USING GIS TO ASSESS FAUNMAP AND DETERMINE GEOGRAPHIC RANGE
CHARACTERISTICS OF MAMMOTHS AND MASTODONS,
GREAT LAKES, USA

By

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ABSTRACT

USING GIS TO ASSESS FAUNMAP AND DETERMINE GEOGRAPHIC RANGE CHARACTERISTICS OF MAMMOTHS AND MASTODONS, GREAT LAKES, USA

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During the Terminal Pleistocene, many now extinct megafauna roamed across North America. Two of the most widely studied genera from this time period are *Mammut* (or mastodons) and *Mammuthus* (or mammoths). While paleoenvironmental studies on individual site localities have been performed, no one has attempted to do a regional study on such species. Additionally, most research on fauna during this time focuses on community dynamics rather than individual species (or genera). The prime source of data for these studies is the FAUNMAP database; however, some studies reveal issues with using the database. During this investigation, the FAUNMAP database was compared to a database I created, consisting of the original database and other sites previously published, yet not included, in the FAUNMAP database. To limit the spatial extent for the study, only site localities for the Great Lakes region were used, due to the large concentration of mammoth and mastodon fossils and palynology and plant macrofossil studies. After adding 528 new sites, the hypothesis stating FAUNMAP was an effective database for studies concerning individual species (or genera) was rejected. Further objectives, using the modified database, determined geographic range characteristics, such has size, range shift through time, and associated vegetation. Assuming the site localities are located near their feeding grounds, the associated vegetation may provide a geographic understanding of their diets; however, the results for this study were inconclusive.

ACKNOWLEDGEMENTS

First of all, I would like to acknowledge Dr. Catherine Yansa, my Graduate Advisor, for setting me on the path leading to this investigation. Without the inspiration received from your presentation, this research would have never been started. Additionally, I would like to thank the members of my committee, Dr. Gary Roloff and Dr. Alan Arbogast, for the guidance and support received during my graduate career. Additional gratitude goes to Dr. Roloff; for without him, I would still be lost with the statistics used for this research. I would also like to thank Dr. Richard Slaughter, University of Wisconsin- Madison Geology Museum, for helping compile mammoth and mastodon localities in the state of Wisconsin.

Finally, I am extremely grateful for my family: Mark, Cathy, Brandon, Ben, Carly, Kaden, and Collin Adams, who all showed me love and support through this entire process; encouraging me when I was having trouble and celebrating with me when I was not.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF SYMBOLS/ABBREVIATIONS

$\delta^{13}C$: (δ- Greek letter "delta") Change in carbon-13 isotope

^{14}C years BP: Radiocarbon years Before Present

^{87}Sr: Strontium isotope

^{86}Sr: Strontium isotope

ANOVA: Analysis of Variance

AP: Arboreal pollen

DJF: Winter months (December, January, February)

Cal yr BP: Calendar years Before Present

ka: thousand years (calendar years BP)

JJA: Summer months (June, July, August)

LGM: Last Glacial Maximum

MCP: Minimum Convex Polygons

NAP: Non-arboreal pollen

NAPD: North American Pollen Database

NCDC: National Climatic Data Center

NOAA: National Oceanic and Atmospheric Administration

USPLS: United States Public Land Survey

ZINB: Zero-inflated Negative Binomial

INTRODUCTION

While climatologists are focusing on understanding and assessing global climate change in the future (IPCC, 2007), biologists and biogeographers are attempting to determine how such climate change may affect biotic communities (e.g., Durner et al., 2009, Bradshaw and Holzapfel, 2010, Van der Putten et al., 2010). According to Patterson (2010: 3019), one method of determining the possible biotic response to climate change is “To use the 'lessons of the Pleistocene' to forecast the biotic effects of climate change.” However, before such forecasts can be performed, the how and why of such responses must first be determined.

Worldwide, climate fluctuated back and forth between glaciations and interglaciations during the Quaternary Period of the last 2.59 million years BP (Gibbard et al., 2010). North American glaciations were characterized by the expansion of alpine glaciers downslope and the formation of two large ice sheets over the northern part of this continent, the Laurentide Ice Sheet in eastern and central United States and Canada and the Cordilleran ice sheet in western North America. Numerous glacial-interglacial cycles have been reconstructed from oxygen isotope ratios of the cores of both glaciers and ocean bottom sediments (Shackleton, 1967, 1987, 2000; Taylor et al., 1993). These core data have been used to create paleoclimate models that simulate past atmospheric circulation patterns with respect to massive continental and alpine glaciers (e.g., Kutzbach et al., 1998; Ganopolski et al., 2010). There are many explanations concerning the cause of such climate change, including (1) Milankovitch’s theory of variations in the earth’s orbit (eccentricity, precision, and obliquity) affecting incoming solar radiation (Huybers and Wunsch, 2005; Crowley and Hyde, 2008), (2) variations in solar radiation due to sun spot activity (Dergachev et al., 2009), and (3) unknown internal forcings (Lehman and Keigwin, 1992; Soon, 2007; Ganopolski and Roche, 2009). Regardless of the cause(s) of Quaternary climate change, the effects of shifting temperature and precipitation regimes and the expansion and contraction of massive glaciers had profound effects on plant and animal geographies.

In eastern North America, the overall climate of the terminal Pleistocene (~18,000-11,500 cal yr BP) was colder than now, with temperatures ranging between 2-16˚C lower than modern depending on the season, latitude, and time (e.g., Webb et al., 1998). The Laurentide Ice Sheet had earlier reached its maximum southward extent (i.e., the Last Glacial Maximum, LGM) to about 38°N between 24,000 and 18,000 cal yr BP (Dyke and Prest, 1987). Locales closest to the receeding ice-sheet margin during the terminal Pleistocene were obviously colder than those situated farther south. Fossil pollen from lakes and wetlands in this area have documented shifting plant ranges in response to ice sheet recession and local changes in annual and seasonal temperature and precipitation over time (e.g., Webb et al., 1998; Williams et al., 2002; Willard et al., 2005; Yansa, 2006; Wagner et al., 2009). These changes in climate and attenuated shifts in plant distributions had profound effects on mammalian populations in North America.

During the LGM and the terminal Pleistocene, extremely large animals, such as mammoths, mastodons (mastodonts), giant beavers, giant sloths, saber-toothed tigers, and American lions, lived south of the North American ice sheets (Kurten and Anderson, 1980). Generally, such animals are combined into a non-taxonomic group called megafauna, but the definition of the group is largely debatable since there is no standard definition (Kurten and Anderson, 1980; Gingerich, 1984; Graham and Lundelius, 1984; Horton, 1984; Marshall, 1984; Martin, 1984; Webb, 1984). These animals disappeared at the end of the Pleistocene, the cause(s) of which have been debated for decades (e.g., Marshall, 1984; Graham, 1990; Guthrie, 1990; Martin, 1990; Haynes, 2002; Firestone et al., 2007; Gill et al., 2009), and will be later discussed in some depth.

Mammoths and mastodons are two of the most widely studied Pleistocene megafauna, because of their iconic status as "charismatic megafauna" and their sometime association with Paleo-Indian materials (Agenbroad et al. (eds.), 1990; Holman, 1995a; Agenbroad, 2005). Mammoths (Family Elephantidae) and mastodons (also spelled mastodonts; Family Mammutidae) belong to the Order Proboscidea along with the Family Gomphotheriidae and Family Stegodontinae. The order largely became extinct during the terminal Pleistocene with the exception of the extant *Elephas maximus* (Asian Elephant) and *Loxodonta africana* (African Elephant; Kurten and Anderson, 1980). Three extinct proboscidean species have been identified within the Great Lakes region of the USA and Ontario, Canada: the Jefferson mammoth (*Mammuthus jeffersonii*), the woolly mammoth (*Mammuthus primigenius*), and the American mastodon (*Mammut americanum;* Kurten and Anderson, 1980; FAUNMAP Working Group, 1994; Holman, 2001). Pollen and plant macrofossil studies have provided insight to mammoth and mastodon habitats and diet (e.g., Kapp, 1986, 1999; McAndrews and Jackson, 1988; McAndrews, 2003; Yansa and Adams, 2012), but there has been no prior attempt to establish geographic ranges for these megafauna.

The purpose of this thesis research was to determine whether the two species of mammoths and one species of mastodon in the Great Lakes region occupied different habitats and if not, the amount of overlap between them. To do this, the first step was to acquire fossil data from FAUNMAP, which is one of the most widely used databases for Pleistocene mammals (http://www.ucmp.berkeley.edu/faunmap/).

FAUNMAP was created with the goal of analyzing the evolution of mammal communities in the United States throughout the Pleistocene epoch (FAUNMAP Working Group, 1994). Understanding the evolution and changes in mammal communities during the Pleistocene climate fluctuations is an important application to understanding present and future range changes of extant species (Burns et al., 2003; Martínez-Meyer et al., 2004; Keane et al., 2008; Davies et al, 2009). When the database became available electronically (FAUNMAP Working Group, 1996a), the data could be queried by anyone. Since then, scientists have used it for a number of studies, ranging from reconstructing past community structures (FAUNMAP Working Group, 1996b), endemism (Riddle, 1996), and range shifts in response to environmental changes (Walker, 2000; Burns et al., 2003; Lyons, 2003, 2005).

Although FAUNMAP has proven to be a useful database, problems have been shown to exist concerning the validity of the inherent data. A previous study by Walker (2000) tested the validity of the FAUNMAP data concerning the American Pronghorn (*Antilocarpa americana*). He found that the database lacks significant amounts of data due to the focus on data acquisition from major journals and often lacks data documented in less known journals, government or museum reports, or newspapers. The database also lacks data significant in reconstructing habitats, such as associated pollen and plant macrofossil studies at the same sites with reported megafauna or if other vertebrate taxa were found in nearby locales (FAUNMAP Working Group, 1994).

Controversies surrounding the taxonomy of the chosen taxa may cause additional problems. Riddle (1996) stated that skewed data would result from the misidentification of species. While the quantity of data for mammoths and mastodons is large compared to those for other Pleistocene taxa, debates on proboscidean taxonomy are prevalent (Osborn, 1922, 1925, 1936, 1942; Kurten and Anderson, 1980; Madden, 1981a; Holman, 1995b; Pasenko and Schubert, 2004). While only one mastodon species is known, the American mastodon (*Mammut americanum*), mammoth identifications in eastern and midwestern North America are controversial. All vertebrate paleontologists recognize the woolly mammoth (*Mammuthus primigenius*), however there are disagreements over the validity of a second species, the Jefferson mammoth (*Mammuthus* jeffersonii). Various researchers have classified the Jefferson mammoth as: (1) a valid species (e.g., Osborn, 1922; Holman, 2001), (2) a subspecies of the Columbian mammoth (*Mammuthus columbi*) common to the western United States (e.g., Kurten and Anderson, 1980; Agenbroad, 2005), (3) a synonym for the Columbian mammoth (e.g., Maglio, 1973), and (4) a hybrid between the Columbian and woolly mammoths (e.g., Fisher 2001, 2009). Therefore, in the Great Lakes region where two species of mammoths have been found, some of the skeletons identified as woolly mammoth *may* be those of Jefferson mammoths, but were not recognized as such. Due to this debate amongst paleontologists, some aspects of this thesis research will group all mammoth species, but where identified, data for the Jefferson mammoth are provided.

A simple observation of mammoth and mastodon data in FAUNMAP shows 206 records of *Mammut americanum* (American mastodon), 58 records for *Mammuthus jeffersonii* (Jefferson mammoth), and 28 for *Mammuthus primigenius* (woolly mammoth) across the continental United States. Abraczinkas (1992) documented 211 mastodon sites and 49 mammoth sites in Michigan alone, indicating both that the FAUNMAP database does not capture all reported fossil sites and that mastodon and mammoths are fairly common fossil occurrences in Michigan. Therefore, I collected additional mammoth and mastodon data from sources from the Great Lakes region not reported in FAUNMAP, such as from state scientific society publications, news reports and other lesser known print materials to compile a more complete database for analysis.

In the past, the best way to determine geographic ranges was through the use of Minimum Convex Polygons (MCP; Mohr, 1947). First introduced to study the ranges of modern animals, this method has become one of the main ways of assessing home ranges of animals around the world (e.g., Larter and Gates, 1994; Andrekas et al., 1999; Hanski et al., 2000; Davison et al., 2009). However, many prior investigations documented biases involved in this technique (e.g., Burgman and Fox, 2003; Downs and Horner, 2008; Nilsen et al., 2008), finding that it is highly dependent on sample size and range shape. Therefore, Kernel-based methods and Directional Distribution Ellipses were performed for this investigation. Using these data sources and methods (Worton, 1989; Seamon and Powell, 1996; Naparus and Kuntner, 2012), my research addressed the following questions.

