetation. However, the methods used here should be transferable to other areas of interest. Indeed, as much as I am is interested in studying the past as a means to understand the present, this is a methodological work designed to provide new and/or enhanced procedures to help better map historic vegetation.

The unique nature of PLS data for a portion of present-day Oklahoma affords broader regional analysis using similar methods. To date, studies utilizing repeat PLS survey data have only been conducted in Carter County, Oklahoma (Shutler and

Hoagland 2004) and this study of the Arbuckle Mountains (Chapter 3). However, the Chickasaw Nation (see Figure 1.2) occupies 12 counties in south-central Oklahoma. An expansion of the methods employed here to the whole of the region may provide greater insight into the dynamics and the biological consequences thereof occurring throughout the region.

This study also only looked at two discrete time periods. However, to revisit our Heraclitian axiom, change is a persistent feature of any landscape. While a comparison between the 1870s and 1890s provided valuable insight to the ecological changes corresponding with a rapid demographic shift, the contemporary landscape of the Arbuckle Mountains (Figure 5.1) indicates that a great deal of change has occurred subsequent to the time periods encompassed by this study. To take it a step further, each habitat patch has followed a unique trajectory (see Figure 3.12). Repeat analysis at various discrete time intervals throughout the past century could provide further insight to individual patch history, as well as the biological communities supported therein.

This study has also been unidirectional—a glance backwards. However, by looking backwards and gaining an understanding of the biological and ecological consequences of various trajectories of change, we may be able to look forward to predict the consequences of proposed land conversions. Although this research has not been explicitly about advocacy, I do possess a particular point of view (POV) on matters of biological conservation. A pragmatic and academic application of these data would help sate this POV. On that note, I not only foresee the possible utility of these or similar methods in future conservation initiatives, but this information may also be used for restoration purposes, with the understanding that such restoration represents merely one transient point along a continuum.

Another potential contribution of this research is the introduction of the weights-of-evidence (WofE) method (Chapter 4) to historical vegetation reconstructions. Although this method was designed initially for medical diagnosis and, later, mineral exploration, it has proven to be an effective geospatial technique for probabilistic mapping (see Chapter 4 for a brief overview of other uses of this method). As discussed on several previous occasions, a major limitation of PLS data in historic vegetation reconstructions is the coarse nature of the witness tree data. This research demonstrates that the WofE method is a viable method to map individual taxon distributions from PLS data at finer resolutions than that afforded by the data, themselves.

The weights-of-evidence method also has great potential in other ecological applications. Consider the species listed in Table 5.1, for instance. By nature of being in the biodiversity data management system, these are species that the ONHI wishes to track. However, due to the rarity of some of these organisms, there may be limited occurrence data associated with these species. The weights-of-evidence method could be used in such instances to predict probabilistic distributions of these species based on the known occurrences.

A Final Note

The English playrwright and novelist, William Somerset Maugham wrote in *The Razor's Edge* (1943), "[i]f change is the essence of existence one would have thought it would be sensible to make it the premise of our philosophy." If not our philosophy, we ought to make that essence the principle by which we study contemporary landscapes and biological assemblages.

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Table 5.1. A list of tracked species in the Arbuckle Mountains, OK from the Oklahoma Natural Heritage's Biotics database.

Scientific Name	Common Name	Taxonomic Group
Carex fissa	A Sedge	Vascular Plant
Coryphantha vivipara	Ball Prickly-Pear	Vascular Plant
Dalea frutescens	Black Dalea	Vascular Plant
Isoetes melanopoda	Blackfoot Quillwort	Vascular Plant
Quercus sinuata var. *breviloba*	Durand Oak	Vascular Plant
Epipactis gigantea	Giant Helleborine	Vascular Plant
Setaria grisebachii	Grisebach Foxtail	Vascular Plant
Arenaria benthamii	Hilly Sandwort	Vascular Plant
Andrachne phyllanthoides	Missouri Buck-Brush	Vascular Plant
Penstemon oklahomensis	Oklahoma Beardtongue	Vascular Plant
Sporobolus ozarkanus	Ozark Dropseed	Vascular Plant
Penstemon cobaea var. purpureus	Purple Beardtongue	Vascular Plant
Echinocereus reichenbachii	Reichenbach Hedgehog-Cactus	Vascular Plant
Psoralea reverchonii	Rock Scurf-Pea	Vascular Plant
Cheilanthes horridula	Rough Lipfern	Vascular Plant
Alnus maritima	Seaside Alder	Vascular Plant
Dichromena nivea	Snowy White-Top	Vascular Plant
Carex hyalina	Tissue Sedge	Vascular Plant
Opuntia tunicata	Tuna Cholla	Vascular Plant
Orconectes neglectus	A Crayfish	Invertebrate Animal
Orconectes palmeri longimanus	A Crayfish	Invertebrate Animal
Atrytone arogos	Arogos Skipper	Invertebrate Animal
Hesperia attalus	Dotted Skipper	Invertebrate Animal
Atrytonopsis hianna	Dusted Skipper	Invertebrate Animal
Hesperia viridis	Green Skipper	Invertebrate Animal
Villosa lienosa	Little Spectaclecase	Invertebrate Animal
Allocrangonyx pellucidus	Oklahoma Cave Amphipod	Invertebrate Animal
Ptychobranchus occidentalis	Ouachita Kidneyshell	Invertebrate Animal
Quadrula cylindrica	Rabbitsfoot	Invertebrate Animal
Orconectes virilis	Virile Crayfish	Invertebrate Animal
Macroclemys temminckii	Alligator Snapping Turtle	Vertebrate Animal
Ictalurus nebulosus	Brown Bullhead	Vertebrate Animal
Aquila chrysaetos	Golden Eagle	Vertebrate Animal
Nocomis asper	Redspot Chub	Vertebrate Animal

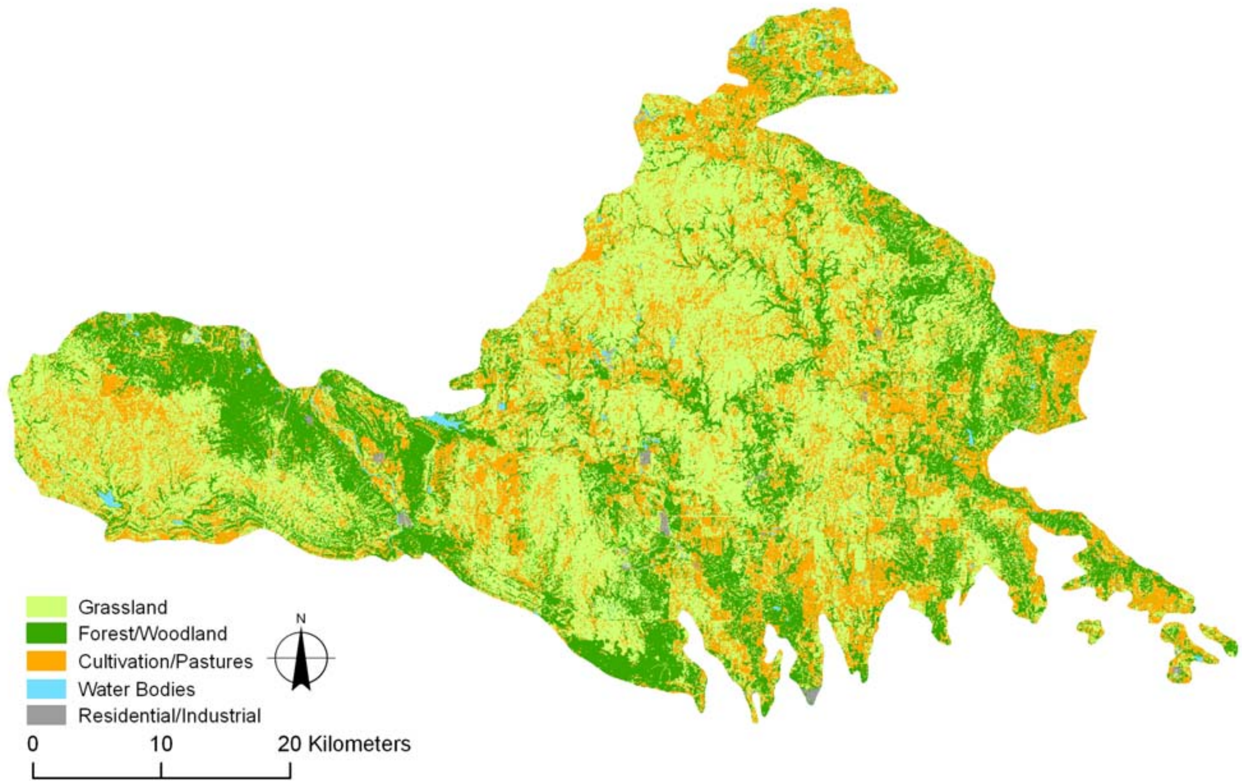

Figure 5.1. The contemporary landscape of the Arbuckle Mountains. Source: Reclassified Gap Analysis Map of Oklahoma (2001). U.S. Department of Interior, U.S. Geological Survey.

APPENDIX A:

DISTRIBUTION MAPS OF TREE SPECIES RECORDED BY GENERAL LAND OFFICE SURVEYORS IN THE ARBUCKLE MOUNTAIN, OKLAHOMA

The following maps portray the distribution of tree taxa encountered during the Public Land Survey (PLS) conducted by the General Land Office (GLO) in the Arbuckle Mountains of Oklahoma. At the intersection of section lines and at each quarter section point (0.8 km along a section line), surveys noted the nearest tree in each of the adjoining sections, recording its identification and diameter at breast height (DBH), as well as the compass direction and distance from the corner or quarter section point. These are commonly called witness trees. Trees encountered during both the 1870s and 1890s surveys are mapped.

Maps were developed by determining the x,y coordinates of the intersections of section lines and each quarter section point using a GIS and a digital township, range, and section dataset obtained from the Bureau of Land Management's Land Survey Information System (LSIS) for reference. The x,y coordinates for each point from which trees were recorded were then joined to the tree distribution data. The location of individuals were then determined by calculating the new x,y locations based on the compass bearing and distance from each monument point (the point from which trees were recorded).

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A5. *Celtis laevigata*

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A10. *Gymnocladus dioicus*

A11. *Juglans nigra*

A12. *Juniperus* spp.

A13. *Maclura pomifera*

A14. *Malus ioensis*

A15. *Morus rubra*

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A30 *Sideroxylon lanuginosum*

A31. *Ulmus* spp.

Figure A1. Occurrences of all trees recorded by General Land Office surveyors in the Arbuckle Mountains.

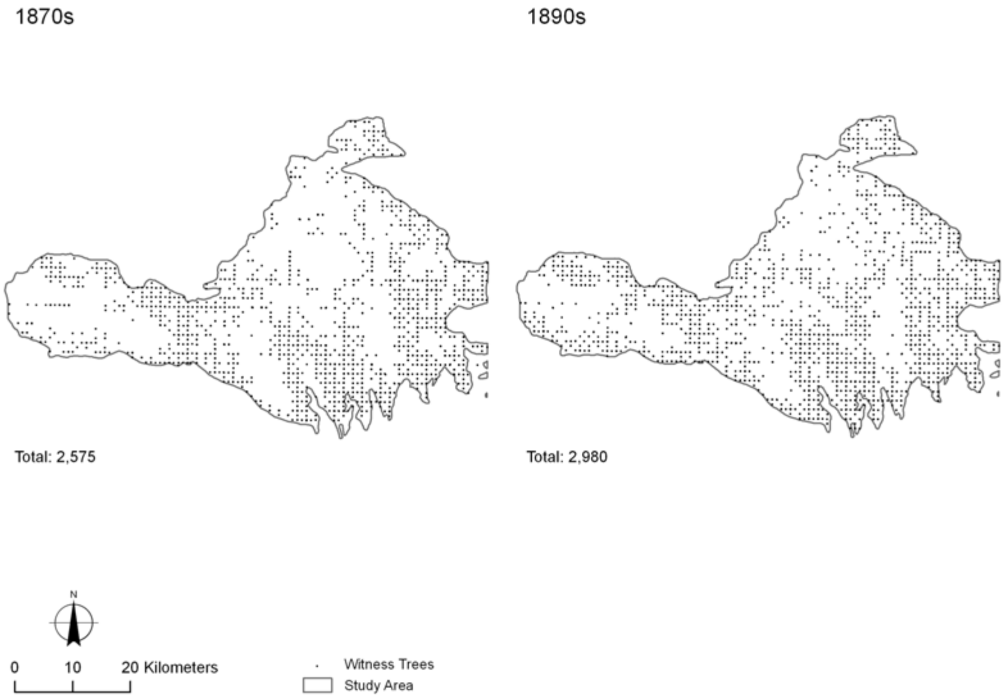


Figure A2. Recorded occurrences of *Acer negundo* listed as "box elder" by the General Land Office surveyors. *Acer negundo* is a bottomland forest species in the eastern two-thirds of Oklahoma.

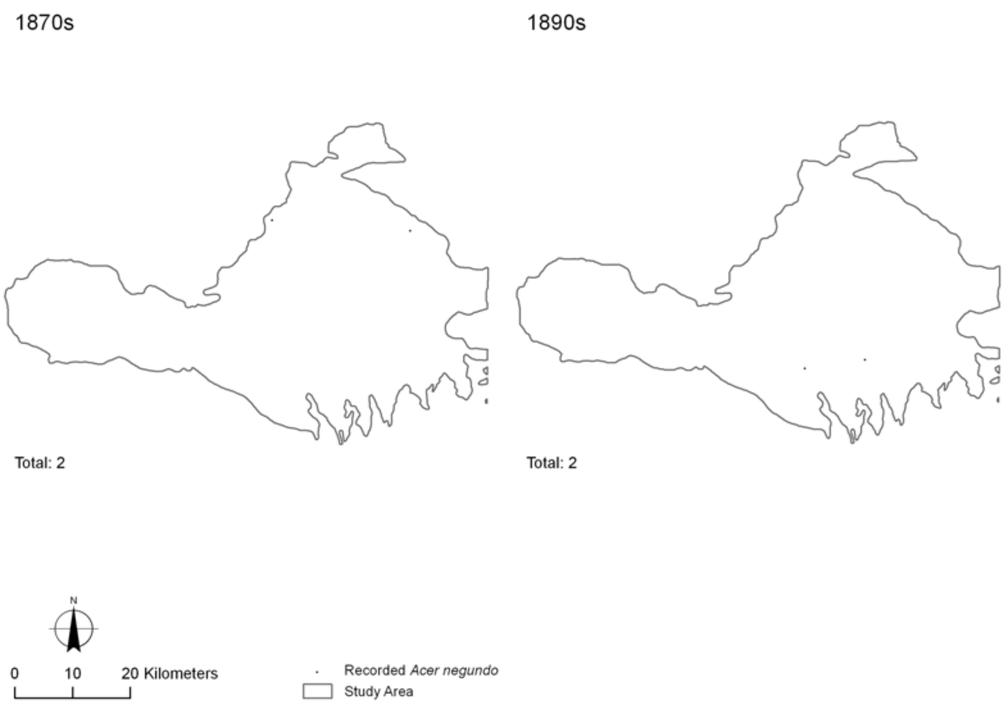


Figure A3. Recorded occurrences of *Carya illinoinensis*, , listed as “pecan” by the General Land Office surveyors. *Carya illinoinensis* is an important bottomland species in central Oklahoma.