Research Questions

Specifically, four questions were investigated in my M.S. research:

1) Are FAUNMAP-derived data of sufficient quantity and quality to permit accurate biogeographic studies on individual species during the Late Quaternary (terminal Pleistocene)? Or do they need to be augmented by the collection of additional data from lesser known journals, museum reports, newspapers and other items from the "gray literature?"

2) Can accurate mammoth and mastodon geographic ranges in the Great Lakes region be determined using presence-only data?

3) If so, can geographic range shifts for mammoth and mastodons be detected between two time periods, the LGM (Last Glacial Maximum, 24,000 to 18,000 cal yr BP) and the terminal Pleistocene (a time of ice sheet recession, 18,000-11,500 cal yr BP), using both dated and undated proboscidean locality data reported for the Great Lakes region?

4) Are mammoths and mastodons associated with different vegetation types in this region? If so, what plant communities were associated with each type of proboscidean?

While the ultimate aim of the research is to contribute data useful for forecasting future biotic changes in response to 21st century climate change, many steps must be done before this goal can be accomplished. Specifically, my research provides a preliminary step towards this ultimate goal and hopefully future research outside the scope of this thesis will involve such modeling. Even though this thesis research is preliminary, I hope it introduces significant improvements in the methods currently used to assess Pleistocene biogeographic range shifts in response to past climate change.

CHAPTER ONE: LITERATURE REVIEW

Mammoth and Mastodon Evolution, Biology and Biogeography

Megafauna

Mammoths and mastodons, along with giant sloths, giant beavers, saber-toothed tigers, Irish elk, and modern elephants, are called megafauna, which is a general term used to describe any large terrestrial animal and includes both those that are extinct and extant (Kurten and Anderson, 1980). Typically, the definition of megafauna includes an arbitrary body weight, but there is no agreement on what that weight should be (Marshall, 1984). The body weights range from >5 kg (Webb, 1984) to >44 kg (Martin, 1984). Kurten and Anderson (1980) created size categories: small (1 g to 907 g), medium (908 g to 181 kg), large (182 kg to 1.9 tons), and very large (>2 tons), with the term "megafauna" only applying to those in the large and very large categories. Some (Horton, 1984; Martin, 1984) simplified use of the term megafauna to that group of relatively large animals that became extinct before the Holocene, which began at 11,500 cal yr BP.

The large size of such animals has been attributed to Bergmann's Rule (*In* Schrieder, 1950). According to this rule, taxa found in colder climates are generally larger than those found in warmer locations; an adaptation to reduce their surface area to volume ratio. Larger animals have less surface area compared to the total volume, so they would lose less heat than smaller taxa during the Pleistocene glaciations. Due to their large size, megafauna are thought to be keystone species, taxa in which the structure of their habitat is intimately associated with their presence in the landscape (Owen-Smith, 1987; Barnosky et al., 2004; Johnson, 2009). Owen-Smith (1987), for example, attributed the maintenance of the tundra environments directly to trampling and browsing by megafauna.

Although there is much debate on the definition of megafauna, one thing is known for certain, many of these massive mammals went extinct near the end of the Pleistocene. During this time 29 North American megafauna genera disappeared and another 6 were extirpated (Faith and Surovell, 2009), and, in total, 97 megafauna genera became extinct worldwide (Barnosky et al., 2004). Some of the last to disappear were the mammoths and mastodons, which persisted until 14,800 to 13,000 cal yr BP in North America (e.g., Martin and Klein, 1984; Davies et al. 2009; Gill et al. 2009; Saunders et al. 2010; Faith 2011). However, some megafauna, such as modern elephants, gorillas, hippopotamus, and bears, escaped extinction (Koch and Barnosky, 2006). Questions have arisen concerning the timing (e.g., Stuart et al., 2004; Faith and Surovell, 2009), quantity (Guthrie, 1990), and cause of the extinctions (e.g., Koch and Fisher, 1989; Ugan and Byers, 2007; Firestone et al., 2007; Fisher, 2009).

While the actual cause is largely irresolvable (Marshall, 1984; Guthrie, 1990; Martin, 1990), four main hypotheses exist: (1) environmental and climate changes (e.g., Guthrie, 1984; Kiltie, 1984; King and Saunders, 1984), (2) overexploitation by humans, i.e., the “Pleistocene overkill” hypothesis, (e.g., Martin, 1967; Martin, 1984; Johnson, 2006; Surovell and Waguespack, 2008; Fisher, 2009), (3) a combination of both anthropogenic and environmental factors (Barnosky et al., 2004; Gill et al., 2009), and (4) an extraterrestrial impact (Firestone et al., 2007). This thesis will examine the environmental conditions in the Great Lakes region as they relate to mammoths and mastodons during the Late Pleistocene. Specifically, this time interval spans (1) the LGM, when the Laurentide Ice Sheet was at its maximum southern extent and had the greatest climatic influence on the Midwest region (24,000-18,000 cal yr BP), and (2) the termination of the last glaciation, in response to temperature changes and internal ice-sheet dynamics (e.g., Dyke and Prest, 1987; Clark et al., 2009).

Proboscideans

Proboscideans reached the height of their diversity in the Late Pleistocene (e.g., Kurten and Anderson, 1980; Rasmussen et al., 2006; Garza, 2007; Ugan and Byers, 2007; Woodman and Athfield, 2009; Graff and Bigelow, 2011). These extinct megaherbivores once roamed across the northern and southern hemispheres, with fossils recorded on the continents of Europe, Asia, Africa, North America and South America (e.g., Kurten and Anderson, 1980; Surovell and Waguespack, 2005). The Order Proboscidea has four families, Elephantidae, Mammutidae, Gomphotheriidae, and Stegodontinae, each containing many species (Kurten and Anderson, 1980). By the end of the Pleistocene, the species diversity of this order diminished because of extinctions, with only two extant species of proboscideans, the African elephant (*Loxodonta africana*) and the Asian elephant (*Elephas maximus*; Haynes, 1991).

Proboscideans are generally characterized by the presence of a trunk (or proboscis) that functions both as a nose for smell and hand to grasp plant foods. Other characteristics include pillar-like (or columnar) limbs that support the body on a horizontal vertebral column, large heads, modified incisors (tusks), and rounded feet with flattened pads on bottom (Holman, 1995b). Kurten and Anderson (1980) considered other morphological features for identification, such as a long humeri and femurs, short lower limb segments, and five-toed feet. The evolutionary trends for proboscideans are greater size, increased dental specialization, lengthening of limbs and trunk, and the shortening of the neck (Kurten and Anderson, 1980; Shoshani, 1998).

Using molecular studies, it has been determined that proboscideans are most closely related to the Order Sirenia, which includes dugongs, manatees, and sea cows (Tassy, 1996). The split between lineages may have occurred during the Late Cretaceous (Tassy, 1996). The oldest known proboscidean is *Anthracobune* sp., found in shallow or semi-aqueous environments during the early-middle Eocene, and looked much like a modern tapir (Kalbet al., 1996). Tassy (1996) considered *Anthracobune* (or Anthracobunids) to be the sister-taxa to all proboscideans. The monophyletic tree splits into *Moeritherium* spp. and *Deinotherium* spp. before coming to the main group of proboscideans, the Suborder Elephantiformes (Tassy, 1996). From this point, the Elephantiformes diverged into *Paleomastodon* spp. and *Phiomia* sp., which later split into the Elephantidae, a family that includes both elephants and mammoths, and Mammutidae (mastodons). Elephantidae later diverged into the other two families, Gomphotheriidae and Stegodontinae, while Mammutidae evolution remained stable (Figure 1-1; Tassy, 1996; Todd and Roth, 1996; Shoshani, 1998).

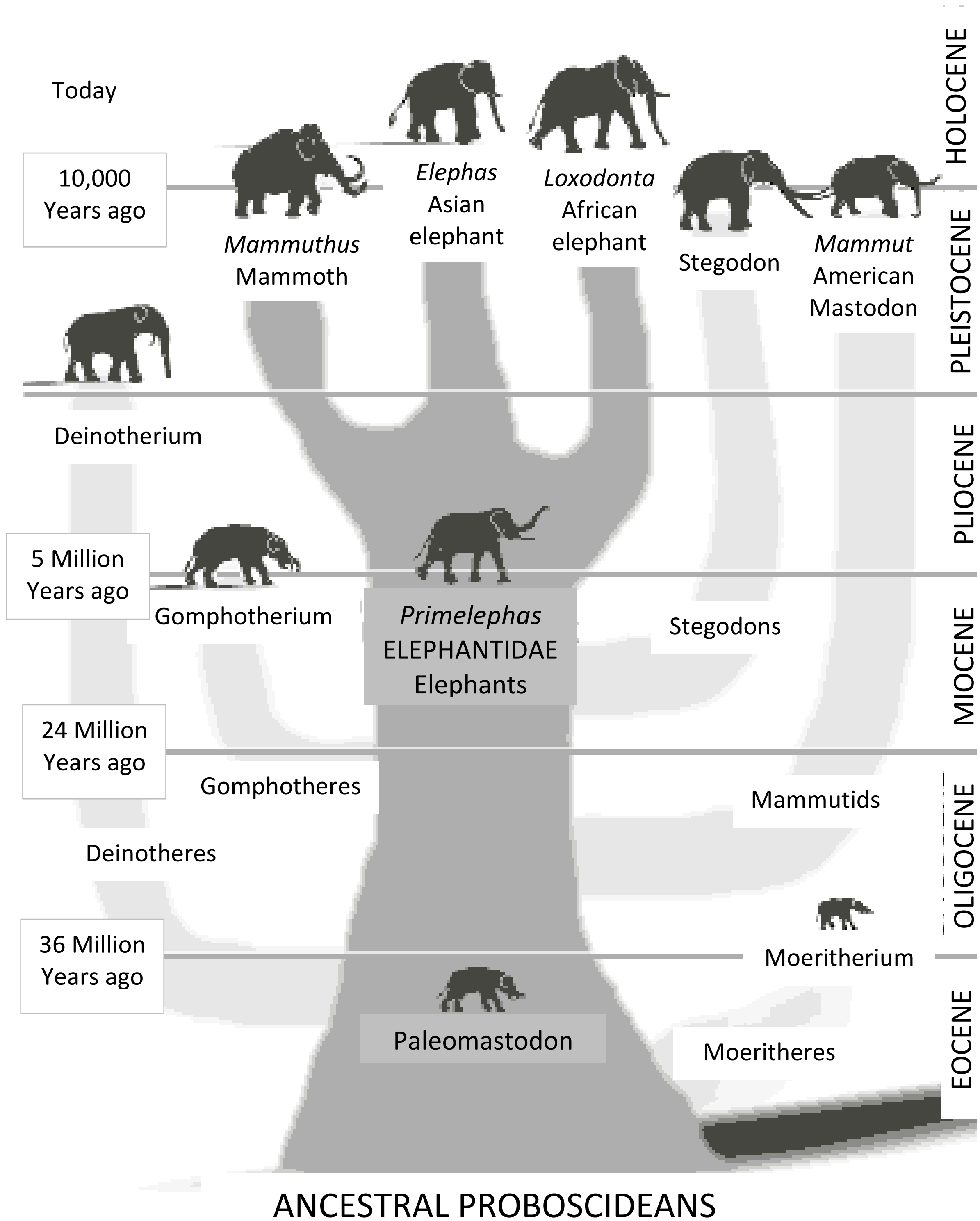

Figure 1-1: Illustration of Proboscidean evolution (from Garza, 2007). Note that *Mammut americanum* diverged early and remained evolutionary stable, while *Mammuthus* spp. and *Elephas* spp. evolved later, from the continuing Elephantidae line.

The first identified proboscideans occurred in Africa during the Upper Cretaceous and Lower Eocene (Osborn, 1922, 1936, 1942). However, due to much taxonomic controversy, it took until quite recently to finalize a modern image of proboscidean evolution (Tassy and Shoshani, 1996). The taxonomy of the order has been questioned and reviewed multiple times since the first discovery. Disputes over systematics resulted from morphological studies, which were severely limited by species identification based on tooth specialization and improper holotype designation of skeletons. In addition, multiple arguments rang out through academia concerning the “lumping” or “splitting” of different lineages. Osborn (1936, 1942) wrote the first monograph of the order, identifying five superfamilies and seven families, and is now considered to be a “splitter.” The modern view of proboscideans is much more conservative, recognizing two superfamilies and four families (Kurten and Anderson, 1980).