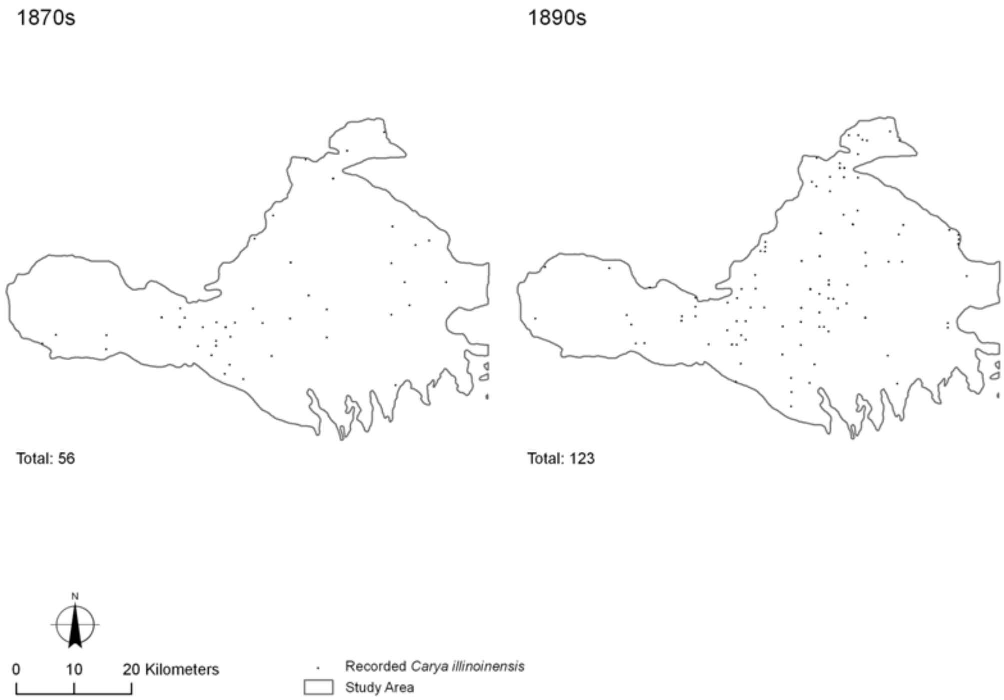


Figure A4. Recorded occurrences of *Carya texana*, listed as “hickory” by the General Land Office surveyors. *Carya texana* is an important upland species in the eastern two-thirds of Oklahoma.

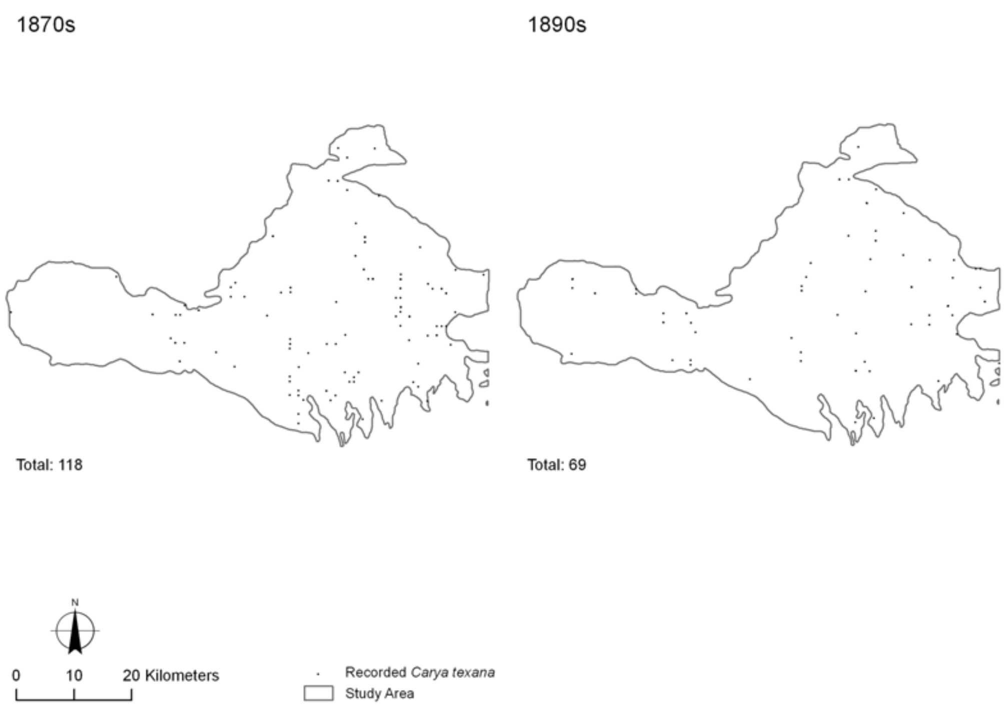


Figure A5. Recorded occurrences of *Celtis laevigata,* listed as "hackberry" by the General Land Office surveyors. *Celtis laevigata* is an important bottomland species in the cross timbers.

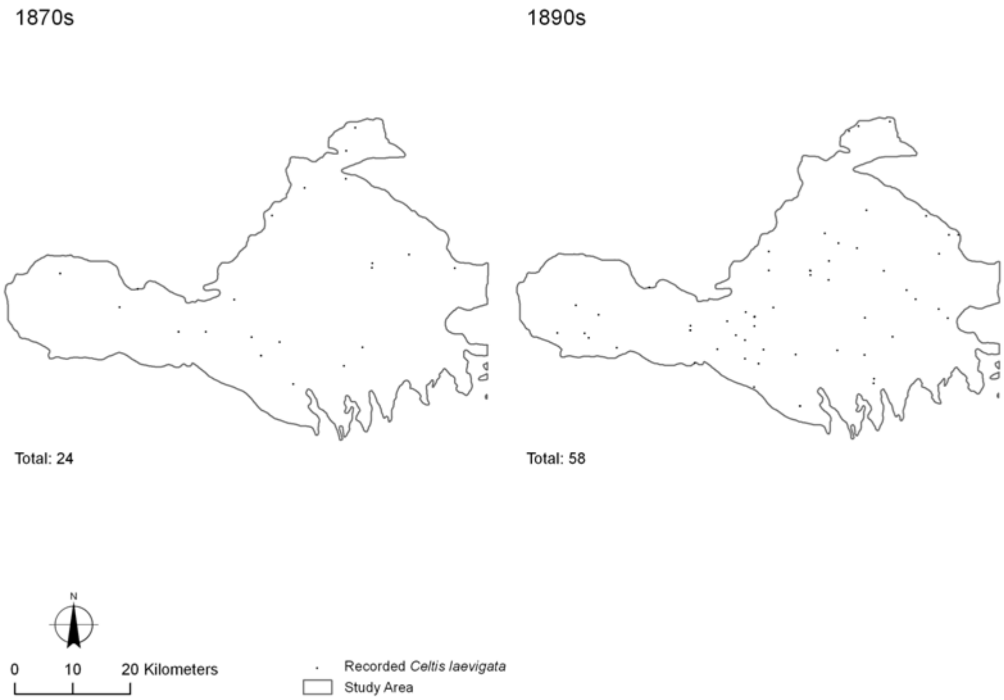


Figure A6. Recorded occurrences of *Cercis canadensis,* listed as "red bud" by the General Land Office surveyors.

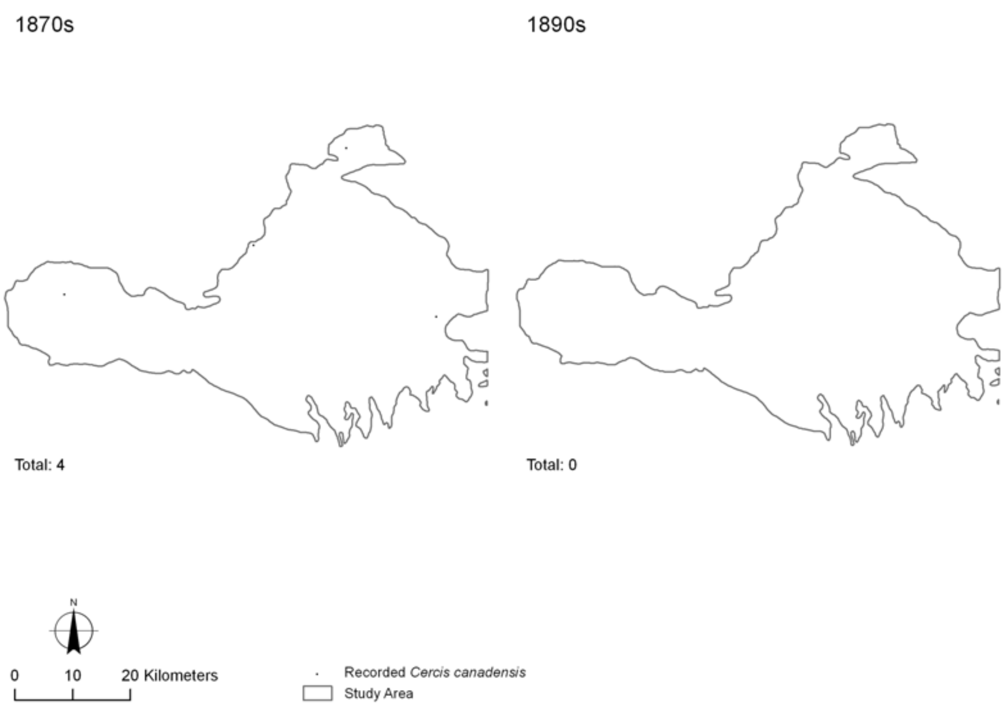


Figure A7. Recorded occurrence of *Crataegus* sp. Several species of *Crataegus* occur in the Arbuckle Mountains. Surveyors identified this tree as "hawthorn."

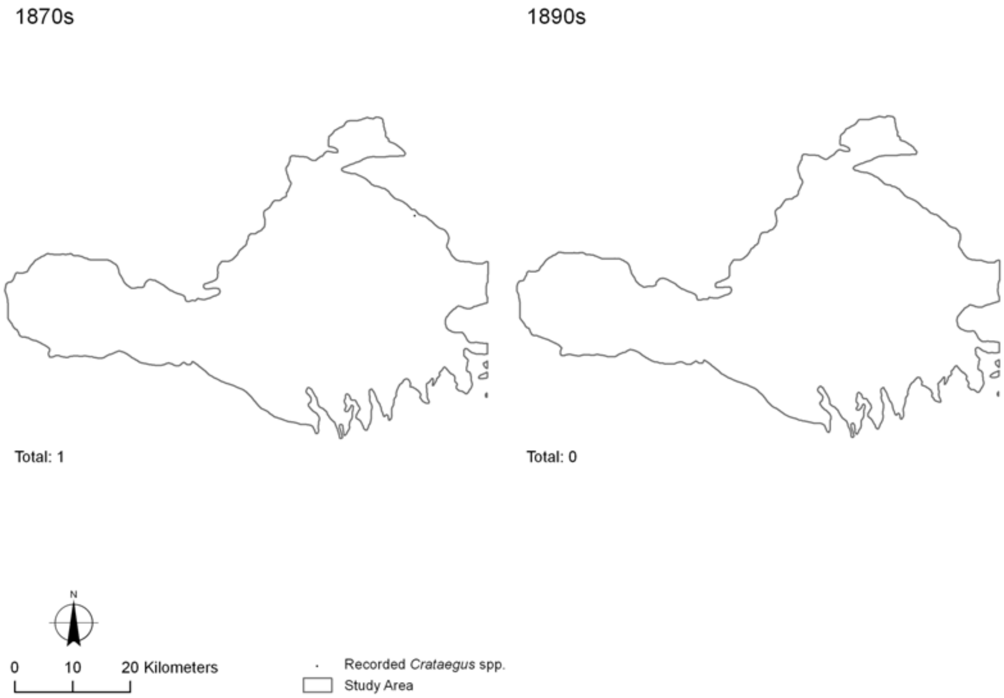


Figure A8. Recorded occurrences of *Diospyros virginiana*, listed as "persimmon" General Land Office surveyors, an old-field and secondary forest species throughout much of Oklahoma.

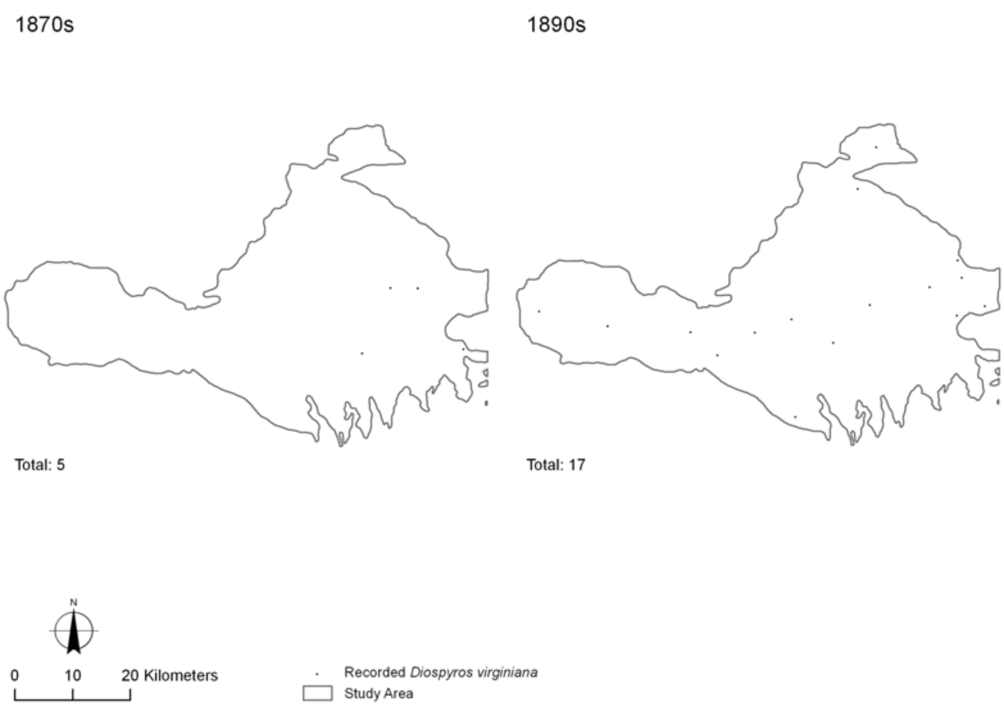


Figure A9. Recorded occurrences of *Fraxinus* spp. Three species of *Fraxinus* are recorded from the Arbuckle Mountains; *F. americana, F. pennsylvanica,* and *F. texana*. Surveyor listed only "ash" and did not differentiate species.

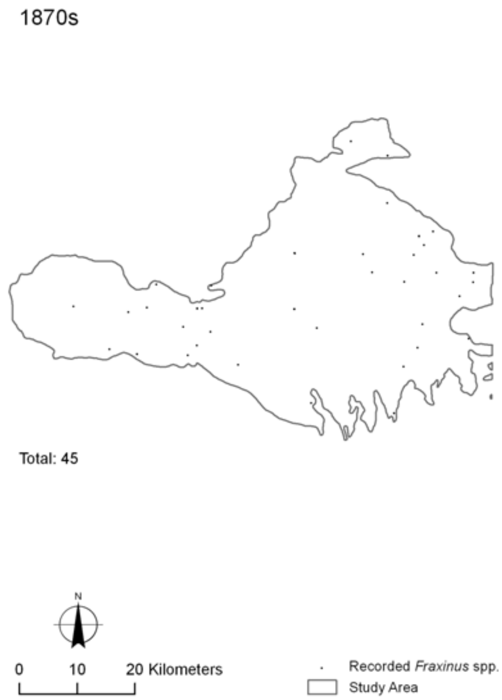


Figure A10. Recorded occurrences of *Gymnocladus dioicus*. Surveyors identified this tree as "coffee tree."

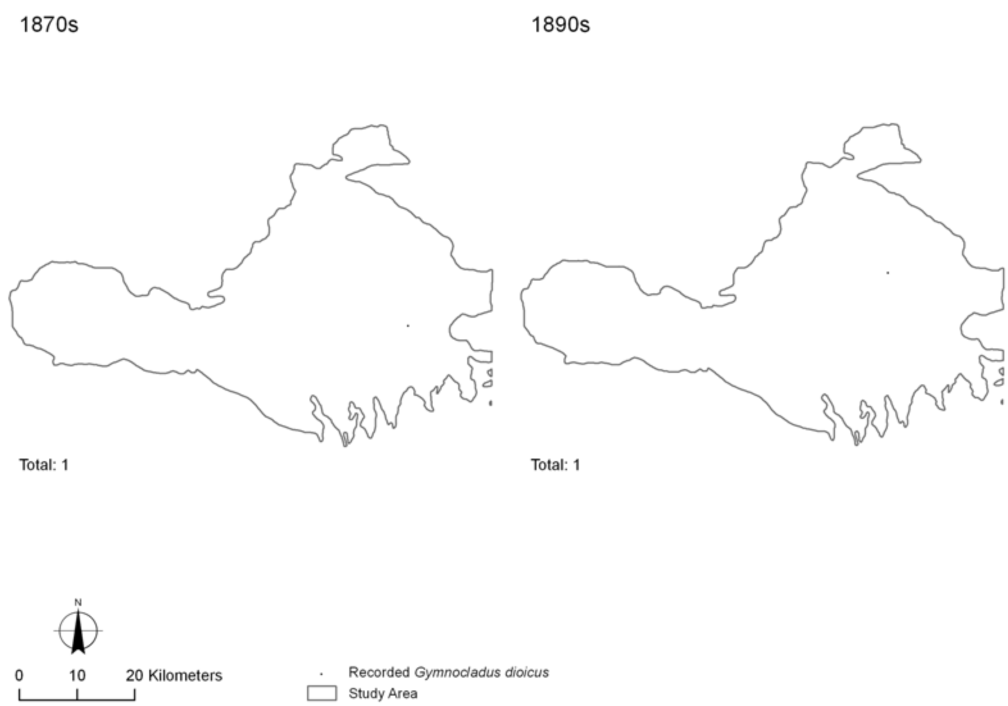


Figure A11. Recorded occurrences of *Juglans nigra,* listed as "walnut" General Land Office surveyors, an important bottomland species in the cross timbers.

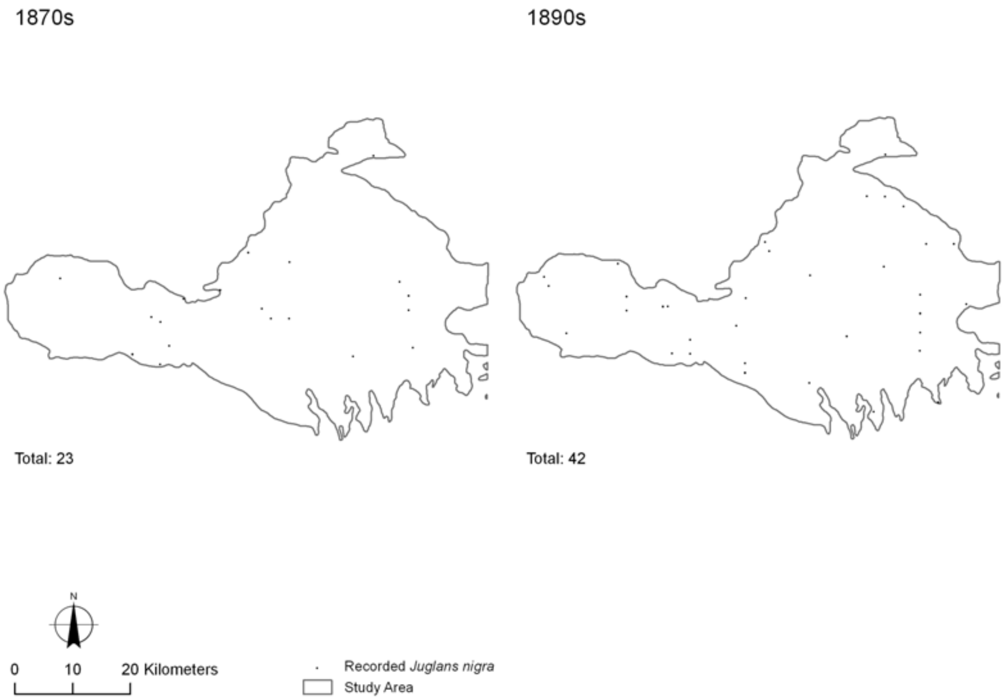


Figure A12. Recorded occurrences of *Juniperus* spp, listed as "cedar" by the General Land Office surveyors. Two *Juniperus* spp. occur within the Arbuckle Mountains, *J. virginiana* and *J. ashei*, both of which have increased in abundance since historic times due to fire suppression and land use practices.

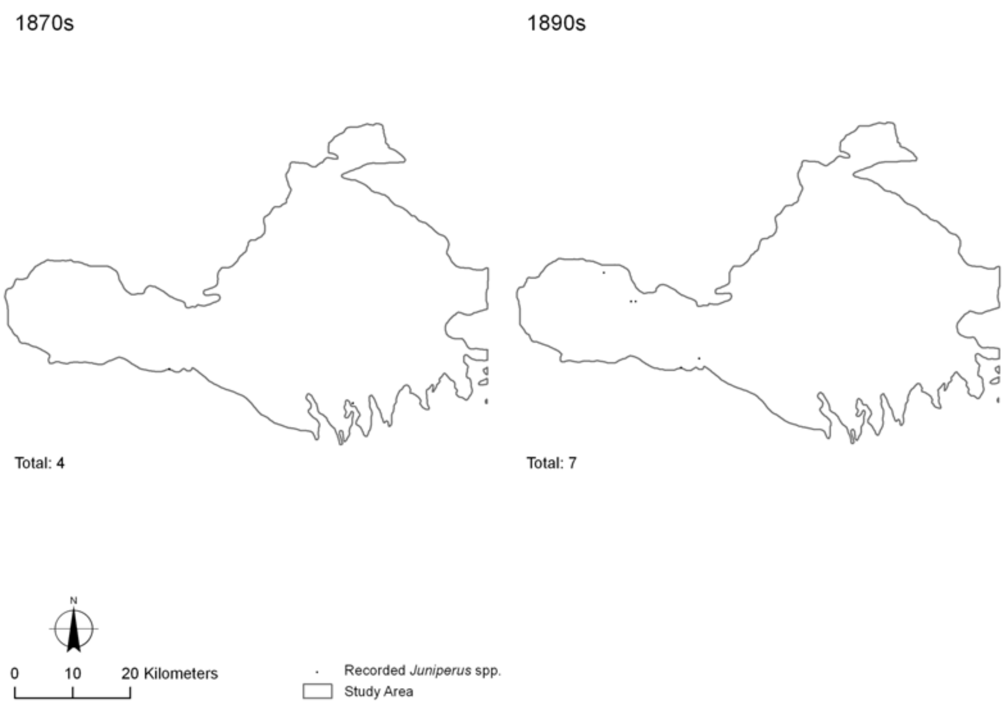


Figure A13. Recorded occurrences of *Maclura pomifera*, listed as “bois d’arc” General Land Office surveyors,

Figure A14. Recorded occurrences of *Malus* ioensis, listed as “crabapple” by the General Land Office surveyors.

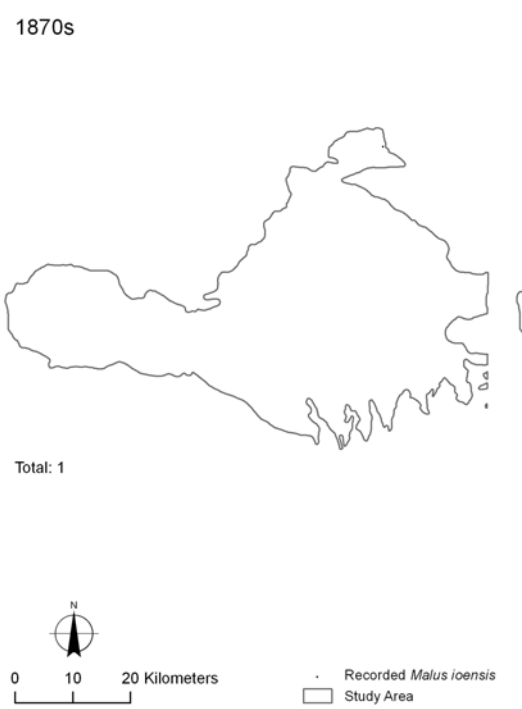


Figure A15. Recorded occurrences of *Morus rubra*, listed as "mulberry" by the General Land Office surveyors.

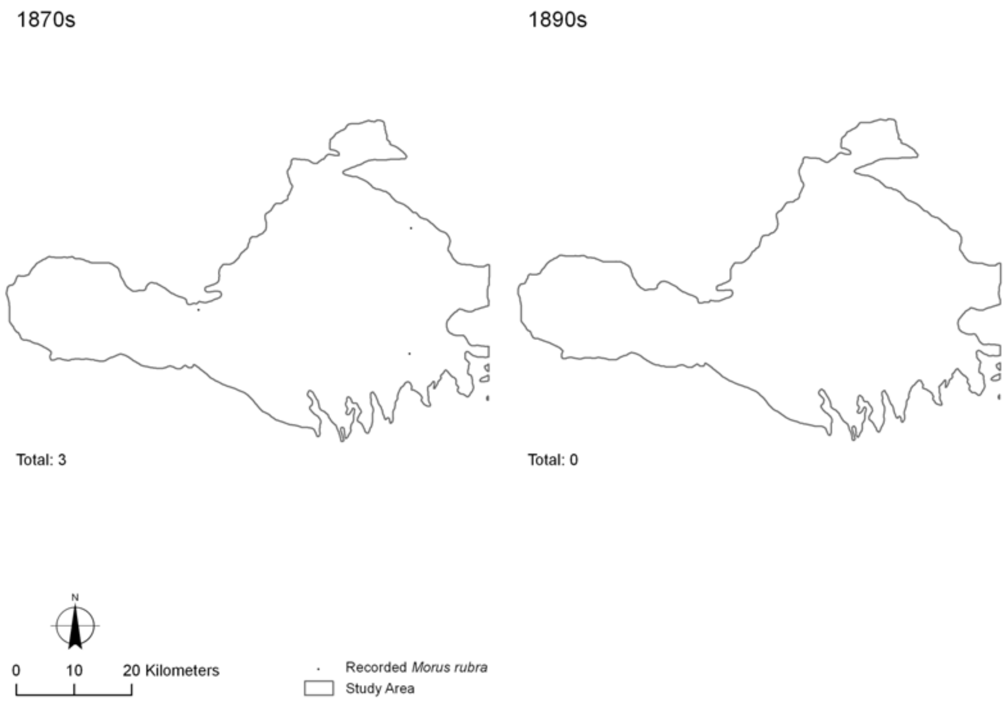


Figure A16. Recorded occurrences of *Platanus occidentalis,* listed as "sycamore" by the General Land Office surveyors. *Platanus occidentalis* is an important riparian species in the cross timbers.