Mammoths and Mastodons

Mammoths (Family Elephantidae) and mastodons (Family Mammutidae) are two of the most studied taxa from the Pleistocene Epoch. Immunological and molecular studies place both the mammoths and mastodons firmly within the Order Proboscidea, separating them into different, but sister families on the same phylogenetic tree (Figure 1-1; Shoshani et al., 1985; Lowenstein and Shoshani, 1996). The geographic distributions of the taxa were very different from one another, however. Haynes and Klimowicz (2003), using FAUNMAP as a source, showed that mammoths and mastodons were highly segregated. Mastodons were typically found in the eastern United States and mammoths were more common in the Great Plains and western

United States.   Mastodons are considered to be the evolutionarily simpler taxa when compared to mammoths and therefore, will be described first.

Mastodons

During the Pleistocene, an ancestral mastodon species migrated from Eurasia into North America via the Bering land bridge, and evolved to become the American mastodon, *Mammut americanum*. This species was also the first mastodon to be named as *Elephas americanus* by Osborn (1936). Since then, the American mastodon has been renamed five times, ending with its current name, *Mammut americanum* (Skeels, 1962).

The earliest records for American mastodons date to the Blancan North American Land Mammal Age (4.9 to 1.8 million years ago), but the largest distribution was during the Rancholabrean Age (300,000 to 11,000 years ago), where they ranged from Alaska to Florida (Kurten and Anderson, 1980). Figure 1-2 shows the distribution of mastodons in the contiguous United States during the Late Quaternary and features three main clusters of sites, just south of the Great Lakes region, the Atlantic Coast, and California.

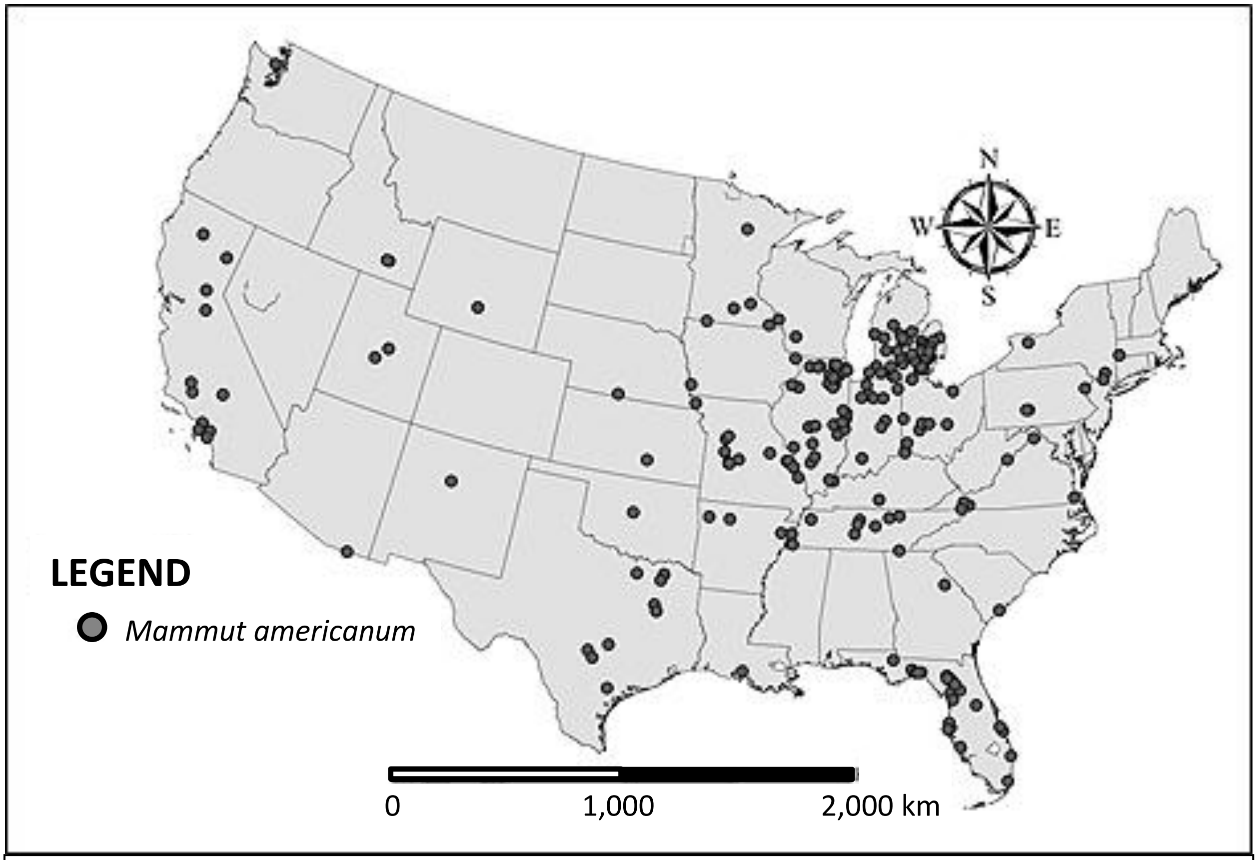

Figure 1-2: Mastodon distribution in the contiguous United States (from the FAUNMAP database). One can see three main clusters of site localities for the species: southern Great Lakes Region, Atlantic Coast, and California.

Morphological characteristics of the mastodon include a flat skull with tusks that exit the skull horizontally, curving outwards and then downward (Figure 1-3). They are also characterized by a robust, piglike body, with all legs being the same length (Skeels, 1962; Kurten and Anderson, 1980; Holman 1995b, 2001), as shown in Figure 1-3. Skeels (1962) stated that the average shoulder height of the American mastodon is 2.7 - 3.0 meters with an average body length of 45 meters. Holman (2001) estimated that the species most likely weighed four to six tons.

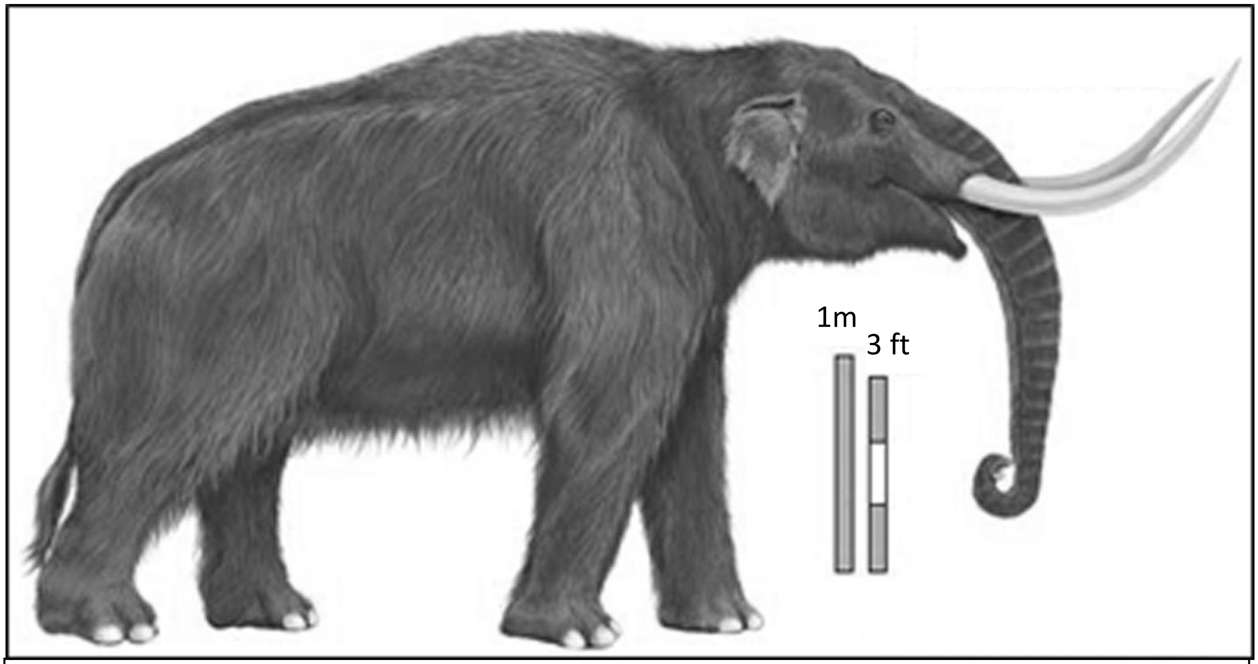

Figure 1-3: Illustration of *Mammut americanum* (from Encyclopaedia Brittanica, 2006). Typical morphological characteristics of this species include a flat skull, tusks that first curve outward then downward, and a robust, pig-like body.

Figure 1-4: Illustration of *Mammut americanum* tooth. The tooth morphology of this species is characterized by a series of large knobs arranged in parallel rows.

Mastodon diet is reflected in the dental morphology, which consists of a series of large knobs, usually arranged in two parallel rows, as seen in Figure 1-4. This pattern provides the origin of their name, which literally means "nipple tooth" (Holman, 2001, 1995b). The chewing motion of mastodons was a crushing movement, with the lower jaw moving up and down against the upper jaw (Kurten and Anderson, 1980). Between the dental morphology and chewing motion, it has been determined that mastodons were primarily browsers, eating woody materials in woodlands and shrub areas (Shoshani, 1998). Studies analyzing dental enamel wear confirm the preference of twigs in the mastodon diet (Green et al., 2005). Furthermore, pollen and macrofossil studies associated with mastodon skeletons, and the analysis of their dung, have shown that mastodons preferred spruce open woodlands and forests in the northern portion of their range, which includes the Great Lakes region (Kapp, 1986; McAndrews and Jackson, 1988; McAndrews, 2003). However, Gobetz and Bozarth (2001) showed an unexpected high number of grass phytoliths embedded in the mastodon teeth they studied. This disparity may show that mastodons had a wide ranging diet highly dependent on their location. This interpretation is supported by studies of mastodons from Florida and other southern locales in the United States that indicate that these megafauna occupied a variety of habitats, including those dominated by broadleaf deciduous trees (Taggart, 1983; Newsom and Mihlbachler, 2006).

Mammoths

Mammoths are the more complicated of the two taxa, consisting of many species instead of one. The phylogenetics of mammoths starts in the early Eocene, when Elephantidae diverged into three different lineages: *Loxodonta*, *Elephas*, and *Mammuthus* (Todd and Roth, 1996). The *Loxodonta* spp. remained in Africa, eventually evolving into the modern day African elephant (*Loxodonta africana*). The *Elephas* lineage left Africa before the end of the Pliocene, becoming a dominant group throughout Eurasia. Remnants of the group can be seen in southeastern Asia as the Asian elephant (*Elephas maximus*). The third lineage (*Mammuthus*) entered Eurasia during the early Pleistocene and spread throughout the northern hemisphere. All species of

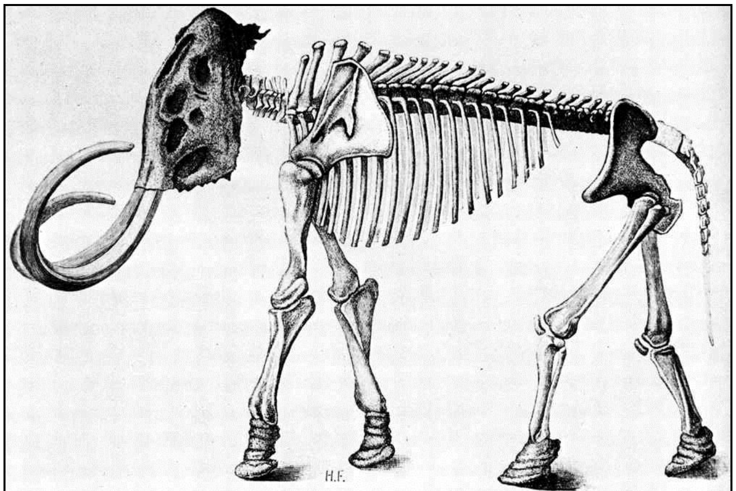

Figure 1-5: Skeleton view of mammoth (from Holman, 2001). Morphological characteristics of mammoths include domed skulls, tusks that first exit downwards and then curve outwards, longer front legs, and an arched back.

mammoths were descended from this lineage (Kurten and Anderson, 1980; Todd and Roth, 1996; Shoshani, 1998).

Due to their common ancestry, extinct mammoths and modern elephants look very similar (Haynes, 1990, 1991). The morphological characteristics of mammoths include a domed skull with tusks that exit the skull vertically first and then curve downward and then outward (Skeels, 1962), as depicted in Figure 1-5. Compared to mastodons, mammoth have longer front legs, with the rear end being lower to the ground, and an arched back that ended in a hump directly behind the neck (Anderson, 1984).