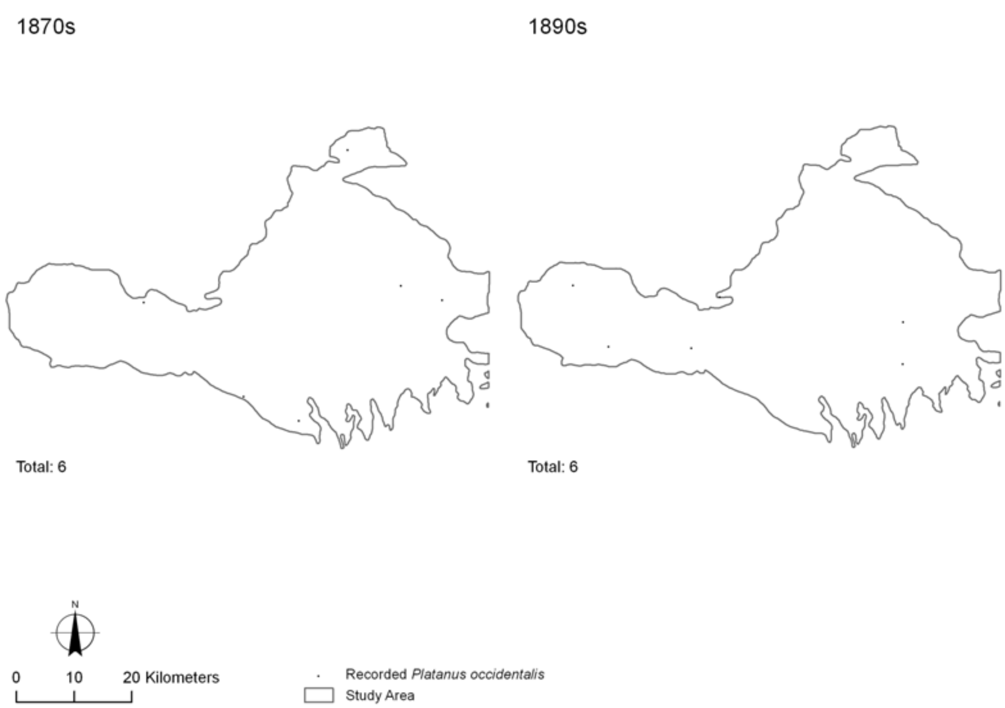


Figure A17. Recorded occurrences of *Populus deltoides,* listed as “cottonwood” by the General Land Office surveyors. *Populus deltoides* is an important riparian species in the cross timbers.

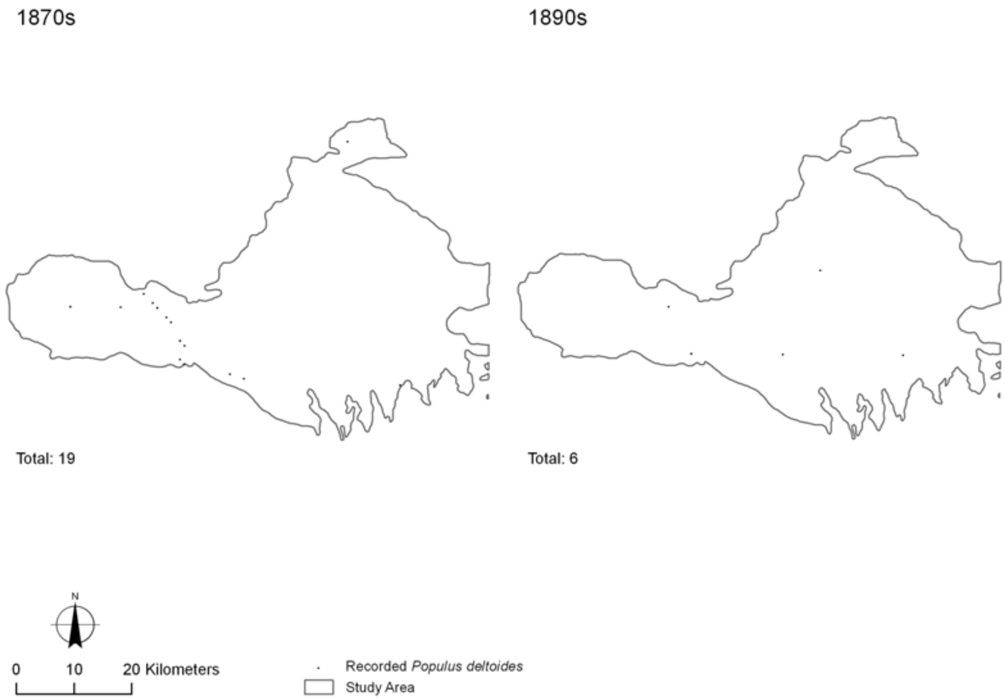


Figure A18. Recorded occurrences of *Prunus* spp, listed as “plum” by the General Land Office surveyors. There are several species of *Prunus* in the Arbuckle Mountains, including *P. americana*, *P. angustifolia*, and *P. mexicana*.

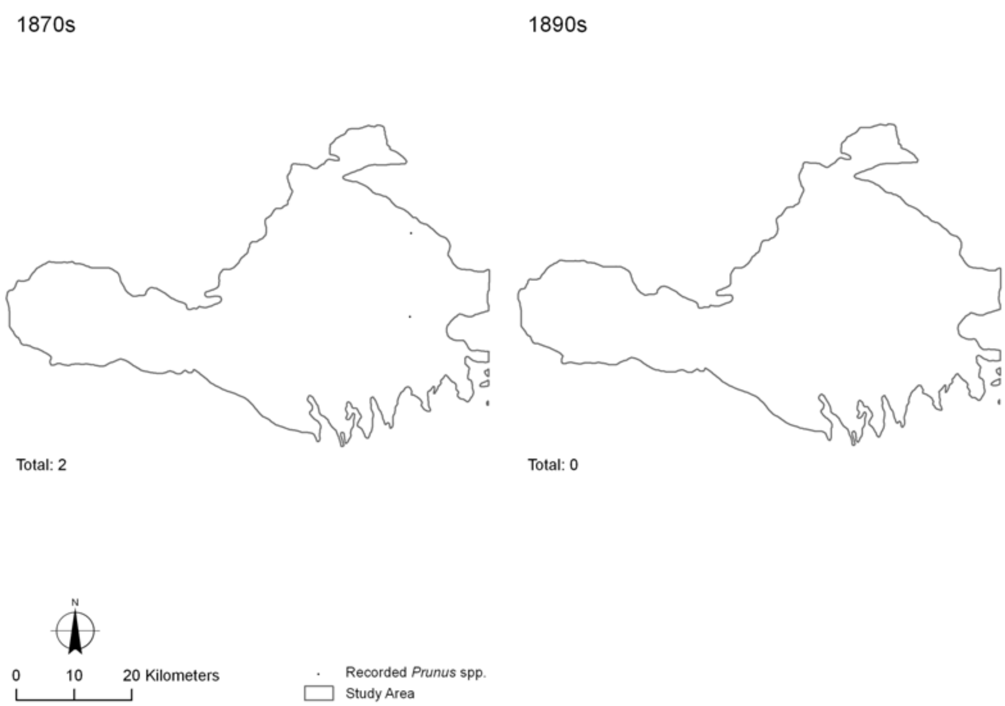


Figure A19. Recorded *Quercus alba,* listed as "white oak" by the General Land Office surveyors. *Quercus alba* is not known to occur in the Arbuckle Mountains and this is likely a misidentification.

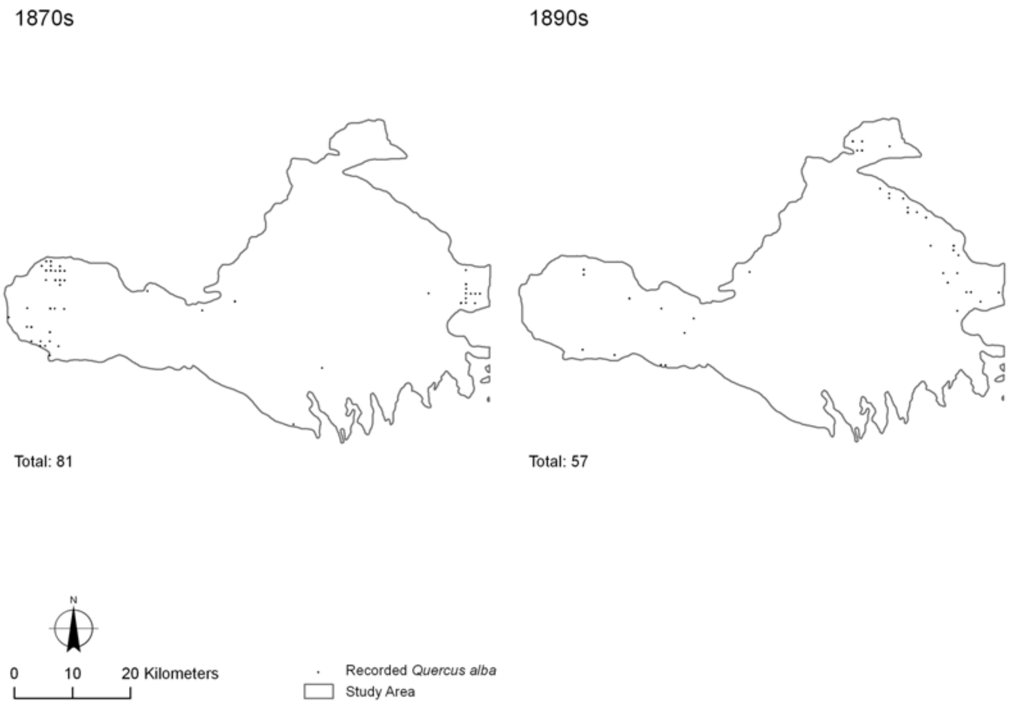


Figure A20. Recorded *Quercus falcata* listed as "red oak" by the General Land Office surveyors. However, this may refer to any member of the *Erythrobalanus* subgenus in the Arbuckle Mountains, including *Q. buckleyi* and *Q. shumardii*. *Quercus falcata* is uncommon in the Arbuckle Mountains.

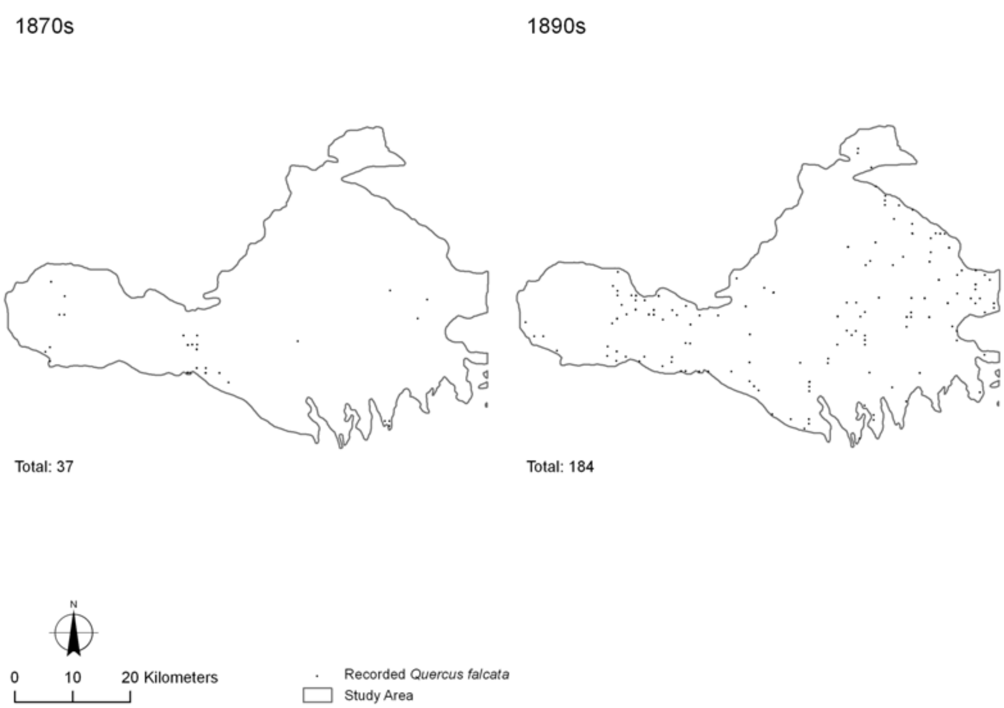


Figure A21. Recorded occurrences of *Quercus macrocarpa,* listed as “bur oak” by the General Land Office surveyors.

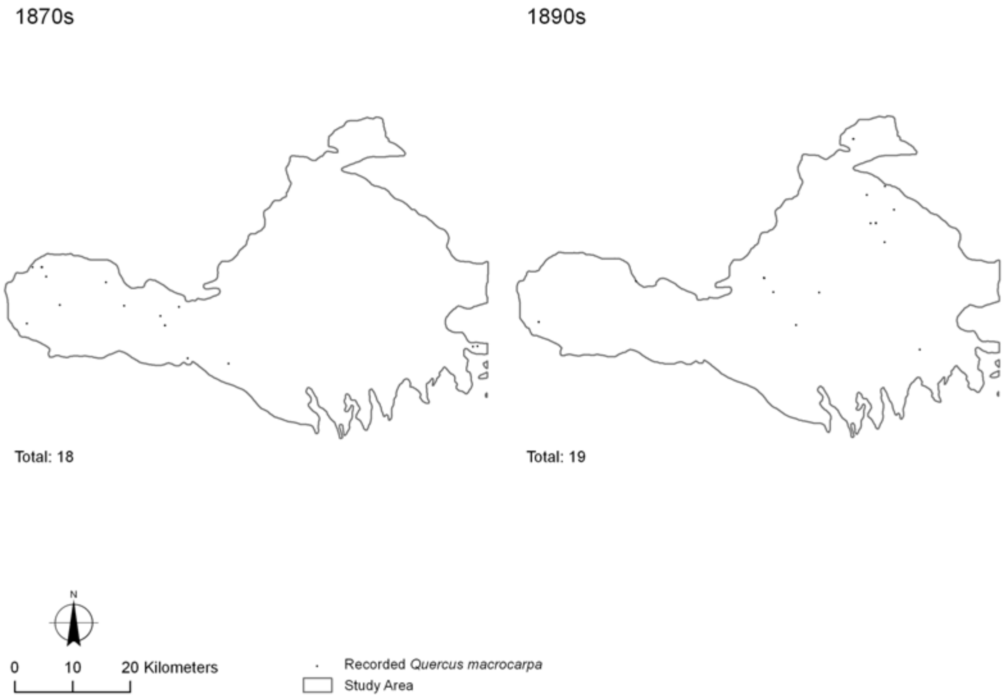


Figure A22. Recorded occurrences of *Quercus marilandica,* listed as “blackjack” by the General Land Office surveyors. *Quercus marilandica* is considered the second most important woody species in the modern cross timbers. Thus its low abundance in the 1870s is noteworthy.

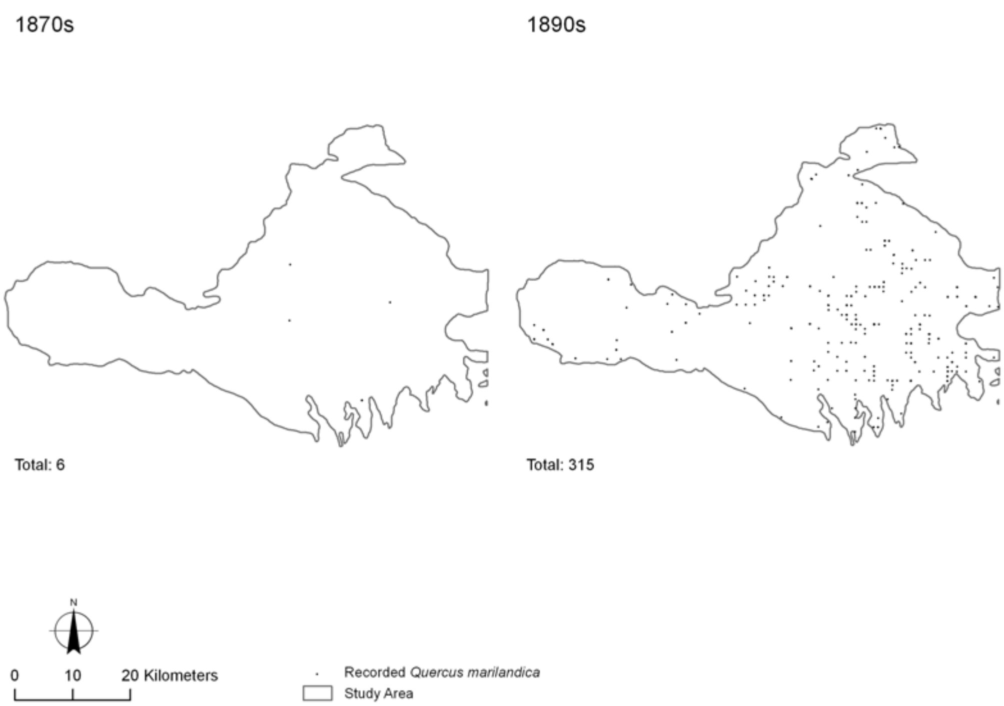


Figure A23. Recorded occurrences of *Quercus nigra,* listed as "water oak" by the General Land Office surveyors. *Quercus nigra* is not known to occur in the Arbuckle Mountains, however, so this is likely a misidentification by the surveyors.

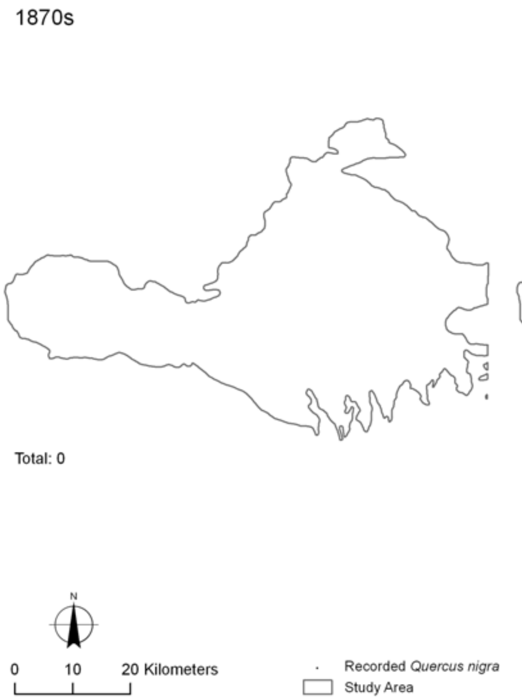


Figure A24. Recorded occurrences of *Quercus palustris,* listed as "pin oak" by the General Land Office surveyors. *Quercus palustris* is not known to occur in the Arbuckle Mountains, however, so this is likely a misidentification by the surveyors.

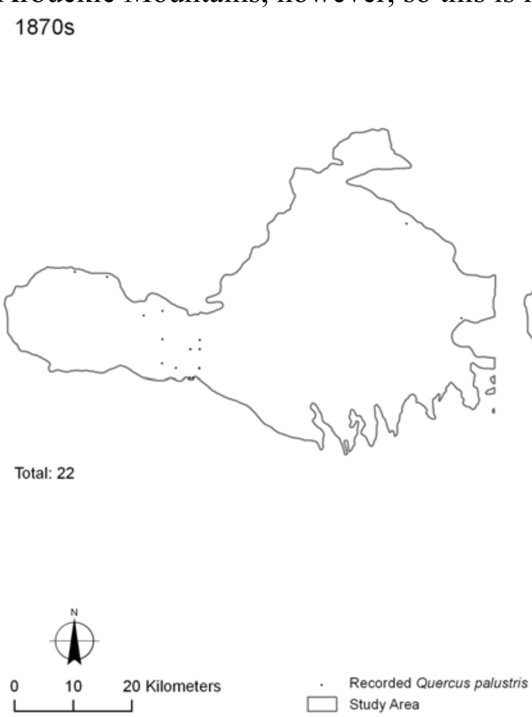


Figure A25. Recorded occurrences of trees listed simply as "oak" by the General Land Office surveyors. Members of the genus *Quercus* known to occur in the Arbuckle Mountains include *Q. buckleyi, Q. falcata, Q. macrocarpa, Q. marilandica, Q. muehlenbergii, Q. shumardii, Q. sinuata, Q. stellata*, and *Q. velutina*

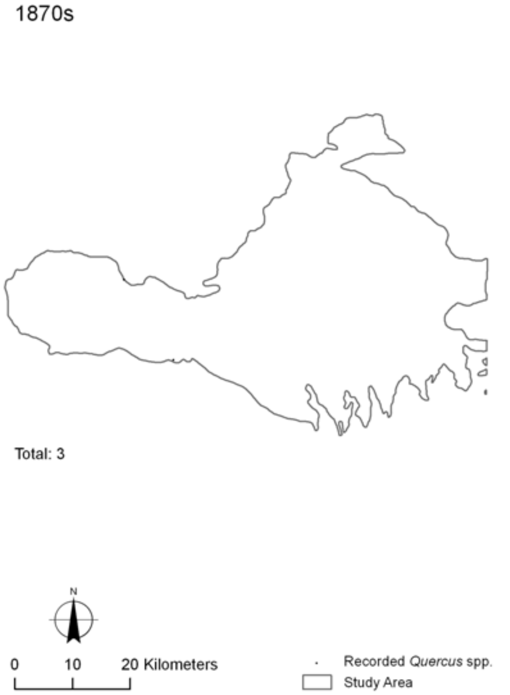


Figure A 26. Recorded occurrences of *Quercus stellata,* listed as "post oak" by the General Land Office surveyors. *Quercus stellata* is considered the most important woody species in the modern cross timbers.

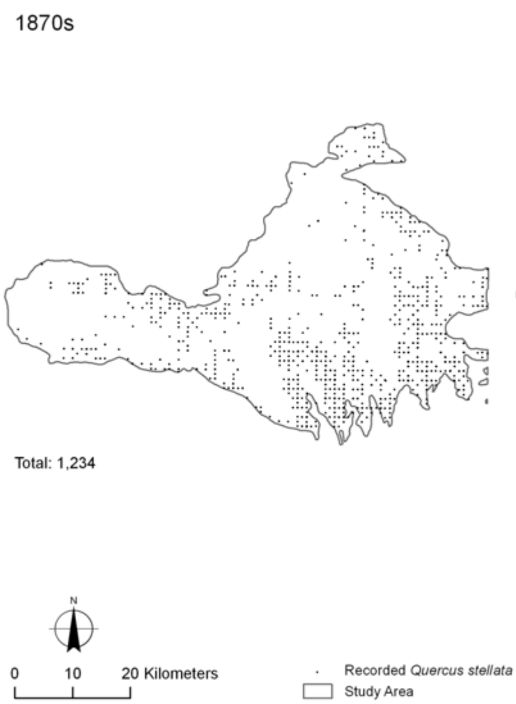


Figure A27. Recorded occurrences of *Quercus velutina, ,* listed as “black oak” by the General Land Office surveyors.. *Quercus velutina* is not a dominant woody species in the Arbuckle Mountains today, perhaps indicating selective harvesting during the period of early European settlement.

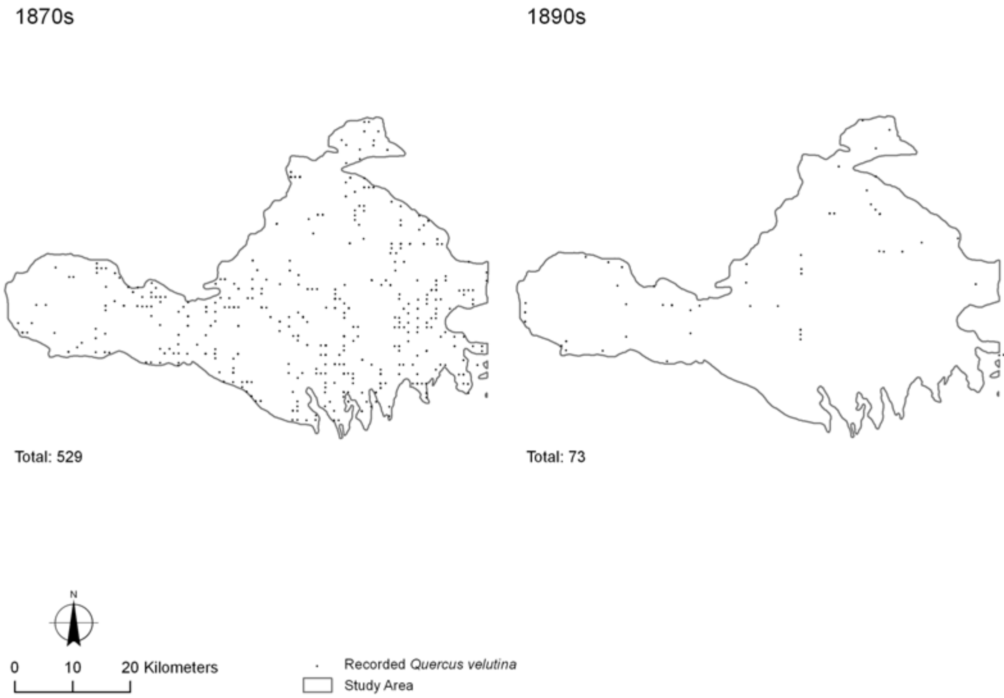


Figure A28. Recorded occurrences of “willows” by General Land Office surveyors in the Arbuckle Mountins. There are there species of *Salix* in the region: *S. caroliniana, S. exigua,* and *S. nigra*.

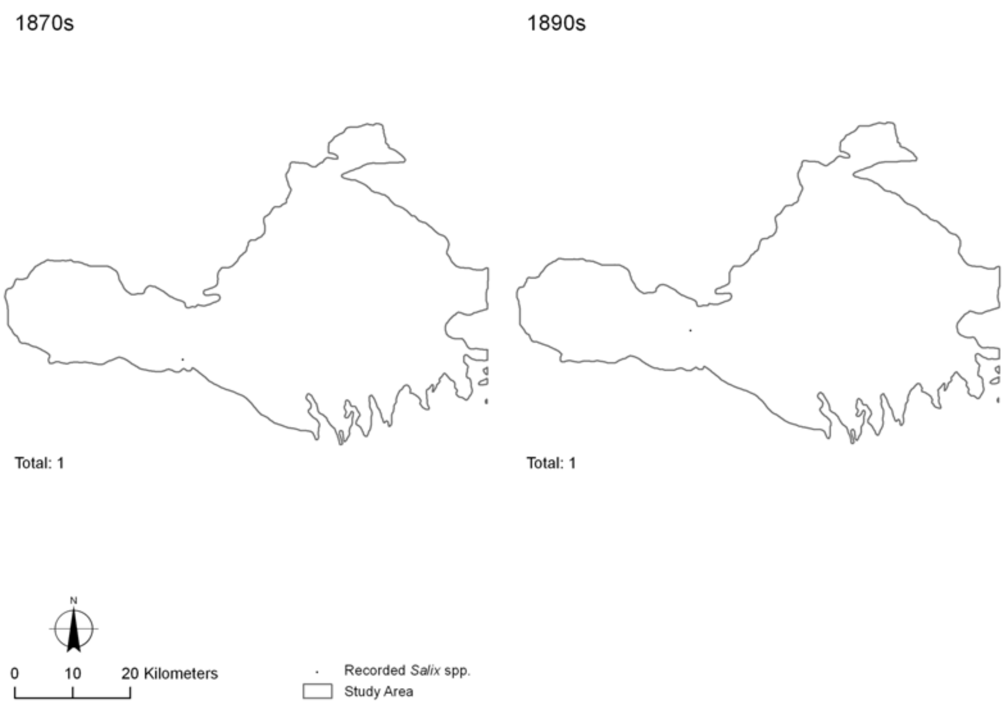


Figure A29. Recorded occurrences of *Sapindus saponaria,* listed as “chinaberry” by the General Land Office surveyors.

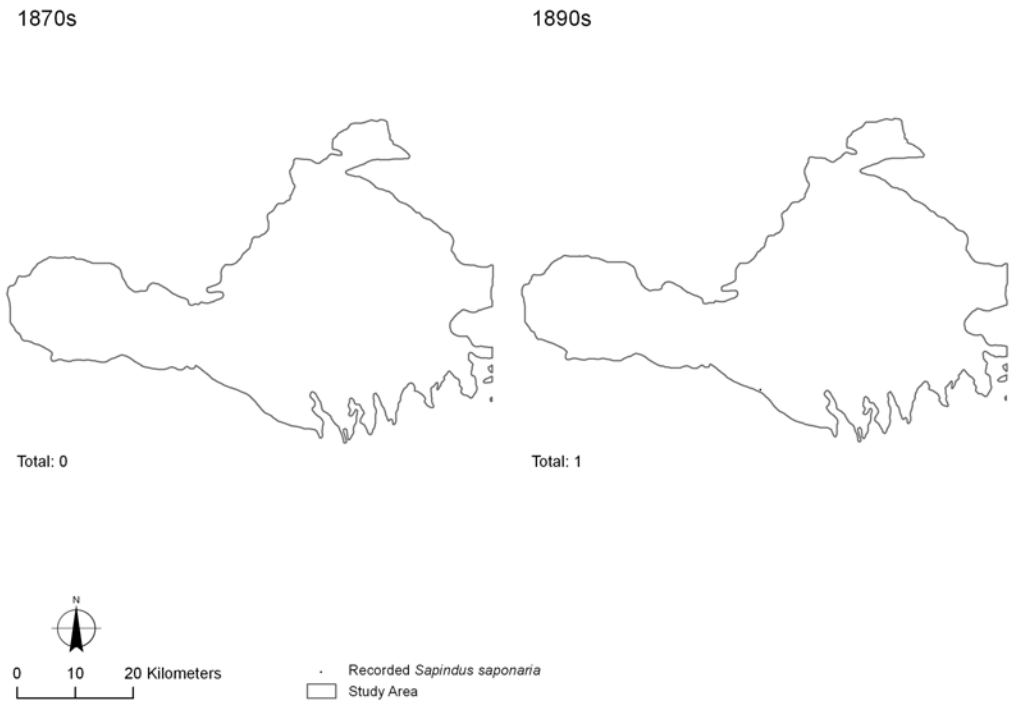


Figure A30. Recorded occurrences of *Sideroxylon lanuginosum*, listed either as “chittam” or “shittam” by the General Land Office surveyors.