Available fossil data indicate that the first mammoths (probably *Mammuthus trogontherii*, steppe mammoth) had crossed the Bering land bridge from Siberia into North America (Alaska) by about 1.1 million years ago (Lister and Bahn, 2007). This mammoth species spread and eventually evolved into *M. columbi* (Columbian mammoth) in the western United States, and roamed as far south as Nicaragua (Kurten and Anderson, 1980). Available data suggest that the Columbian mammoth consumed grasses and herbaceous plants as well as the leaves and fruits of deciduous trees and shrubs in a “savanna-like” environment (Lister and Bahn, 2007). The ranges of *M. columbi* and other mammoth species, as reported in FAUNMAP, are shown in

Figure 1-6. Although *M. imperator* is shown in this figure, most mammoth experts contend that it is not a valid species, and it has been reclassified as *M. columbi* (e.g., Osborn, 1942; Kurten and Anderson, 1980).

Mammuthus primigenius (woolly mammoth) is well accepted to have arrived later in North America (via the land bridge), at about 100,000 yr BP (Kurten and Anderson, 1980). This species was especially adapted to cold climates and, as shown in Figure 1-6, had a distribution around the southern Great Lakes during the Late Pleistocene (Kurten and Anderson, 1980; Lister and Bahn, 2007). As mentioned above, recognition of *Mammuthus jeffersonii* (Jefferson mammoth) as a separate species, as depicted in Figure 1-6, is controversial, and will be discussed in detail below.

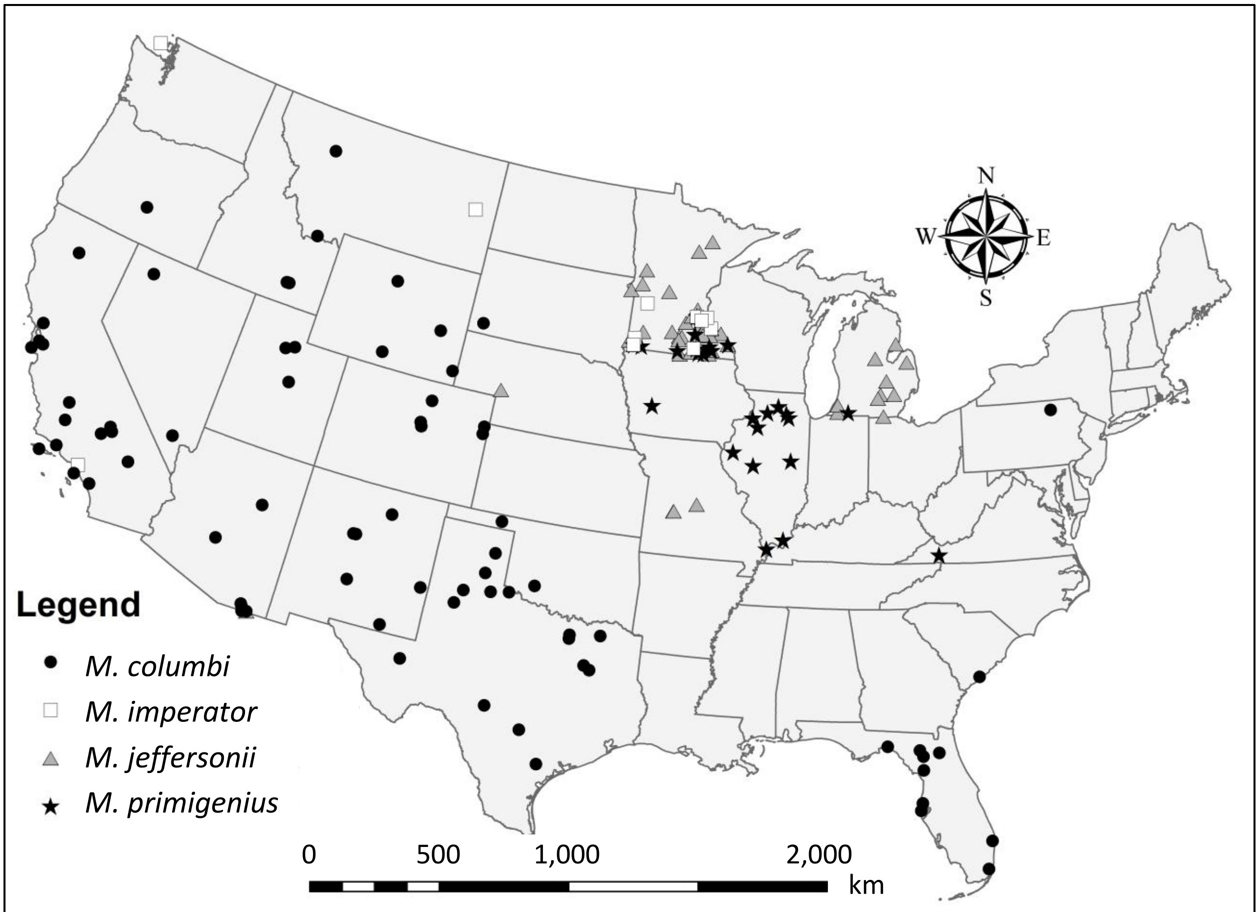

Figure 1-6: Mammoth distribution in the contiguous United States using the FAUNMAP database. Clusters of sites can be seen in the western portion of the United States as well as around the Great Lakes region and Florida.

Dental morphologies are the main differences between mammoth species (Osborn, 1942). In general, mammoth teeth were composed of a series of thin, transverse rows of enamel (Skeels, 1962), as shown in Figure 1-7. The number of plates, distance between plates, and thickness of enamel varies between species, and is therefore recognized as a valid way of differentiating species. However, since many of these characteristics are gradational, the firm identification of species can still be questioned (Madden, 1981a).

Figure 1-7: Picture of a mammoth tooth (from Lister and Bahn, 2007). Mammoth teeth are composed of a series of thin, transverse rows of enamel.

Due to this controversy, the actual number of mammoth species is highly debated. From the time Blumenbach named the first mammoth, *Elephas primigenius,* in 1799 (Osborn, 1936), the taxonomic divisions of species have been questioned, and the actual number depends on the researcher doing the revision. Holman (1995b) stated there are two general views concerning the number of mammoth species, one consist of five individual species while the other consists of one highly variable species. The most widely used taxonomic revision is within Kurten and Anderson (1980). They identified four North American species (*M. meridionalis, M. columbi*, *M. jeffersonii*, and *M. primigenius*), agreeing with Osborn's (1942) reclassification of what was called *M. columbi* to *M. jeffersonii*, and what was *M. imperator* to *M. columbi*. In addition to Kurten and Anderson's (1980) recognition of four mammoth species, other sources state the number of mammoth species to be five (Pasenko and Schubert, 2004; Holman, 1995b), six (Madden, 1981a), or as many as 16 (Osborn, 1942).

Based on dental morphology it appears that mammoths chewed like other grazers, with the lower jaw moving back and forth along the upper jaw (Holman, 1995b, 2001). Confirming this interpretation, ecological studies associated with mammoths indicate that they preferred open grassland or steppe habitats (Guthrie, 2001; Haynes and Klimowicz, 2003). Studies of mammoth dung (Agenbroad and Mead, 1989; van Geel et al., 2008) indicate that their diet consisted primarily of graminoids, grasses and grasslike sedges. Freeze-dried woolly mammoth carcasses recovered in Siberia have preserved stomach contents that are ~90% composed of grasses and sedges, with small amounts of browse of boreal trees and arctic shrubs (Lister and Bahn, 2007). Saunders et al. (2010) discussed a Jefferson mammoth find associated with pollen data indicative of spruce- or black ash-dominated woodlands in Illinois. These studies suggest that mammoths were primarily grazers, consuming grasses and sedges. But both woolly and Jefferson mammoths could also browse on the leaves of shrubs and trees, and thus could have had a slight overlap in habitats with mastodons in the Great Lakes region (Yansa and Adams, 2012). Given that two species have been identified in the Great Lakes region, *Mammuthus primigenius* (woolly mammoth) and *Mammuthus jeffersonii* (Jefferson mammoth), they are thus described in further detail below.

Woolly mammoth (*Mammuthus primigenius*)

Woolly mammoths (or *Mammuthus primigenius*) were present throughout the continent from the mid to late Sangamon interglacial (sometime between 100,000 and 75,000 cal yr BP) to the Late Wisconsin glacial. They inhabited what are thought to be tundra and northern taiga (boreal forest) habitats in Europe and North America (Holman, 2001), however, the environment at that time lacked an exact modern analog. Guthrie (2001) describes it in Siberia as a cold and arid “mammoth steppe” with a somewhat more mesic environment restricted to the Bering land bridge (Beringia) that linked Siberia and Alaska. The environment mammoths and other megafauna occupied in the Midwest and eastern United States also was novel, lacking an exact modern counterpart (e.g., Webb et al., 2004; Gill et al., 2009).

This species is considered to be at the most advanced stage in mammoth evolution and reflect their adaptation to a cold glacial climate (Madden, 1981a; Kurten and Anderson, 1980). They are the smallest of the mammoths, with a shoulder height of 2.8 meters (Kurten and Anderson, 1980). They are characterized by greatly curving tusks and long, shaggy hair. In addition to the typical mammoth characteristics, the woolly mammoth also had a short tail, small ears, and the trunk had two “fingers” at the tip (modern elephants only have one; Kurten and Anderson, 1980; Haynes, 2001). Their more dexterous trunks would have allowed them to pick up delicate and small plant leaves and flowers (Lister and Bahn, 2007).

The dental morphology of the woolly mammoth was characterized by more plates on their cheek teeth, as well as the plates being more compressed together, than other mammoth species (Madden, 1981a). The third molar is the typical tooth used for identification between mammoth species. For the woolly mammoth, the third molar had between 24 and 27 plates, with a density of 9 to 13 plates per 100 millimeters (average 10; Skeels, 1962).

Jefferson mammoth (*Mammuthus jeffersonii*)

Named for President Thomas Jefferson, the Jefferson mammoth (*Mammuthus jeffersonii*) was first documented by Osborn (1922), who determined that the holotypes of the previously identified *M. jacksoni* and *M. imperator* were indistinguishable. He combined the two species into one group and renamed it *M. jeffersonii.* Kurten and Anderson (1980) agreed with Osborn (1922), but Madden (1981a) gave the name *M. jacksoni* priority and dismissed *M. jeffersonii*. Therefore, even with the clarification of Osborn (1922) and Kurten and Anderson (1980), the taxonomic identification of *M. jeffersonii* is still debated (Osborn, 1942; Skeels, 1962; Pasenko and Schubert, 2004). Pasenko and Schubert (2004) proposed that *M. jeffersonii* only represents a geographic variant of *M. columbi* and others (e.g., Holman, 2001) believe it is simply a hybrid between *M. primigenius* and *M. columbi*. For these reasons, very few fossil skeletons have been identified as *M. jeffersonii*. So, if this species designation is indeed valid, then some of the *M. primigenius* and *M. columbi* remains have been misidentified and could instead be those of *M. jeffersonii* (Skeels, 1962). Obviously, a comprehensive re-examination of all mammoth fossils needs to be done to sort out this taxonomic quandary, but for the purposes of this thesis, I accept the validity of *Mammuthus jeffersonii*, which is in agreement with Saunders et al. (2010) and several other mammoth experts.

Occurring from sometime in the Sangamon interglacial to the Late Wisconsin, the Jefferson mammoth is viewed to be the culmination of the *Mammuthus meridionalis – M. columbi* line, and is considered to be the northern equivalent of *M. columbi* (Holman, 2001). Standing at 3.2 to 3.4 meters tall at the shoulder, it is one of the largest mammoths identified (Kurten and Anderson, 1980). Several specimens of a smaller example of the Jefferson mammoth (*M. jeffersonii exilis*) have recently been identified on islands off the coast of California and the Siberian Arctic (2.4 to 2.7 meters tall; Kurten and Anderson, 1980; Azzaroli, 1981; Madden, 1981a,b; Vartanyan et al., 1993; Roth, 1996; Graham, 2001).

Skeels (1962) first described the dental morphology of *M. jeffersonii* as having 25 plates on the upper third molar and 24 plates on the lower third molar. Kurten and Anderson (1980) further identified the dental characteristics to have between 20 to 24 plates on each molar, with a frequency of 5 to 7 plates per 100 millimeters, and an enamel thickness of 2.0 to 2.3

millimeters. However, they also recognized more advanced individuals with 24 to 30 plates, a plate frequency of 7 to 9 per 100 millimeters, and an enamel thickness of 1.5 to 2.0 millimeters. The dental overlap of *M. primigenius* and *M. jeffersonii* is recognized to be one of the major causes of species misidentification (Pasenko and Schubert, 2004). In addition to the physical characteristics of mammoths and mastodons, behavioral characteristics must also be understood in order to gain an understanding on how these mammals interacted with their environments.

Social and Migratory Characteristics of Mammoths and Mastodons

Mammoth and mastodon social behavior has been hypothesized using modern elephants as an example. Since the two living lineages of Elephantidae are largely social creatures, Haynes (1990, 1991) inferred that mammoth and mastodon social structure was likely similar. Some inferred behaviors include the separation of females and bulls in different herds except for breeding and nomadic migration. While herd structure is largely unknown, the concept of migration has been studied using age profiles (Churcher, 1980) and isotope studies (Hoppe et al., 1999).

Churcher (1980) used circumstantial evidence, such as age profiles (histograms of the populations' ages based on skeletal growth characteristics and teeth), faunal associations, and geological settings, as a basis for determining whether mammoths migrated. He concluded that mammoths (*M. columbi* and *M. primigenius*) were hunted by humans as they made their seasonal migrations that covered distances as long as 2,400 kilometers one way. In contrast, Haynes (1991) observed modern elephants only exhibited shorter distance nomadic migratory patterns, and hence he assumed mammoths would exhibit the same. Hoppe et al. (1999) attempted to determine which of these two viewpoints is most correct. Using strontium isotope chemistry, they determined the migratory patterns of mammoths and mastodons. The strontium isotope ($^{87}Sr/^{86}Sr$) ratio in vertebrate fossils varies according to the environment and differences are recorded in the mineralized structures, such as bone or tooth enamel. By mapping local strontium isotope ratios across an area, the isotope analysis can pinpoint the locations where a particular piece of bone originated. By comparing where the bone was found and where the strontium isotope analysis indicated the bone mineralized, a migration route can be determined. They concluded that mastodons may have undertaken migrations with distances between 120 and 300 kilometers, but no more than 700 kilometers. Mammoth strontium isotopes did not vary, suggesting they did not range more than a few hundred kilometers, showing a more local, nomadic migratory pattern.

Mammoth and Mastodon Biogeographies

Using the current extent of knowledge about mammoths and mastodons and their living relatives, the elephants, a biogeography study can be conducted based on their inferred behavior, morphology, and habitats. By studying the biogeography of proboscideans, and other extinct megafauna, we can attain a better understanding about range shifts of large herbivores during times of rapid climate change, such as what we are experiencing today and into the near future (e.g., Burns et al., 2003; Thuiller et al., 2006; Davies et al, 2007; Keane et al., 2007). Biogeography studies of mammoths and mastodons in the past have mostly consisted of integrating sources into a total list of fossil-bearing sites (Anderson, 1905; MacAlpin, 1940;

Skeels, 1962; McAndrews and Jackson, 1988; Shoshani, 1989; Abraczinkas, 1992, 1993; Agenbroad, 2005) and general observations of range locations (Holman, 1991), and distributions related to geologic features (Abraczinkas, 1992), but other studies have tried to use modern elephants as a basis for site preference.

In the Great Lakes region, the Mason-Quimby Line is a line drawn across the northern extent of all valid mammoth and mastodon records in Michigan, as well as the northern extent of most of the Paleoindian discoveries in the state. It was first introduced by University of Michigan archaeologists R.J. Mason (1958) and G.I. Quimby (1958, 1960). While reference to this line has been questioned in the past (Cleland, 1966), it is still mentioned in most publications, including in Yansa and Adams (2012) where the line was extended westward across Wisconsin and Minnesota. Holman (1991) also noted that this line encompassed the northern limit of all previously reported sites of extinct Pleistocene vertebrates in Michigan. Reasons for the Mason-Quimby Line are not clear, but Holman (1991) hypothesized the line represented a boundary between the sterile environment left behind after the glacial retreat to the north and the land to the south recolonized by plants and animals.

Abraczinkas (1992) tried to determine whether there was a spatial relationship between mammoth and mastodon site locations and surface saline water. Modern elephants have a physiological need for sodium and are known to travel to sodium-rich locations to correct the deficit. Using a self-generated database of proboscidean sites across the state of Michigan and salt sites, Abraczinkas (1992) calculated distances and frequency distributions in relation to known salt-water sources. She concluded that the mammoth and mastodon locations were not significantly different than a random distribution. Alternatively, McAndrews (2003) proposed that mastodons consumed salt-laden clays to help detoxify the chemicals found in the spruce needles and twigs they consumed, based on his identification of clay and spruce browse in the dung recovered from the Hiscock mastodon site in New York.

One problem with biogeography studies associated with historical ranges is the difficulty in attaining distribution data. For example, Abraczinkas (1992) had fourteen collaborators to help document mammoth and mastodon sites in Michigan and they still mentioned the possibility of missing sites. With more documented sites across the continental United States, a higher sample number would have resulted in more powerful statistics and a different conclusion could have resulted. Due to this problem, the number of studies focusing on historic distributions is severely lacking. However, with the creation of databases that were previously unavailable, the number of these types of studies will hopefully begin to increase. This research hopes to address the problem of obtaining distribution data by assessing the most used database for these types of studies, FAUNMAP, as well augmenting the available data by incorporating site localities previously published in obscure locations, such as state academy journals and museum reports.

FAUNMAP

FAUNMAP Database

With the realization of the difficulties attaining data to perform biogeography studies, databases documenting animal site locations became common in the late 20th century.

FAUNMAP is an example of one of these databases. Under the direction of Drs. Russell W. Graham and Ernest L. Lundelius, Jr., FAUNMAP focused on documenting the presence of Pleistocene mammals through the United States and was initially published in 1994 by the Illinois State Museum (FAUNMAP Working Group, 1994).

In addition to the directors, the FAUNMAP Working Group (1994) consisted of three compilers and fifteen regional collaborators. Using paleontological and archaeological sources, over 2,919 fossil mammal sites were documented across the United States. The selection criteria for each site were that each site must have a known geographic location, chronology, and voucher specimens in a public institution. The FAUNMAP database also consists of two separate databases – archival and research. The archival database contains data as they were originally reported while the research database has been filtered to standardize the taxonomy, eliminate mixed faunal assemblages, and to accept or reject chronologies (FAUNMAP Working Group, 1994).

The primary objective of FAUNMAP was to create a database that could be used to investigate questions concerning the evolution of mammal communities during the fluctuating climatic conditions of the late Quaternary (FAUNMAP Working Group, 1994). With the advent of geographic information systems (GIS), the database could be used for spatiotemporal studies focusing on the analysis of mammal communities. The database was made electronically available in 1996, allowing anyone to query the database for any of the documented species. Current ranges of extant species were also added during this time, allowing a qualitative assessment of faunal distribution change (FAUNMAP Working Group, 1996a). A few years ago the FAUNMAP database was merged into a larger umbrella database containing electronic data from numerous fossil proxies called NEOTOMA (http://www.neotomadb.org/). But for the purpose of this thesis the original name for the vertebrate database, FAUNMAP, is used as it was this dataset that I acquired and incorporated in my newly expanded database.

Biogeography Studies Utilizing FAUNMAP Data

From the first publication of the FAUNMAP data, many scientists (e.g., Burns et al., 2003; FAUNMAP Working Group, 1996b; Riddle, 1996) have used the data to assess changes in mammalian communities through the Pleistocene. FAUNMAP Working Group (1996b) used the data to determine whether mammalian communities during the Pleistocene followed the Clementsian or Gleasonian models. Clementsian communities consist of large groups of species that are in equilibrium with climate and would have moved north or south with climatic fluctuations as a whole. The Gleasonian model assumes species exhibit a more individual approach in response to climate fluctuations, changing their ranges in accordance to their individual tolerances. The end product of a Gleasonian model would show varying rates, times, and directions of migrations. Using the FAUNMAP Data, the FAUNMAP Working Group (1996b) determined that species responded to climate fluctuations in a Gleasonian fashion.

Riddle (1996) used FAUNMAP data to assess endemism during the Pleistocene. Endemism is an ecological term meaning that a species is unique to a particular area. Utilizing the outcomes of the FAUNMAP Working Group (1996b), Riddle examined the ranges of North American mammals to determine whether the data provided evidence for range-shifting that resulted in a breaking of barriers associated with endemism. Examples of barriers associated with endemism are physical features, such as mountains, water bodies, or ecological features, such as habitat boundaries. By combining geomorphologic provinces across the United States and the FAUNMAP data of rodent populations, he determined that very little range-shifting occurred outside of the geomorphologic provinces in which they currently reside. Riddle's (1996) conclusion supports the concept of endemism within Late Pleistocene communities.

The majority of studies utilizing FAUNMAP data have attempted to determine the responses of mammalian communities in response to climate change. Burns et al. (2003) used the data to assess the ability of the United States national parks in protecting the mammalian diversity as their ranges shift in response to 21st century climate change. They identified eight parks across the United States, each associated with different vegetation. Using Pleistocene mammal analogs, they determined the likely range shifts of the species under different climate change scenarios. Burns et al. (2003) thusconcluded that if the carbon dioxide levels doubled, the U.S. national parks could lose between 0% and 20% of the current mammal diversity in any one park.

Lyons (2005, 2003) used FAUNMAP data to quantitatively assess the amount of range shift that occurred throughout the Pleistocene. Using the outcomes of the FAUNMAP Working Group (1996b), her hypothesis was that range shifts of individual species were independent of one another. The conclusions of the research shows that communities were more similar than the Gleasonian model would predict. She found that very few species show large range shifts, but much variation existed between the degree of shifting, in both size and direction.

Problems Associated with FAUNMAP Data

Although FAUNMAP has proven to be a useful database, problems still exist as far as database limitations are concern (FAUNMAP Working Group, 1994). They cited limitations in the search function, such as the inability to query sites older than 40,000 yr BP and younger than 500 yr BP (Post-Columbian) sites. Many site data published prior to 1950 were not incorporated into the database due to the lack of radiocarbon (^{14}C) or other temporal controls. The database is also restricted to mammals even though it has been recognized that other Phylum (Aves, Reptilia, Amphibia, Pisces) play important roles in animal communities (FAUNMAP Working Group, 1994). In addition, other environmental data are not included in the database, such as pollen and plant macrofossil studies or associated vertebrate and invertebrate remains found nearby (FAUNMAP Working Group, 1996a).

Other problems have been mentioned in literature utilizing FAUNMAP data (Walker, 2000; Riddle, 1996). Riddle (1996) stated that skewed data would result from the misidentification of species. Additional review of FAUNMAP was performed by Walker (2000), who focused specifically on the American pronghorn (*Antilocapra americana*). Some limitations mentioned were the necessity to query each individual time period to get all of the distribution data, and that if an exact age is unknown for a particular site, the data would not show up. He also stated that the time periods overlap, sometimes having the same record appear twice. In addition, since the records are only for the United States, range shifts for species are skewed if they extend into Canada. Lyons (2003, 2005) also recognized this problem. In general, Walker (2000) concluded that FAUNMAP is highly incomplete, citing the problem as being that only a few cultural resource management reports were included in the database and data published in newspapers, or state journals, were largely ignored. Hence the main goal of this thesis was to address these shortcomings of FAUNMAP by compiling a more accurate and complete database that incorporated data from the “gray literature” and in doing so better address biogeographic research questions.

Summary

In summary, during the terminal Pleistocene, many species went extinct, but those most affected were the largest mammals, the megafauna, and of these the Order Proboscidea was greatly impacted. Consisting of four families, Elephantidae, Mammutidae, Stegodontinae, and Gomphotheriidae, proboscideans reached the peak of their diversity during the terminal Pleistocene, but only two elephant species survived into modern day (*Loxodonta africana* and *Elephas maximus*; Kurten and Anderson, 1980). Many controversies surround both the term “megafauna” and explanations for their extinction, but that is not the focus of this thesis. Instead, I propose that by improving the knowledge of these taxa and their biogeography, specifically by reconstructing the home ranges and habitats of proboscideans in the Great Lakes region, will result in a better understanding of modern species extinctions and range shifts in response to the changing climate of the 21st century and beyond.

Even though mammoths and mastodons went extinct during the terminal Pleistocene, they are two of the most widely recognized proboscideans and are much loved by the public, as evident in numerous movies and TV documentaries. The main difference between the two taxa is dental morphology (knobs for mastodons versus ridges for mammoths), but they also differ in body shape. Mastodons are characterized by flat skulls, and robust, piglike bodies, while mammoths have domed skulls and have longer front legs with a sloped back. From associated plant fossil and isotope studies, it has been determined that mastodons and mammoths may have occupied different niches (e.g., Yansa and Adams, 2012). Mastodons were browsers, typically associated with spruce woodlands, and mammoths were predominately grazers of graminoids (grasses and grass-like plants, such as sedges; Kurten and Anderson, 1980; Madden, 1981a; Holman, 2001).