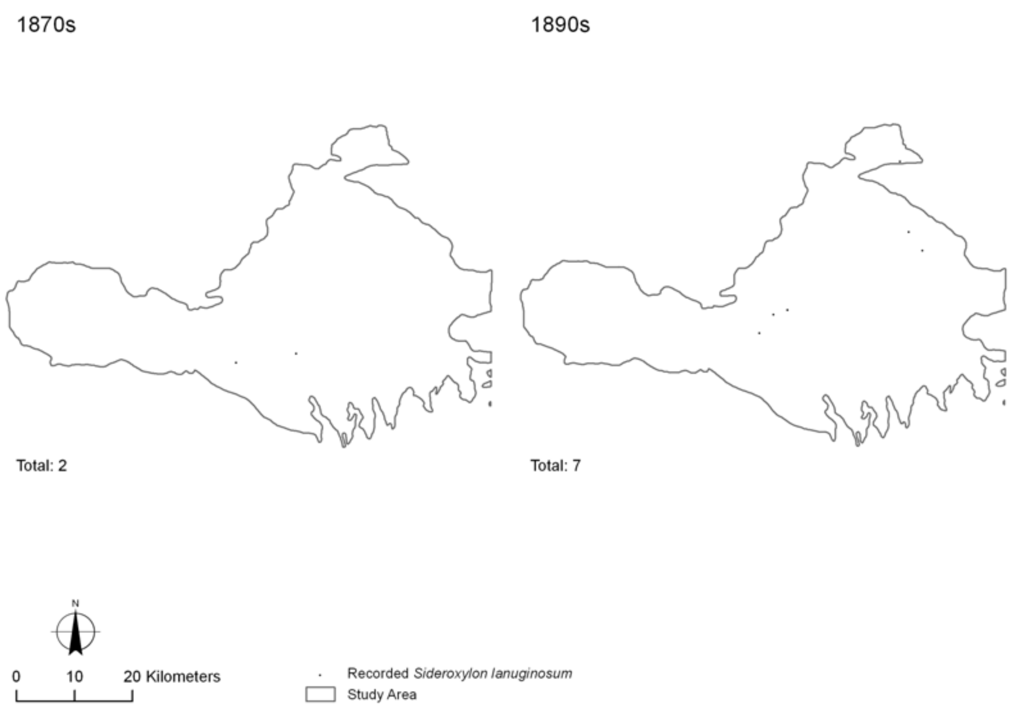
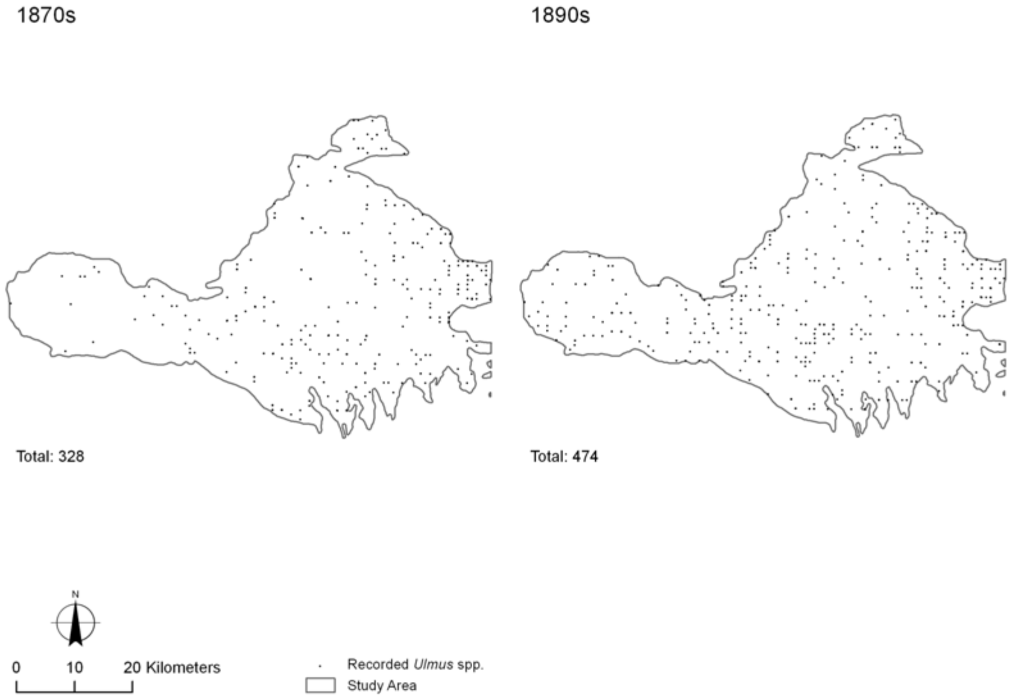


Figure A31. Recorded occurences of "elm" by the General Land Office surveyors in the Arbuckle Mountains. There are four species of *Ulmus* in the region: *U. alata*, *U. americana*, *U. crassifolia*, and *U. rubra*.



APPENDIX B:

CALCULATED WEIGHTS FOR MODELS OF TREE DISTRIBUTIONS IN THE ARBUCKLE MOUNTAINS IN RELATIONSHIP TO ENVIRONMENTAL FACTORS

Weights-of-evidence (WofE) is a discrete, multivariate method based on a log-linear form of Bayes' rule. Weights-of-evidence modeling combines known locations of a phenomenon under investigation with a series of predictor maps (evidential layers) to determine the spatial associations between occurrence points and each class of an evidential layer. The WofE method involves a series of calculations, including positive (W^+) and negative (W^-) weights for each class in each evidential layer; the contrast (C); and the studentized contrast (C_s).

W^+ and W^-, are estimated for each class of an evidential layer using the following formulae (for derivation of weights, see Bonham-Carter (1994)):

$$W_i^+ = \log_e \frac{P\{B_i|D\}}{P\{B_i|\overline{D}\}} \tag{1}$$

$$W_i^- = \log_e \frac{P\{\overline{B}_i|D\}}{P\{\overline{B}_i|\overline{D}\}} \tag{2}$$

The weights represent a measure of spatial association between occurrences and classes of an evidential layer. If the spatial association is greater than would be expected by chance, W^+ is positive and W^- is negative. If the spatial association is less than would be expected by chance, W^+ is negative and W^- is positive. A value nearing zero indicates randomness (Kemp *et al.* 1999; Raines *et al.* 2000). The difference between W^+ and W^- is known as the contrast C. Thus $C = W^+ - W^-$. The larger the value of C is, the greater the spatial association (Bonham-Carter *et al.* 1989). The studentized value of C (C_s) is C divided by its standard deviation and provides a measure of confidence (Bonham-Carter 1994).

As discussed in Chapter 4, we combined occurrence records for 6 woody plant taxa (*Quercus stellata, Q. marilandica, Q. velutina, Carya texana, C. illinoinensis*, and *Juniperus* spp.) with five evidential layers (surficial geology, soil association, elevation, moisture availability index, and historic land cover) to estimate the posterior probability of occurrence of each taxon. However, Chapter 4 presents the results of these calculations in a condensed form. Here, the full weights (W^+ and W^-) for each class are shown with the exception of those classes on which a witness tree record did not occur and, therefore, no weights were calculated. These tables also include the area occupied by each of the classes, the number of points that occurred on each class, the contrast, and studentized contrast. For a complete discussion of the methods, see Chapter 4.

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Table B1. USGS class code, geological formation name, area of class, number of occurrences, calculated weights (W^{+}, W^{-}), contrast, and studentized contrast (C_s) for *Quercus stellata* and the geology evidential layer.

CLASS	GEOLOGICAL FORMATION	AREA (ha)	#POINTS	W+	W-	CONTRAST	Cs
IPo	Pennsylvanian Oscar Group (Shale)	210.15	1	1.5043	-0.0032	1.5075	1.4313
IPa	Pennsylvanian Ada Formation (Shale)	1,602.00	2	0.0916	-0.0007	0.0923	0.1283
Md	Mississippian Delware Creek Shale	4,949.91	12	0.7796	-0.0275	0.8071	2.6614
Dw	Devonian Woodford Shale	8,880.48	27	1.0191	-0.0762	1.0953	5.2143
DSh	Devonian, Silurian Hunton Group (Limestone/Shale)	7,219.98	9	0.0900	-0.0033	0.0933	0.2712
Osfv	Ordovician Sylvan Shale, Fenvale Limestone, and Viola Limestone	12,967.47	14	-0.0572	0.0036	-0.0608	-0.2183
Obm	Ordovician Bromide, Tulip Creek, and McLish Formations	22,346.37	28	0.0953	-0.0117	0.1069	0.5260
Ooj	Ordovician Oil Creek and Joins	16,419.78	28	0.4128	-0.0427	0.4555	2.2310
Ows	Ordovician West Spring Creek	31,490.19	6	-1.8097	0.1373	-1.9470	-4.7001
Ok	Ordovician West Spring Creek	10,164.96	4	-1.0804	0.0328	-1.1132	-2.1992
Mg	Mississippian Goddard Shale	2,253.60	2	-0.2571	0.0024	-0.2595	-0.3622
Owk	Ordovician West Spring Creek	23,096.16	10	-0.9840	0.0740	-1.0580	-3.2613
Cth	Cambrian Timbered Hills Group	2,157.03	6	0.9246	-0.0150	0.9397	2.2101
Cbf	Cambrian Butterfly Dolomite	7,676.28	3	-1.0873	0.0247	-1.1120	-1.9065
Cp	Cambrian Colbert Porphyry	1,466.01	1	-0.5244	0.0028	-0.5273	-0.5226
Ocm	Ordovician Cool Creek	22,027.23	3	-2.1466	0.0983	-2.2449	-3.8586
pCt	Precambrian Tishimingo and Troy Granites	33,698.79	87	0.8458	-0.2733	1.1191	8.2144
Ka	Cretaceous Antlers Sand	2,794.05	2	-0.4756	0.0050	-0.4806	-0.6720

Table B2. USDA soil code, soil association name, area of class, number of occurrences, calculated weights (W^{+}, W^{-}), contrast, and studentized contrast (C_s) for *Quercus stellata* and the soil association evidential layer.

CLASS	SOILS CLASS	AREA (ha)	#POINTS	W+	W-	CONTRAST	Cs
s6316	Shidler-Scullin-Rock outcrop-Lula-Claremore	80,886.69	52	-0.5853	0.2412	-0.8265	-5.2464
s6314	Normangee-Heiden-Durant	8,686.26	16	0.4920	-0.0268	0.5188	1.9698
s6313	Garvin-Fitzhugh-Durant-Bates	4,672.35	1	-1.6938	0.0184	-1.7121	-1.7049
s6351	Shidler-Rock outcrop	14,897.79	14	-0.1996	0.0135	-0.2131	-0.7667
s6328	Hector-Endsaw-Bolivar	815.85	3	1.2221	-0.0087	1.2308	2.0400
s6315	Rock outcrop-Kiti	58,780.98	46	-0.3858	0.1152	-0.5010	-3.0356
s6310	Durant-Clarita-Chigley	5,410.44	12	0.6855	-0.0252	0.7108	2.3486
s6309	Garvin-Clarita-Chigley	1,742.13	5	0.9570	-0.0128	0.9698	2.0845
s6308	Rock outcrop-Chigley-Agan	33,669.90	88	0.8580	-0.2798	1.1378	8.3716
s6339	Bosville-Bernow	777.24	1	0.1217	-0.0005	0.1221	0.1203
s6304	Konsil	898.47	2	0.6893	-0.0041	0.6934	0.9548
s6279	Yahola-Reinach-McLain-Dale	2,939.31	5	0.4095	-0.0070	0.4164	0.9060

Table B3. Elevation class code, elevation range, area of class, number of occurrences, calculated weights (W^{+}, W^{-}), contrast, and studentized contrast (C_s) for *Quercus stellata* and the elevation evidential layer.

CLASS	ELEVATION RANGE	AREA (ha)	#POINTS	W+	W-	CONTRAST	Cs
2	630 - 710	4,937.49	4	-0.3501	0.0070	-0.3571	-0.7025
3	710 - 790	15,329.43	33	0.6549	-0.0721	0.7270	3.8060
4	790 - 870	23,811.93	60	0.8200	-0.1668	0.9868	6.4975
5	870 - 950	30,341.16	55	0.4759	-0.1040	0.5799	3.7246
6	950 - 1030	33,748.65	45	0.1589	-0.0325	0.1914	1.1449
7	1030 - 1110	39,167.28	29	-0.4415	0.0774	-0.5189	-2.6029
8	1110 - 1190	37,202.85	13	-1.2003	0.1393	-1.3396	-4.6813
9	1190 - 1270	21,843.90	4	-1.8498	0.0931	-1.9430	-3.8464
10	1270 - 1350	6,475.14	2	-1.3245	0.0230	-1.3475	-1.8918

Table B4. Moisture index Moisture class code, moisture class, area of class, number of occurrences, calculated weights (W^{+}, W^{-}), contrast, and studentized contrast (C_s) for *Quercus stellata* and the moisture availability index evidential layer.

CLASS	MOISTURE CLASS	AREA (ha)	#POINTS	W+	W-	CONTRAST	Cs
-4	Xeric	15,846.93	6	0.5843	-0.0643	0.6485	1.4547
-3		8,499.87	2	0.0938	-0.0041	0.0979	0.1337
-2		47,767.23	10	-0.0257	0.0073	-0.0330	-0.0913
-1		17,104.23	2	-0.6175	0.0396	-0.6571	-0.9034
0		3,895.20	0	0.0000	0.0000	0.0000	0.0000
1		31,697.82	13	0.6675	-0.1755	0.8430	2.5293
2		48,650.67	5	-0.7480	0.1458	-0.8939	-1.8757
3		9,878.76	2	-0.0599	0.0028	-0.0627	-0.0859
4	Mesic	30,926.97	6	-0.1034	0.0165	-0.1199	-0.2711

Table B5. Land cover Land cover class code, land cover class, area of class, number of occurrences, calculated weights (W^{+}, W^{-}), contrast, and studentized contrast (C_s) for *Quercus stellata* and the 1870s land cover evidential layer.