Many biogeography studies have concerned Pleistocene mammals, such as mammoths and mastodons, during the terminal Pleistocene (e.g., Agenbroad et al., 1990; FAUNMAP Working Group, 1996b, Bearrs and Kapp, 2003). FAUNMAP was originally created to study the relationships between such mammal distributions (FAUNMAP Working Group, 1994). Since that initial publication, many studies have used the data to determine mammal community dynamics, endemism, and even to hypothesize the loss of biodiversity for future climate changes (FAUNMAP Working Group, 1996b; Riddle, 1996; Burns et al., 2003). Although FAUNMAP has been useful, studies have also shown limitations in the electronic database, such as missing data and the complexity of querying (Riddle, 1996; Walker, 2000,).

While mammoths and mastodons are considered by many to be keystone species, few studies have specifically focused on geographic ranges for these taxa. Instead recent research is primarily focused on vegetation analyses of individual sites or genetic analyses of paleontological materials. Additionally, while there are many biogeography studies utilizing the

FAUNMAP database, very few of them are focused on individual taxa, such as proboscideans, or on specific regions, such as the southern Great Lakes region. Hence, this thesis is designed to reconstruct mammoth and mastodon geographic distributions in the southern Great Lakes region and associate them with paleohabitats, as inferred from fossil pollen data, to test several biogeographic research questions.

CHAPTER TWO: STUDY AREA

Great Lakes Region

The study area for this investigation is the Great Lakes region of the United States, specifically, Minnesota, Wisconsin, Illinois, Indiana, Michigan, and Ohio. This study area was chosen due to the numerous pollen and plant macrofossil studies (e.g., Kapp, 1986, 1999; McAndrews and Jackson, 1988; McAndrews, 2003) and extensive mammoth and mastodon sites (e.g., Anderson, 1905; Skeels, 1962; Abraczinkas, 1992; FAUNMAP Working Group, 1994; Holman, 2001) investigated in the area.

As seen earlier in Figures 1-2 and 1-6, there are large clusters of both mammoth and mastodon sites in the Great Lakes region when viewing the plotted FAUNMAP data. When looking at individual species within the region (Figure 2-1), one can see that smaller clusters exist, which may indicate habitat partitioning. However, the FAUNMAP data portrayed in Figure 2-1 are incomplete; most notable are the absence of data for Wisconsin, which is an artifact of these data not published and hence not entered into FAUNMAP. In my research for this thesis, I acquired data for Wisconsin and filled in other gaps in the expanded database I created, which is significantly more complete than FAUNAMP, and will elucidate more and newly discovered, patterns in mammoth and mastodon range distributions and habitats.

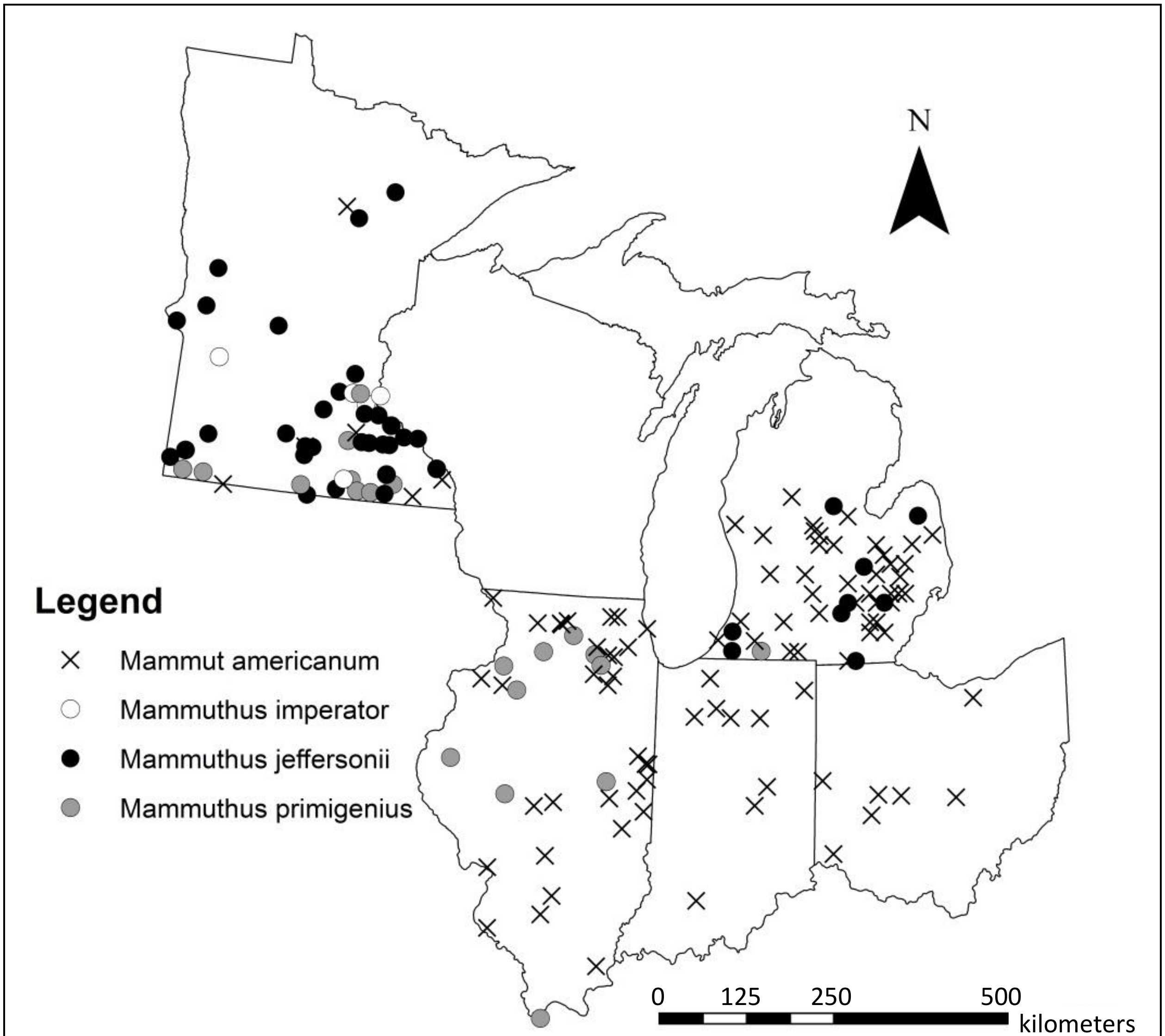

Figure 2-1: Mammoth and mastodon distribution in the Great Lakes region, based on the FAUNMAP dataset, which suggest that each species appears to have a different range. *Mammuthus jeffersonii* occurrences appear to cluster in southeastern Minnesota and southern Lower Michigan, *Mammuthus primigenius* sites in southeastern Minnesota and Illinois, and *Mammut americanum* locales primarily found in the eastern Great Lakes states (Illinois, Indiana, and Michigan). Note the absence of data for Wisconsin, which is discussed in text.

Geologic Setting

The temporal setting for this study is during the Late Pleistocene, specifically during the Last Glacial Maximum (LGM, 24,000-18,000 cal yr BP) and the terminal Pleistocene (18,000-11,500 cal yr BP). The reason for this is that mammoths and mastodon populations had reached their peak in diversity as well as in range size and had become extinct near the end of the Pleistocene. The Pleistocene epoch is the part of the Quaternary period that is generally considered to be the last ice age. Ranging in time from 2,590,000 to 11,500 years ago, the Pleistocene is known for numerous advances and retreats of continental ice sheets and alpine glaciers over much of the northern hemisphere (Anderson, 1984; Holman, 1995b; Breckenridge and Johnson, 2009; McIntosh et al., 2011).

The study area had been repeatedly impacted by these Pleistocene glaciations. The best understood glacial period is the Wisconsin Glaciation (Figure 2-2), because it was the most recent advance and retreat. The Wisconsin glacial interval lasted from about 110,000 to 11,500 cal yr BP, during which time, the Laurentide Ice Sheet advanced and retreated many times over eastern and central North America (Dreimanis, 1977; Attig et al, 2011; Curry and Petras, 2011). The most extensive advance of ice during this interval occurred approximately 24,000-18,000 cal yr BP, during the LGM of the Late Wisconsin, when the Laurentide Ice Sheet covered the Great Lakes (Andrews, 1987; Dyke and Prest, 1987; Holman, 2001; Larson and Schaeztl, 2001; Krist and Lusch, 2004). This ice sheet stretched from Alberta to Maine, extending southward to almost identical latitudes in present-day Illinois, Indiana, and Ohio, and completely covered Ontario, Michigan and eastern Wisconsin with ice (Figure 2-2; Holman, 1995b, 2001). The ice sheet then began to melt at a few places along its margin at 21,000 cal yr BP, in earnest starting at ~18,000 cal yr BP, eventually uncovering all of the Great Lakes by 12,000 cal yr BP, and largely disappeared in the Hudson Bay area by 6,800 cal yr BP (e.g., Mielke, 1989; Carlson et al., 2008).

Figure 2-2: Map showing the maximum glacial extent of the Illinoisan and Wisconsin glaciations in the Great Lakes region (from Holman, 2001). During the Wisconsin glaciation, the Laurentide ice sheet extended as far south as Illinois, Indiana, and Ohio, completely covering the northern portions of the states as well as Ontario, Michigan, and eastern Wisconsin.

In the Great Lakes region, the legacy of the last glaciation is clearly evident in the landforms that were created by the recession of the Laurentide Ice Sheet. Glacial landforms, such as drumlins, eskers, moraines, and kettles, can be seen across the Great Lakes region. Drumlins are formed from glacial till that has been modified into a streamlined shape according to the direction of the ice flow. Their shape is usually an elongated, symmetrical ellipse, with the steeper side pointing upstream of the glacial migration (Chorley, 1957; Bennett and Glasser, 2009). Moraines, or terminal moraines, form as the glacier temporarily suspends migration, allowing till to be deposited in front of the stationary glacier due to the internal movement of sediments. Terminal moraines are the most distinctive glacial landform, marked by the winding ridges with poorly sorted deposits (Ashworth, 1987; Bennett and Glasser, 2009). Like drumlins and moraines, eskers are also depositional landforms, but they form from the deposition of sediment by flowing water under the ice (Ashworth, 1987; Bennett and Glasser, 2009; Blewett et al., 2009). Typically looking like long, winding ridges, or s-shaped, eskers are formed as outwash deposits, located in the postglacial valley (Ashworth, 1987). Kettles are hollows formed after an ice block that had previously fallen off the glacier and buried melts (Ashworth, 1987). Often filled with water, they are also known as kettle lakes (Bennett and Glasser, 2009; Blewett et al., 2009). An additional landform formed indirectly from glacial activity is dunes. During times of glacial retreat, large areas of land devoid of vegetation were revealed. Sand dunes often formed during these times, when large amounts of glacial outwash small enough for wind-blown travel, such as sand, were available. Many types of sand dunes exist, such as barchans, longitudinal, dome, or transverse, but the most common forms throughout the Great Lakes region, especially among the inland dunes, are parabolic (USGS Publications Service

Center, 1997). Parabolic dunes are formed when some vegetation exists, stabilizing the arms of the dune during migration and maintaining a semi-circular, c-shaped landform (Odynsky, 1958; Arbogast et al., 2002).

Climate Change

Specifically, the time period of focus in this thesis is at the end of the Pleistocene glaciation, and during this time, temperature and precipitation greatly fluctuated. Evidence for climate fluctuation is present in oxygen isotope analyses of ice cores, such as the Greenland and Antarctica ice cores (e.g., Alley, 2000). Using data derived by the ice cores, climate models (e.g., Community Climate Model, Version 1) are run to estimate climate change based on oxygen isotope readings (e.g., Kutzbach et al., 1998).