CLASS	LAND COVER CLASS	AREA (ha)	#POINTS	W+	W-	CONTRAST	Cs
1	Forest/Woodland	96,351.93	220	0.6972	-1.7231	2.4203	11.2109
2	Grassland/Savanna	113,132.70	24	-1.7214	0.6951	-2.4166	-11.1937

Table B6. USGS class code, geological formation name, area of class, number of occurrences, calculated weights (W^+, W^-), contrast, and studentized contrast (C_s) for *Quercus marilandica* and the geology evidential layer.

CLASS	GEOLOGICAL FORMATION	AREA (ha)	#POINTS	W+	W-	CONTRAST	Cs
Md	Mississippian Delware Creek Shale	4,949.91	3	-0.4589	0.0087	-0.4677	-0.7979
Msw	Mississippian Sycamore and Welden Limestones	509.49	1	0.7512	-0.0026	0.7538	0.7333
Dw	Devonian Woodford Shale	8,880.48	15	0.5939	-0.0349	0.6288	2.2958
DSh	Devonian, Silurian Hunton Group (Limestone/Shale)	7,219.98	5	-0.3234	0.0096	-0.3330	-0.7291
Osfv	Ordovician Sylvan Shale, Fenvale Limestone, and Viola Limestone	12,967.47	5	-0.9168	0.0384	-0.9552	-2.0990
Obm	Ordovician Bromide, Tulip Creek, and McLish Formations	22,346.37	33	0.4540	-0.0681	0.5221	2.6979
Ooj	Ordovician Oil Creek and Joins	16,419.78	10	-0.4540	0.0301	-0.4841	-1.4810
Ows	Ordovician West Spring Creek	31,490.19	32	0.0683	-0.0122	0.0806	0.4132
IPm	Pennsylvanian McAlester Formation (S	61.02	1	3.3502	-0.0047	3.3550	2.5738
Ok	Ordovician West Spring Creek	10,164.96	4	-0.8962	0.0294	-0.9256	-1.8237
Mg	Mississippian Goddard Shale	2,253.60	1	-0.7748	0.0058	-0.7806	-0.7743
Owk	Ordovician West Spring Creek	23,096.16	12	-0.6151	0.0546	-0.6697	-2.2352
Cth	Cambrian Timbered Hills Group	2,157.03	3	0.3918	-0.0048	0.3966	0.6700
Cp	Cambrian Colbert Porphyry	1,466.01	1	-0.3388	0.0020	-0.3408	-0.3370
Ocm	Ordovician Cool Creek	22,027.23	26	0.2223	-0.0287	0.2510	1.1784
pCt	Precambrian Tishimingo and Troy Granites	33,698.79	50	0.4589	-0.1129	0.5718	3.4540
Ka	Cretaceous Antlers Sand	2,794.05	2	-0.2897	0.0033	-0.2931	-0.4087

Table B7. USDA soil code, soil association name, area of class, number of occurrences, calculated weights (W^+, W^-), contrast, and studentized contrast (C_s) for *Quercus marilandica* and the soil association evidential layer.

CLASS	SOIL CLASS	AREA (ha)	#POINTS	W+	W-	CONTRAST	Cs
s6316	Shidler-Scullin-Rock outcrop-Lula-Claremore	80,886.69	98	0.2485	-0.1851	0.4336	3.0548
s6314	Normangee-Heiden-Durant	8,686.26	9	0.0875	-0.0039	0.0914	0.2645
s6313	Garvin-Fitzhugh-Durant-Bates	4,672.35	3	-0.4011	0.0074	-0.4085	-0.6966
s6351	Shidler-Rock outcrop	14,897.79	14	-0.0126	0.0009	-0.0135	-0.0483
s6315	Rock outcrop-Kiti	58,780.98	26	-0.7788	0.1890	-0.9678	-4.5788
s6310	Durant-Clarita-Chigley	5,410.44	2	-0.9601	0.0161	-0.9762	-1.3673
s6308	Rock outcrop-Chigley-Agan	33,669.90	49	0.4381	-0.1063	0.5443	3.2664
s6304	Konsil	898.47	1	0.1611	-0.0007	0.1618	0.1591
s6279	Yahola-Reinach-McLain-Dale	2,939.31	2	-0.3421	0.0040	-0.3461	-0.4829

Table B8. Elevation class code, elevation range, area of class, number of occurrences, calculated weights (W^+, W^-), contrast, and studentized contrast (C_s) for *Quercus marilandica* and the elevation evidential layer.

CLASS	ELEVATION RANGE	AREA (ha)	#POINTS	W+	W-	CONTRAST	Cs
2	630 - 710	4,937.49	2	-0.8672	0.0138	-0.8810	-1.2334
3	710 - 790	15,329.43	11	-0.2875	0.0192	-0.3066	-0.9801
4	790 - 870	23,811.93	33	0.3879	-0.0602	0.4481	2.3179
5	870 - 950	30,341.16	31	0.0737	-0.0126	0.0863	0.4369
6	950 - 1030	33,748.65	42	0.2766	-0.0608	0.3374	1.9199
7	1030 - 1110	39,167.28	49	0.2821	-0.0748	0.3569	2.1457
8	1110 - 1190	37,202.85	34	-0.0406	0.0083	-0.0489	-0.2574
9	1190 - 1270	21,843.90	2	-2.3622	0.1000	-2.4622	-3.4606

Table B9. Moisture index Moisture class code, moisture class, area of class, number of occurrences, calculated weights (W^+, W^-), contrast, and studentized contrast (C_s) for *Quercus marilandica* and the moisture availability index evidential layer.

CLASS	MOISTURE CLASS	AREA (ha)	#POINTS	W+	W-	CONTRAST	Cs
-4	Xeric	15,846.93	14	-0.0766	0.0059	-0.0824	-0.2944
-3		8,499.87	17	0.7695	-0.0476	0.8171	3.1476
-2		47,767.23	39	-0.1571	0.0411	-0.1982	-1.1012
-1		17,104.23	22	0.3094	-0.0317	0.3411	1.4873
0		3,895.20	6	0.4963	-0.0118	0.5081	1.2025
1		31,697.82	32	0.0601	-0.0108	0.0709	0.3634
2		48,650.67	45	-0.0296	0.0085	-0.0381	-0.2232
3		9,878.76	12	0.2504	-0.0137	0.2641	0.8742
4	Mesic	30,926.97	17	-0.5596	0.0706	-0.6302	-2.4692

Table B10. Land cover class code, land cover class, area of class, number of occurrences, calculated weights (W^+, W^-), contrast, and studentized contrast (C_s) for *Quercus marilandica* and the 1890s land cover evidential layer.

CLASS	LAND COVER CLASS	AREA (ha)	#POINTS	W+	W-	CONTRAST	Cs
1	Forest/Woodland	74,316.60	100	0.3334	-0.2410	0.5744	4.0463
2	Grassland/Savanna	119,028.06	93	-0.2247	0.2372	-0.4619	-3.2449
6	Cultivated	16,220.79	11	-0.3690	0.0258	-0.3948	-1.2624

Table B11. USGS class code, geological formation name, area of class, number of occurrences, calculated weights (W^{+}, W^{-}), contrast, and studentized contrast (C_s) for *Quercus velutina* and the geology evidential layer.

CLASS	GEOLOGICAL FORMATION	AREA (ha)	#POINTS	W+	W-	CONTRAST	Cs
IPv	Pennsylvanian Vanoss Group (Shale)	177.30	1	4.0785	-0.0216	4.1001	2.6940
IPa	Pennsylvanian Ada Formation (Shale)	1,602.00	1	1.1116	-0.0148	1.1264	1.0793
Md	Mississippian Delware Creek Shale	4,949.91	1	-0.0605	0.0014	-0.0619	-0.0606
Dw	Devonian Woodford Shale	8,880.48	9	1.6386	-0.1790	1.8176	4.6750
DSh	Devonian, Silurian Hunton Group (Limestone/Shale)	7,219.98	3	0.6826	-0.0339	0.7165	1.1756
Osfv	Ordovician Sylvan Shale, Fenvale Limestone, and Viola Limestone	12,967.47	9	1.2251	-0.1585	1.3837	3.6097
Obm	Ordovician Bromide, Tulip Creek, and McLish Formations	22,346.37	5	0.0438	-0.0052	0.0490	0.1024
Ooj	Ordovician Oil Creek and Joins	16,419.78	4	0.1309	-0.0116	0.1425	0.2690
Ows	Ordovician West Spring Creek	31,490.19	5	-0.3058	0.0446	-0.3504	-0.7336
Ok	Ordovician West Spring Creek	10,164.96	2	-0.0875	0.0042	-0.0917	-0.1255
Cth	Cambrian Timbered Hills Group	2,157.03	1	0.7972	-0.0121	0.8093	0.7819
IPd	Pennsylvanian Deese Group (Limestone)	346.41	1	2.9192	-0.0208	2.9400	2.4598
pCt	Precambrian Tishimingo and Troy Granites	33,698.79	1	-1.9961	0.1524	-2.1485	-2.1213
Ka	Cretaceous Antlers Sand	2,794.05	3	1.7031	-0.0555	1.7586	2.7905

Table B12. USDA soil code, soil association name, area of class, number of occurrences, calculated weights (W^{+}, W^{-}), contrast, and studentized contrast (C_s) for *Quercus velutina* and the soil association evidential layer.

CLASS	SOIL CLASS	AREA (ha)	#POINTS	W+	W-	CONTRAST	Cs
s6316	Shidler-Scullin-Rock outcrop-Lula-Claremore	80,886.69	18	0.0375	-0.0234	0.0608	0.1992
s6314	Normangee-Heiden-Durant	8,686.26	1	-0.6325	0.0198	-0.6523	-0.6414
s6351	Shidler-Rock outcrop	14,897.79	2	-0.4769	0.0282	-0.5051	-0.6937
s6315	Rock outcrop-Kiti	58,780.98	17	0.3064	-0.1438	0.4502	1.4553
s6310	Durant-Clarita-Chigley 0	5,410.44	1	-0.1520	0.0037	-0.1557	-0.1525
s6309	Garvin-Clarita-Chigley 0	1,742.13	1	1.0217	-0.0141	1.0358	0.9950
s6308	Rock outcrop-Chigley-Agan 0	33,669.90	1	-1.9960	0.1524	-2.1483	-2.1212
s6279	Yahola-Reinach-McLain-Dale	2,939.31	5	2.2354	-0.1034	2.3387	4.5358

Table B13. Elevation class code, elevation range, area of class, number of occurrences, calculated weights (W^{+}, W^{-}), contrast, and studentized contrast (C_s) for *Quercus velutina* and the elevation evidential layer.

CLASS	ELEVATION RANGE	AREA (ha)	#POINTS	W+	W-	CONTRAST	Cs
3	710 - 790	15,329.43	6	0.6201	-0.0670	0.6871	1.5404
4	790 - 870	23,811.93	4	-0.2488	0.0273	-0.2760	-0.5230
5	870 - 950	30,341.16	1	-1.8910	0.1336	-2.0246	-1.9987
6	950 - 1030	33,748.65	6	-0.1911	0.0321	-0.2232	-0.5050
7	1030 - 1110	39,167.28	15	0.5974	-0.1969	0.7943	2.4852
8	1110 - 1190	37,202.85	9	0.1235	-0.0279	0.1514	0.4024
9	1190 - 1270	21,843.90	5	0.0668	-0.0079	0.0747	0.1559

Table B14. Moisture class code, moisture class, area of class, number of occurrences, calculated weights (W^+, W^-), contrast, and studentized contrast (C_s) for *Quercus velutina* and the moisture availability index evidential layer.

CLASS	MOISTURE CLASS	AREA (ha)	#POINTS	W+	W-	CONTRAST	Cs
-4	Xeric	15,846.93	6	0.5843	-0.0643	0.6485	1.4547
-3		8,499.87	2	0.0938	-0.0041	0.0979	0.1337
-2		47,767.23	10	-0.0257	0.0073	-0.0330	-0.0913
-1		17,104.23	2	-0.6175	0.0396	-0.6571	-0.9034
0		3,895.20	0	0.0000	0.0000	0.0000	0.0000
1		31,697.82	13	0.6675	-0.1755	0.8430	2.5293
2		48,650.67	5	-0.7480	0.1458	-0.8939	-1.8757
3		9,878.76	2	-0.0599	0.0028	-0.0627	-0.0859
4	Mesic	30,926.97	6	-0.1034	0.0165	-0.1199	-0.2711

Table B15. Land cover class code, land cover class, area of class, number of occurrences, calculated weights (W^+, W^-), contrast, and studentized contrast (C_s) for *Quercus velutina* and the 1890s land cover evidential layer.

CLASS	LAND COVER CLASS	AREA (ha)	#POINTS	W+	W-	CONTRAST	Cs
1	Forest/Woodland	74,316.60	22	0.3759	-0.2839	0.6597	2.1381
2	Grassland/Savanna	119,028.06	17	-0.3686	0.3446	-0.7132	-2.2635

Table B16. USGS class code, geological formation name, area of class, number of occurrences, calculated weights (W^+, W^-), contrast, and studentized contrast (C_s) for *Carya texana* and the geology evidential layer.

CLASS	GEOLOGICAL FORMATION	AREA (ha)	#POINTS	W+	W-	CONTRAST	Cs
IPh	Pennsylvanian Holdenville Format	217.17	1	2.9291	-0.0125	2.9416	2.4104
Md	Mississippian Delware Creek Shale	4,949.91	2	0.1354	-0.0034	0.1388	0.1909
Dw	Devonian Woodford Shale	8,880.48	4	0.2474	-0.0121	0.2595	0.4972
DSh	Devonian, Silurian Hunton Group (Limestone/Shale)	7,219.98	1	-0.9542	0.0215	-0.9757	-0.9645
Osfv	Ordovician Sylvan Shale, Fenvale Limestone, and Viola Limestone	12,967.47	8	0.5740	-0.0501	0.6241	1.6351
Obm	Ordovician Bromide, Tulip Creek, and McLish Formations	22,346.37	6	-0.2830	0.0284	-0.3115	-0.7251
Ooj	Ordovician Oil Creek and Joins	16,419.78	19	1.2433	-0.2128	1.4562	5.3109
Ows	Ordovician West Spring Creek	31,490.19	5	-0.8162	0.0931	-0.9092	-1.9531
Ok	Ordovician Kindblade Formation (Limestone)	10,164.96	8	0.8301	-0.0642	0.8943	2.3298
Mg	Mississippian Goddard Shale	2,253.60	1	0.2319	-0.0028	0.2347	0.2295
Owk	Ordovician West Spring Creek	23,096.16	2	-1.4275	0.0895	-1.5171	-2.1100
Ocm	Ordovician Cool Creek	22,027.23	2	-1.3799	0.0838	-1.4637	-2.0355
Pg	Permian Garber Sandstone	366.21	1	2.2296	-0.0118	2.2414	2.0048
IPd	Pennsylvanian Deese Group (Limestone)	346.41	1	2.2988	-0.0119	2.3107	2.0529
Ipdo	Pennsylvanian Dornick Hills Grou	643.68	1	1.5686	-0.0105	1.5791	1.4817
pCt	Precambrian Tishimingo and Troy Granites	33,698.79	12	0.0056	-0.0010	0.0066	0.0208

Table B17. USDA soil code, soil association name, area of class, number of occurrences, calculated weights (W^{+}, W^{-}), contrast, and studentized contrast (C_s) for *Carya texana* and the soil association evidential layer.