During the Late Wisconsin Glaciation, the Laurentide Ice Sheet reached its maximum extent (LGM) between approximately 24,000 and 18,000 cal yr BP. Climate modeling simulations of Kutzbach et al. (1998) are summarized here as they are the authoritative source for the Great Lakes region. Their modeling efforts revealed very cold continental conditions at 21,000 cal yr BP, estimating summer temperatures (JJA) at less than -20° Celsius over the Laurentian Ice Sheet and winter temperatures (DJF) below -20°C for areas north of 30°N. A large glacial anticyclone also existed over the ice sheet during the winter months, creating two areas with extreme winds, those north (~60°N) and south (~30°N) of the ice sheet. According to their models, the climate was also very dry at 21,000 cal yr BP, with most areas receiving less than 1-2 mm/day of precipitation. At 18,000 cal yr BP, climate models indicated slight warmer conditions, but still the temperatures were colder than modern, with a sharp temperature gradient at the southern edges of the ice sheets. COHMAP Members (1988) also noted that the large Laurentide and Cordilleran ice sheets also split the west-to-east flow of the jet stream during LGM winters in North America.

The climate of 16,000 cal yr BP was colder and very similar to that of 21,000 cal yr BP. Winter temperatures (DJF) showed little change between these two time periods due to the decreased seasonal insolation, but summer temperatures (JJA) were greater at 16,000 cal yr BP because of insolation-induced warming. While climate conditions were still colder than present, the slowly increasing summer temperatures introduced seasonality to the Northern Hemisphere. Due to the increasing summer temperatures, precipitation rates also increased.

A significant spike in temperatures occurred at 14,700 cal yr BP, at the beginning of the Bølling-Allerød chronozone, a warm stadial during the terminal Pleistocene (Panyushkina et al., 2008; Clark et al., 2009). By this time, the Laurentide ice sheet had receded north, only covering the northern borders of present day Wisconsin and Lower Michigan, and this warm chronozone caused rapid melting of the ice sheet into Canada until the end of this interval at 12,900 cal yr BP (Andrews 1987; Krist, Jr and Lusch, 2004; Clark et al., 2009).

The climate model simulations of Kutzbach et al. (1998) for 14,000 cal yr BP are similar to those at 16 ka except for the more pronounced warming south of the ice sheets, particularly during winters. Specifically, their efforts show a -0.9°C difference between present day and 14,000 cal yr BP for 30°N-60°N during the summer (July) and a -8.3°C difference during the winter (January).

The Bølling-Allerød was succeeded by the Younger Dryas chronozone, a comparative colder period that lasted from 12,900 to 11,500 cal yr BP, when the Laurentide ice sheet and other glaciers expanded to a limited extent (Panyushkina et al., 2008; Clark et al., 2009). This cooling event was relatively short-lived, because summertime solar radiation continued to increase, reaching a peak between 12,000 and 9,000 cal yr BP with a subsequent decline in insolation that continues to this day (COHMAP Members, 1988; Kutzbach et al., 1998). By 12,000 cal yr BP, the Laurentide ice sheet was diminished in size and had retreated far enough north so that it no longer divide the polar jet stream, and the glacial anticyclone had also weakened (COHMAP Members, 1988). Greater temperatures began during the Holocene interglaciation at 11,600 or 11,500 cal yr BP (e.g., Dyke and Prest, 1987; Clark et al., 2009), the epoch in which we currently live.

Vegetation Reconstructions

The plant communities of the terminal Pleistocene responded to these changes in climate and ice sheet coverage in the Great Lakes region, as indicated by pollen and plant macrofossil studies of lake and wetland sediments. From 24,000 to 18,000 cal yr BP, plants and animals existed in a “refugium,” that area south of the maximum limit of the Laurentide Ice Sheet where they survived the last glaciation (Delcourt and Delcourt, 1991). Although fossil data are limited, it appears that a type of tundra vegetation occupied the area closest to the ice sheet and a mosaic of habitats dominated by cool-temperate boreal conifer and deciduous hardwood trees existed farther south (King, 1973; Delcourt and Delcourt, 1991; Jackson et al., 2000). Mammoths and mastodons occupied these habitats (Saunders et al., 2010).

Upon glacier retreat, a tundra-like vegetation colonized the recently deglaciated landscape of northeastern Illinois between 21,700 and 16,200 cal yr BP (Curry and Yansa, 2004; Curry et al., 2010), and a few other locales in neighboring states. The southernmost part of Michigan was deglaciated starting at 17,000 cal yr BP, but so far no tundra plant fossil localities have been found, but it presumably existed there (Hupy and Yansa, 2009). Tundra fossils have been found in northern Lower Michigan at a later date, at 13,950 cal yr BP when the Laurentide ice sheet was positioned nearby at that time (Larson et al., 1994).

The vegetation type associated with most mammoth and mastodon remains in the Great Lakes region is the spruce parkland/sedge wetland biome that covered an extensive area, from the northern Great Plains (Yansa, 2006) to the Atlantic seaboard (e.g., Webb et al., 2004). This biome was characterized by an abundance of wetlands inhabited by members of the Cyperaceae family (*Carex* spp. (sedges), etc.) and aquatic plants (Yansa, 2006). The trees that occupied the shorelines of these swamps and bogs included white spruce (*Picea glauca*), black spruce (*P. mariana*), balsam fir (*Abies balsamea*), tamarack (*Larix laricinia*), and a few hardier deciduous trees – black ash (*Fraxinus nigra*) and aspen (*Populus tremuloides*; Webb, 1974; Kapp, 1999; Yansa and Adams, 2012). The timing of this vegetation varies spatially, with younger ages northward, because of following ice sheet recession and its associated temperature gradient (Yansa, 2006). This parkland/wetland occupied northern Illinois from 19,000 to 14,100 cal yr BP (Gonzales & Grimm 2009; Saunders et al. 2010), southern Wisconsin from 15,500 to 14,100 cal yr BP (Fredlund et al. 1996; Yansa et al. 2009), and southern Lower Michigan from 15,300 to 11,400 cal yr BP (Hupy & Yansa 2009), for example. This vegetation shifted into a closed forest that included more species, such as pine (*Pinus*) and additional hardwoods (including oak, *Quercus*), again in a time-transgressive manner, and by the early Holocene the conifers were largely restricted to the northern part of the Great Lakes region (e.g., Webb et al., 2004; Grimm and Gonzales, 2009).

Summary

The study area for this investigation is the southern Great Lakes region of the United States, consisting of the states of Minnesota, Wisconsin, Illinois, Indiana, Michigan, and Ohio. This area was primarily chosen due to the number of mammoth and mastodon sites (e.g., Anderson, 1905; Skeels, 1962; Abraczinkas, 1992) and the numerous pollen and plant macrofossil studies (e.g., Kapp, 1986, 1999; McAndrews and Jackson, 1988; McAndrews, 2003). However, this study area also has an extensive glacial and climate history, especially during the chosen time period, the Late Pleistocene (24,000-11,500 cal yr BP). The geologic history consists of massive glacial activity, with the most applicable to this research being the Wisconsin glaciation (110,000-11,500 cal yr BP), when large glacial formation advanced and retreated many times (Dreimanis, 1977; Attig et al., 2011; Curry and Peters, 2011). At approximately 24,000-18,000 cal yr BP, the LGM (Last Glacial Maximum) occurred, covering almost the entire study area in ice (e.g., Holman, 2001; Krist and Lusch, 2004). By 12,000 cal yr BP, most of the glacier had melted, retreating to north of the study area, such as the Hudson Bay area (e.g., Mielke, 1989; Carson et al., 2009). The glacial activity during this time left behind many different types of landforms, both from glacial till deposits, such as drumlins and moraines, and glacial outwash, such as eskers and kettles. Additionally, sand dunes formed indirectly from glacial activity, taking advantage of the large amounts of unvegetated glacial deposits and strong winds (e.g., Arbogast, 2007; Blewett et al., 2009).

During the Late Pleistocene, the southern Great Lakes region also experienced frequent climate fluctuations. Using climate models based on environmental variables and data derived from oxygen isotope analyses of ice cores, climate conditions were estimated for different periods of time throughout the Late Pleistocene (e.g., COHMAP Members, 1988; Kutzbach et al., 1998). Temperatures were as low as -20°C over the Laurentian Ice Sheet during the summer months of 21,000 cal yr BP (Kutzbach et al., 1998), only warming during the Bølling-Allerød (14,700-12,700 cal yr BP), which only had a ~-0.9°C difference than today (Kutzbach et al., 1988; Panyushkina et al., 2008; Clark et al., 2009), and after a short cooling period, the Younger Dryas chronozone (12,900-11,500 cal yr BP), temperatures began to increase once again upon entering the Holocene (11,500 cal yr BP; Dyke and Prest, 1987; Panyushkina et al., 2008; Clark et al., 2009).

Vegetation reconstructions, created from pollen and plant macrofossil studies, showed how plant communities responded to these frequent climate changes. At the beginning of the terminal Pleistocene (24,000-18,000 cal yr BP), plant communities existed in a "refugium," which was the areas located beyond the southern limit of the Laurentide Ice Sheet (Delcourt and Delcourt, 1991). During this time, vegetation reconstructions, despite limited data, show a tundra-like environment near the ice sheet and a mosaic of habitats farther south (e.g., King, 1973; Delcourt and Delcourt, 1991). As time progressed, glaciers began to retreat and climate conditions changed, vegetation communities also changed. Tundra is assumed to have followed the glacial retreat north (e.g., Curry and Yansa, 2004; Hupy and Yansa, 2009; Curry et al., 2010). The vegetation communities most applicable to this investigation were those associated with mammoth and mastodon remains in the Great Lakes region, the spruce parkland/sedge wetland biome, which extended from the northern Great Plains (Yansa, 2006) to the Atlantic seaboard (e.g., Webb et al., 2004). Generally, this biome appears to have migrated northward through time; however, the timing of this migration varied spatially (Yansa, 2006). Eventually, this vegetation shifted into a closed forest that included more species, with the conifers restricted to the northern part of the Great Lakes region by the beginning of the Holocene (e.g., Webb et al., 2004; Grimm and Gonzales, 2009).

CHAPTER THREE: METHODS

Data

FAUNMAP Database

Data compiled and analyzed in my thesis were derived from the FAUNMAP database and other sources. FAUNMAP was originally created under the direction of Dr. Russell W. Graham and Ernest L. Lundelius, Jr. Using three compilers and fifteen regional collaborators, the Illinois State Museum published the database containing over 2,919 documented Pleistocene mammal site localities (FAUNMAP Working Group, 1994). The site localities documented in the database all had to include a known geographic location, chronology, and voucher specimens stored in a public institution. For its original release, the FAUNMAP database was divided into two separate databases – Archival and Research. The Archival database contained the data as they were originally reported and the Research database had been filtered by these researchers to standardize the taxonomy, eliminate mixed faunal assemblages, and to accept or reject chronologies (FAUNMAP Working Group, 1994). The database was made available electronically through the Illinois State Museum in 1996, allowing the public to submit online queries for any of the documented species.

Data Preparation

Data were obtained from the FAUNMAP electronic database (FAUNMAP Working Group, 1996a; http://www.museum.state.il.us/research/faunmap/). With help from the Illinois State Museum staff, these data were converted into a shapefile appropriate for use in the ArcGIS desktop (9.x, 10; ESRI, 2010), which was then converted into a Microsoft Excel 2010 (Microsoft, 2010) document.

Because the FAUNMAP database is incomplete, additional data were obtained from museum reports, county atlases, historical county records, newspapers, state science academic publications, and state historical society documents, and entered into this Excel file. The focus was on increasing the number of site localities in the database and discovering which sites had associated radiocarbon (^{14}C) dates and/or paleovegetation data. The new sites added to the Excel document were each given a unique identification number. Geographic coordinates were converted to latitude and longitude for ease of projecting in an ArcGIS desktop (ESRI, 2010). When sites were in United States Public Land Survey system (USPLS) coordinates, latitude and longitude coordinates were determined from the central point of the survey rectangle. All such sites were identified to the nearest township and range, or finer, such as to the nearest township or section. For some sites, their locations were only identified in publications by a stated distance from a nearby town, and for these, the latitude and longitude of the identified towns were used. Data were then imported into an ArcGIS 10 Desktop (ESRI, 2010) with a NAD 1983 geographic coordinate system and a NAD 1983 Great Lakes Albers projection, and formatted the same as the FAUNMAP data.

Format

The format of my database was modified from Abraczinkas's (1992) exhaustive survey of proboscidean sites in Michigan. The records included more specific elements than are in FAUNMAP, as described below:

Site Name: All sites were given a specific name. If the site was located on private property, the name is generally derived from the landowner, but if it was located on public property, the site is named based on nearby geographical features.

County Names: County names were included.

Township Names (if possible): Current survey township names for counties were included.

Section Number and Coordinates (if possible): Public Land Survey coordinates are available for all states in the Great Lakes region. The section number follows the Township name, with quarter sections designated if available.

Latitude/Longitude: Most of the older sites found in the Great Lakes used Public Land Survey System coordinates (Township and Range), but recent sites also included latitude and longitude coordinates. The USPLS coordinates were converted to latitude and longitude coordinates.