CLASS	SOILS CLASS	AREA (ha)	#POINTS	W+	W-	CONTRAST	Cs
s6316	Shidler-Scullin-Rock outcrop-Lula-Claremore	80,886.69	44	0.4421	-0.3996	0.8417	3.5758
s6314	Normangee-Heiden-Durant	8,686.26	2	-0.4402	0.0151	-0.4553	-0.6301
s6313	Garvin-Fitzhugh-Durant-Bates	4,672.35	1	-0.5145	0.0090	-0.5235	-0.5161
s6351	Shidler-Rock outcrop	14,897.79	5	-0.0559	0.0041	-0.0599	-0.1280
s6315	Rock outcrop-Kiti	815.85	2	-2.3662	0.3024	-2.6686	-3.7180
s6310	Durant-Clarita-Chigley	44.91	2	0.0431	-0.0011	0.0443	0.0610
s6309	Garvin-Clarita-Chigley	58,780.98	1	0.4980	-0.0052	0.5032	0.4898
s6308	Rock outcrop-Chigley-Agan	5,410.44	13	0.0879	-0.0172	0.1051	0.3403
s6279	Yahola-Reinach-McLain-Dale	1,742.13	6	1.8799	-0.0701	1.9500	4.2646

Table B18. Elevation class code, elevation range, area of class, number of occurrences, calculated weights (W^{+}, W^{-}), contrast, and studentized contrast (C_s) for *Carya texana* and the elevation evidential layer.

CLASS	ELEVATION RANGE	AREA (ha)	#POINTS	W+	W-	CONTRAST	Cs
2	630 - 710	4,937.49	2	0.1377	-0.0035	0.1412	0.1942
3	710 - 790	15,329.43	13	0.9090	-0.1162	1.0252	3.2747
4	790 - 870	23,811.93	10	0.1749	-0.0240	0.1989	0.5777
5	870 - 950	30,341.16	12	0.1131	-0.0199	0.1330	0.4169
6	950 - 1030	33,748.65	19	0.4783	-0.1193	0.5977	2.2162
7	1030 - 1110	39,167.28	9	-0.4418	0.0775	-0.5193	-1.4500
8	1110 - 1190	37,202.85	8	-0.5091	0.0813	-0.5905	-1.5668
9	1190 - 1270	21,843.90	3	-0.9630	0.0689	-1.0319	-1.7426

Table B19. Moisture class code, moisture class, area of class, number of occurrences, calculated weights (W^{+}, W^{-}), contrast, and studentized contrast (C_s) for *Carya texana* and the moisture availability index evidential layer.

CLASS	MOISTURE CLASS	AREA (ha)	#POINTS	W+	W-	CONTRAST	Cs
-4	Xeric	15,846.93	6	0.0670	-0.0055	0.0725	0.1683
-3		8,499.87	3	-0.0051	0.0002	-0.0053	-0.0089
-2		47,767.23	11	-0.4408	0.0984	-0.5393	-1.6394
-1		17,104.23	6	-0.0114	0.0010	-0.0123	-0.0286
0		3,895.20	6	1.5575	-0.0655	1.6229	3.6160
1		31,697.82	9	-0.2276	0.0349	-0.2625	-0.7318
2		48,650.67	22	0.2499	-0.0863	0.3361	1.3095
3		9,878.76	5	0.3665	-0.0214	0.3879	0.8236
4	Mesic	30,926.97	8	-0.3226	0.0458	-0.3684	-0.9762

Table B20. Land cover class code, land cover class, area of class, number of occurrences, calculated weights (W^+, W^-), contrast, and studentized contrast (C_s) for *Carya texana* and the 1870s land cover evidential layer.

CLASS	LAND COVER CLASS	AREA (ha)	#POINTS	W+	W-	CONTRAST	Cs
1	Forest/Woodland	96,351.93	67	0.6757	-1.5383	2.2140	6.2024
2	Grassland/Savanna	113,132.70	8	-1.6550	0.6892	-2.3443	-6.2411
6	Cultivated	181.26	1	3.1850	-0.0127	3.1977	2.4948

Table B21. USGS class code, geological formation name, area of class, number of occurrences, calculated weights (W^+, W^-), contrast, and studentized contrast (C_s) for *Carya illinoinensis* and the geology evidential layer.

CLASS	GEOLOGICAL FORMATION	AREA (ha)	#POINTS	W+	W-	CONTRAST	Cs
Md	Mississippian Delware Creek Shale	4,949.91	1	0.1893	-0.0049	0.1942	0.1896
MsW	Mississippian Sycamore and Weldon Limestones	509.49	1	2.6611	-0.0262	2.6874	2.3816
Dw	Devonian Woodford Shale	8,880.48	2	0.3004	-0.0151	0.3155	0.4288
DSh	Devonian, Silurian Hunton Group (Limestone/Shale)	7,219.98	1	-0.1946	0.0062	-0.2008	-0.1966
Osfv	Ordovician Sylvan Shale, Fenvale Limestone, and Viola Limestone	12,967.47	8	1.3490	-0.1919	1.5409	3.7434
Obm	Ordovician Bromide, Tulip Creek, and McLish Formations	22,346.37	6	0.4806	-0.0735	0.5541	1.2235
Ooj	Ordovician Oil Creek and Joins	16,419.78	6	0.7988	-0.1044	0.9032	1.9859
Ows	Ordovician West Spring Creek	31,490.19	5	-0.0559	0.0093	-0.0653	-0.1343
	Ordovician Kindblade Formations (Limestone)	23,096.16	3	-0.2597	0.0273	-0.2870	-0.4728
Cth	Cambrian Timbered Hills Group	2,157.03	0	0.0000	0.0000	0.0000	0.0000
Ocm	Ordovician Cool Creek	22,027.23	2	-0.6217	0.0520	-0.6738	-0.9216
pCt	Precambrian Tishimingo and Troy Granites	33,698.79	1	-1.7462	0.1453	-1.8915	-1.8618

Table B22. USDA soil code, soil association name, area of class, number of occurrences, calculated weights (W^+, W^-), contrast, and studentized contrast (C_s) for *Carya illinoinensis* and the soil association evidential layer.

CLASS	SOILS CLASS	AREA (ha)	#POINTS	W+	W-	CONTRAST	Cs
s6316	Shidler-Scullin-Rock outcrop-Lula-Claremore	80,886.69	11	-0.2139	0.1109	-0.3248	-0.8909
s6314	Normangee-Heiden-Durant	8,686.26	1	-0.3826	0.0134	-0.3960	-0.3882
s6313	Garvin-Fitzhugh-Durant-Bates	4,672.35	2	0.9628	-0.0357	0.9985	1.3436
s6351	Shidler-Rock outcrop	14,897.79	4	0.4798	-0.0465	0.5264	0.9797
s6315	Rock outcrop-Kiti	58,780.98	9	-0.0936	0.0333	-0.1269	-0.3271
s6310	Durant-Clarita-Chigley	5,410.44	3	1.2348	-0.0625	1.2973	2.0944
s6308	Rock outcrop-Chigley-Agan	33,669.90	1	-1.7461	0.1453	-1.8914	-1.8617
s6279	Yahola-Reinach-McLain-Dale	2,939.31	5	2.4852	-0.1379	2.6231	5.0137

Table B23. Elevation class code, elevation range, area of class, number of occurrences, calculated weights (W^+, W^-), contrast, and studentized contrast (C_s) for *Carya illinoinensis* and the elevation evidential layer.

CLASS	ELEVATION RANGE	AREA (ha)	#POINTS	W+	W-	CONTRAST	Cs
3	710 - 790	15,329.43	6	0.8700	-0.1099	0.9799	2.1522
4	790 - 870	23,811.93	1	-1.3979	0.0911	-1.4890	-1.4648
5	870 - 950	30,341.16	4	-0.2449	0.0353	-0.2802	-0.5247
6	950 - 1030	33,748.65	10	0.5818	-0.1567	0.7385	1.9592
7	1030 - 1110	39,167.28	6	-0.0926	0.0196	-0.1122	-0.2489
8	1110 - 1190	37,202.85	8	0.2528	-0.0619	0.3147	0.7771
9	1190 - 1270	21,843.90	1	-1.3113	0.0806	-1.3919	-1.3690

Table B24. Moisture class code, moisture class, area of class, number of occurrences, calculated weights (W^+, W^-), contrast, and studentized contrast (C_s) for *Carya illinoinensis* and the moisture availability index evidential layer.

CLASS	MOISTURE CLASS	AREA (ha)	#POINTS	W+	W-	CONTRAST	Cs
-4	Xeric	15,846.93	3	0.1215	-0.0103	0.1319	0.2166
-3		8,499.87	1	-0.3615	0.0125	-0.3740	-0.3665
-2		47,767.23	5	-0.4796	0.1045	-0.5842	-1.2051
-1		17,104.23	7	0.9151	-0.1352	1.0503	2.4488
0		3,895.20	5	2.1538	-0.1333	2.2871	4.4666
1		31,697.82	1	-1.6863	0.1343	-1.8207	-1.7920
2		48,650.67	9	0.0980	-0.0306	0.1286	0.3312
3		9,878.76	0	0.0000	0.0000	0.0000	0.0000
4	Mesic	30,926.97	5	-0.0391	0.0065	-0.0456	-0.0938

Table B25. Land cover class code, land cover class, area of class, number of occurrences, calculated weights (W^+, W^-), contrast, and studentized contrast (C_s) for *Carya illinoinensis* and the 1870s land cover evidential layer.

CLASS	LAND COVER CLASS	AREA (ha)	#POINTS	W+	W-	CONTRAST	Cs
1	Forest/Woodland	96,351.93	23	0.3364	-0.4090	0.7454	2.1309
2	Grassland/Savanna	113,132.70	13	-0.4073	0.3344	-0.7417	-2.1204

Table B26. USGS class code, geological formation name, area of class, number of occurrences, calculated weights (W^+, W^-), contrast, and studentized contrast (C_s) for *Juniperus* spp. and the geology evidential layer.

CLASS	GEOLOGICAL FORMATION	AREA (ha)	#POINTS	W+	W-	CONTRAST	Cs
IPa	Pennsylvanian Ada Formation (Shale)	1,602.00	3	3.8004	-0.3123	4.1127	5.6196
Md	Mississippian Delware Creek Shale	4,949.91	3	2.5275	-0.2964	2.8239	4.0746
Owk	Ordovician West Spring Creek	23,096.16	3	0.9377	-0.2055	1.1432	1.6797
pCt	Precambrian Tishimingo and Troy Granites	33,698.79	2	0.1473	-0.0300	0.1773	0.2262

Table B27. USDA soil code, soil association name, area of class, number of occurrences, calculated weights (W^+, W^-), contrast, and studentized contrast (C_s) for *Juniperus* spp. and the soil association evidential layer.

CLASS	SOILS CLASS	AREA (ha)	#POINTS	W+	W-	CONTRAST	Cs
s6315	Rock outcrop-Kiti	58,780.98	9	1.1038	-1.3882	2.4920	3.1816
s6308	Rock outcrop-Chigley-Agan	33,669.90	2	0.1474	-0.0300	0.1774	0.2263

Table B28. Elevation class code, elevation range, area of class, number of occurrences, calculated weights (W^+, W^-), contrast, and studentized contrast (C_s) for *Juniperus* spp. and the elevation evidential layer.

CLASS	ELEVATION RANGE	AREA (ha)	#POINTS	W+	W-	CONTRAST	Cs
3	710 - 790	15,329.43	2	0.9420	-0.1271	1.0691	1.3597
4	790 - 870	23,811.93	3	0.9066	-0.2017	1.1083	1.6286
5	870 - 950	30,341.16	2	0.2527	-0.0484	0.3011	0.3840
6	950 - 1030	33,748.65	2	0.1456	-0.0297	0.1753	0.2236
7	1030 - 1110	39,167.28	2	-0.0041	0.0009	-0.0050	-0.0064

Table B29. Moisture class code, moisture class, area of class, number of occurrences, calculated weights (W^+, W^-), contrast, and studentized contrast (C_s) for *Juniperus* spp. and the moisture availability index evidential layer.

CLASS	MOISTURE CLASS	AREA (ha)	#POINTS	W+	W-	CONTRAST	Cs
-4	Xeric	15,846.93	2	0.9071	-0.1244	1.0315	1.3121
-3		8,499.87	0	0.0000	0.0000	0.0000	0.0000
-2		47,767.23	5	0.7178	-0.3554	1.0732	1.7659
-1		17,104.23	1	0.1307	-0.0122	0.1429	0.1359
0		3,895.20	0	0.0000	0.0000	0.0000	0.0000
1		31,697.82	0	0.0000	0.0000	0.0000	0.0000
2		48,650.67	0	0.0000	0.0000	0.0000	0.0000
3		9,878.76	0	0.0000	0.0000	0.0000	0.0000
4	Mesic	30,926.97	3	0.6409	-0.1633	0.8043	1.1831

Table B30. Class code, land cover class name, area of class, number of occurrences, calculated weights (W^+, W^-), contrast, and studentized contrast (C_s) for *Juniperus* spp. and the 1870s land cover evidential layer.

CLASS	LAND COVER CLASS	AREA (ha)	#POINTS	W+	W-	CONTRAST	Cs
1	Forest/Woodland	96,351.93	7	0.3276	-0.3980	0.7256	1.1548
2	Grassland/Savanna	113,132.70	4	-0.3963	0.3256	-0.7220	-1.1490