Species: Species of mammoth or mastodon found at the site. Also noted if researchers thought specimens were misidentified.

Date (if possible): Date of discovery

Excavators (if possible): Names of people who discovered, excavated, and studied(s) the site.

Geologic Setting (if possible): Type of sediment encasing the skeleton.

Age (if possible): The most recent date designated by radiocarbon dating (with laboratory reference number) or stratigraphic occurrence.

Material (if possible): List of skeletal elements or teeth found at the site. Sex and age of animal if determined.

Current Repository (if possible): Location of storage of the bones and teeth recovered from the site.

Associated Vegetation studies (if possible): List of vegetation associated with the site derived from palynology (pollen) or plant macrofossil studies.

Associated bones (if possible): Additional bones from fauna other than mammoths or mastodon.

Literature: All literature found referencing the particular site.

Testing Research Questions

Objective 1: FAUNMAP Comparison

Since a previous study showed that FAUNMAP data may not be accurate for the study of some species (Walker, 2000), the first step would be to determine whether the number of mammoth and mastodon sites in the database is sufficient for analysis.

First, a comparison between the original FAUNMAP database and my modified database occurred. The modified database contained both the original site localities documented in the FAUNMAP database and the additional site localities documented in museum reports, county atlases, historical county records, newspapers, and publications and reports by state science academies and state historical societies. The comparison consisted of comparing the number of site localities in both database, as a whole, and between the different taxa.

For additional analysis, data were separated into six categories: (1) all FAUNMAP data, (2) all modified-FAUNMAP data, (3) FAUNMAP-only mammoth data, (4) FAUNMAP-only mastodon data, (5) modified-FAUNMAP mammoth data, and (6) modified-FAUNMAP mastodon data. Once the data were imported into ArcGIS 10 (ESRI, 2010), the “Select by Attributes” function was used to separate the six categories. Directional Distribution ellipses to one standard deviation (68%) were created for the six categories. Areas were calculated for all polygons. Percent overlap was calculated between the respective FAUNMAP and modified FAUNMAP polygons. Mean central points were also created for the Directional Distribution ellipses created using the all FAUNMAP data and modified FAUNMAP data categories. Distances and direction of shift were determined by comparing the mean center points between the two databases within the same method.

Objective 2: Geographic Ranges of Mammoths and Mastodons

Assuming fossil sites accurately reflect normal habitat occupation, geographic ranges can be determined. The modified-FAUNMAP database was used for this objective. Using the "Select by Attributes" function in ArcGIS 10 (ESRI, 2010), four new shapefiles were created based on taxa: *Mammut americanum* (American mastodon), *Mammuthus jeffersonii* (Jefferson mammoth), *Mammuthus primigenius* (woolly mammoth), and *Mammuthus* spp. (all mammoth species). Two different methods were utilized to determine geographic ranges for these taxa- Directional Distribution ellipses (one standard deviation) and Kernel Density Estimator functions were created for each of the four datasets. For the Directional Distribution ellipse method, the areas of the polygons were determined and percent overlap was calculated between the different taxa. Kernel Density rasters were qualitatively compared.

Objective 3: Geographic Range Shifts

Data were split into two time periods: the LGM, ~24 to 18 ka, and terminal Pleistocene, and ~ 18 to 11.5 ka. Due to the lack of accurately dated sites, except in a few cases, the basis of this separation was the maximum Wisconsin glacial extent (LGM, ~18,000 cal yr BP; Berggren and Killey, 2000). Using the known dates as a reference, it was assumed sites south of the glacial extent were older than 18,000 cal yr BP and sites north of the glacial extent were younger than 18,000 cal yr BP.

Following these guidelines, the LGM image (Berggren and Killey, 2000) was georeferenced to the Great Lakes region using the ArcGIS Georeferencing Toolbar (ESRI, 2010). A new polygon shapefile was created, tracing the maximum glacial extent from the image. The ~24 to 18 ka period encompassed all data. Using the “Select by Location” function, the sites not located within the Glacial Extent polygon (i.e., south of the LGM margin) were considered to be in the ~24 to 18 ka time period, while those sites completely within the polygon were considered to be within the ~18 to 11.5 ka period. In addition to partitioning the sites by time period, they were once again divided by taxa, with *Mammut americanum* (American mastodon) and *Mammuthus* spp. sites also encompassing individual shapefiles. Overall, there were four different datasets used for the testing of this objective.

After the point shapefiles were created from these datasets, Directional Distribution ellipses (one standard deviation) were produced for each dataset, generating four polygons. In addition to determining the areas of each polygon, the percentage overlap was calculated between the two different time periods for each taxon. The distance shift between ~24 to 18 ka and ~18 to 11.5 ka was determined by calculating the distance from their respective central features. Additionally, the Kernel Density Estimator function was also used on all four datasets to determine whether a qualitative description could be performed.

Objective 4: Habitat Partitioning

Vegetation Data

Vegetation data were acquired from the NCDC Fossil and Surface Pollen database (Grimm et al. (eds.), 2008). Since the vegetation descriptions relating to the sites in the literature were percentages, the top fifteen pollen types by percentage were queried for the study area. Nine different pollen types were chosen based on knowledge of assumed mammoth and mastodon diets and commonness to the time period: the non-arboreal pollen (NAP) herbs *Artemisia* (sage), Cyperaceae (sedge family), and Poaceae (grass family); and the arboreal pollen (AP) taxa, *Fraxinus* (ash, presumably black ash), *Ostrya*-type (hop hornbeam), *Picea* (spruce), *Pinus* (pine), and *Betula* (birch) and Cupressaceae (cedar or juniper). The latter two taxa can be either trees or shrubs. A Microsoft Excel 2010 (Microsoft, 2010) document was created consisting of the geographic coordinates for each pollen study site and thousand year averages for each vegetation class by ka: >18 ka, 18-17 ka, 17-15.7 ka, 15.7-13.9 ka, 13.9-12.9 ka, and 12.9-11.5 ka. The document was imported into an ArcGIS 10 Desktop (ESRI, 2010) with a NAD 1983 geographic coordinate system and a NAD 1983 Great Lakes Albers projection.

Due to the controversy surrounding the identification of the mammoth species for many of the sites in the study area, this objective was limited to dividing the taxa by genera, *Mammut* spp. (mastodon) and *Mammuthus* spp. (mammoth). Additionally, two methods were used to determine whether a vegetation difference exists between the two genera. For the first method, descriptive statistics (i.e., mean, median, mode, standard deviation) were calculated for both the undated and undated sites. Statistics for the undated sites were determined by finding the vegetation percentages associated with the individual site localities in each millennium and statistics calculated for the dated sites used only the vegetation percentages within their dated millennia. The second method consists of using a five thousand year average of the pollen percentages (~18 to 11.5 ka) and the Kernel Density estimated raster for the same time period.

Vegetation Data - Method One

Inverse Distance Weighting was applied to the shapefile created from the preparation described above. Rasters were created for each pollen class during each time period: : >18 ka, 18-17 ka, 17-15.7 ka, 15.7-13.9 ka, 13.9-12.9 ka, and 12.9-11.5 ka. In total, 54 rasters were created. A maximum distance of 200 kilometers was used and the raster extent was set to the Great Lakes shapefile, with a cell size of approximately 5.1 by 5.1 kilometers.

Using the mammoth and mastodon site localities, the Intersect Point Tool function available from Hawth's Tools (ArcGIS 9.2; Beyer, 2004; ESRI, 2006) was used to export the raster attributes to the point shapefile. The shapefile attribute table was then exported into a Microsoft Excel 2010 (Microsoft, 2010) document. Mean, median, standard deviation, and standard error were calculated for each of the vegetation classes for each millennium.

Using the "Select by Attribute" tool, the dated site localities were separated from the undated sites. Descriptive statistics were calculated using the vegetation associated with the millennia for each dated site locality.

Vegetation Data - Method Two

Using the 18 to 11.5 ka shapefile, Kernel Density rasters were created for *Mammut americanum* (mastodon) and *Mammuthus* spp. (mammoth) taxa. The vegetation data for this method encompassed the same time interval, taking the five thousand year mean for the individual vegetation study sites. Once imported into an ArcGIS 10 Desktop (ESRI, 2010), Inverse Distance Weighted rasters were created for data from an arboreal (AP) class, which consisted of *Betula,* Cupressaceae*, Fraxinus, Ostrya*-type*, Picea,* and *Pinus,* and a non-arboreal (NAP) class comprised of *Artemisia,* Cyperaceae, and Poaceae, using a maximum distance of 200 kilometers and the raster extent set to the Great Lakes shapefile (cell size approximately 5.1 by 5.1 kilometers).

Random points were generated in an ArcGIS 9.2 Desktop (ESRI, 2006) utilizing Hawth's Tools (Beyer, 2004). Four different sets of random points were generated to act as multiple runs of the study. The random points used the cell width (approximately five kilometers) as the minimum distance between points and numbered 10% of the total number of cells in the vegetation raster. To minimize error, using the "Select by Location" tool, the random points not within either of the vegetation rasters were deleted.

Using Hawth's Tools (Beyer, 2004) in combination with an ArcGIS 9.2 Desktop (ESRI, 2006), the Intersect Point Tool was used to export the arboreal and non-arboreal raster attributes, as well as the mammoth and mastodon Kernel Density-estimated rasters, to the generated random points. The attribute tables for the four point shapefiles were exported as a comma-deliminated file (.cvs), which were later imported into R (R Development Core Team, 2008).

Two different regression models were run on the exported data. Using the *pscl* package (Jackman, 2011), the first model was a zero-inflated negative binomial regression. The data were further modified for this regression by multiplying the mammoth and mastodon kernel density estimations by 1.0e9 because this regression was created for count data. For this model, each of the four datasets used the vegetation (arboreal and non-arboreal) classes as the independent variables and the mammoth and mastodon probability as the dependent variable.

The second regression model, linear regression, did not need any additional packages. The data were modified by this regression by dividing it into two different datasets. One dataset had all the data for the *Mammut* spp. (American mastodon), deleting the records where the Kernel Density estimations were zero. The second dataset included all the data for *Mammuthus* spp. (mammoths), also deleting the records with zero Kernel Density estimations. Once divided, the Kernel Density estimations were transformed by multiplying them by the natural log in order to normalize the data. Linear regression models were run with the vegetation classes as independent variables and the Kernel Density probabilities as dependent variables. ANOVA tests were also run on all four regression models to determine whether the results were largely due to chance.

Summary

Data for this investigation was originally derived from the FAUNMAP database, which can be found at http://www.museum.state.il.us/research/faunmap/. The database was created by the Illinois State Museum under the direction of Dr. Russell W. Graham and Ernest L. Lundelius, Jr., and used three compilers and fifteen regional collaborators, eventually publishing 2,919 documented Pleistocene mammal site localities throughout the contiguous United States (FAUNMAP Working Group, 1994, 1996a). For this study, additional mammoth and mastodon localities for the Great Lakes region were added to the original FAUNMAP database to create a new modified database. These new localities were discovered by searching previously published museum reports, county atlases, historical county records, newspapers, state science academic publications, and state historical society documents that had been unreported in the original database. Once discovered, these new sites, and any additional information concerning them, were entered into a Microsoft Excel (Microsoft, 2010) document, formatted similarly to Abraczinkas (1992). Latitude and longitude coordinates were calculated for all sites, both new and old.

Ultimately, this investigation had four objectives. Objective one compared the original FAUNMAP database and the new modified database using directional distribution ellipses. The purpose of objective two was to determine the sizes, and overlap, of the three taxa found in the Great Lakes region- the American mastodon, Jefferson mammoth, and woolly mammoth- using Directional Distribution ellipses. Objective three was to discuss the shifts in the proboscideans' geographic ranges that could be observed between the two time periods- 24 to 18 ka and 18 to 11.5 ka- by dividing the localities according to the LGM and creating Directional Distribution ellipses. The purpose of objective four was to determine whether habitat partitioning could be observed between mammoth and mastodon taxa. To do this, pollen data were collected from the NCDC Fossil and Surface Pollen database (Grimm et al., 2008). Overall, nine different pollen taxa were chosen, *Artemisia* (sage), Cyperaceae (sedge family), Poaceae (grass family), *Fraxinus* (ash), *Ostrya*-type (hop hornbeam), *Picea* (spruce), *Pinus* (pine), and *Betula* (birch), and were divided into six different thousand-year time periods determine from radiocarbon dates. Two different methods were used to determine whether habitat partitioning could be observed. The first method used inverse distance weighted rasters created from all nine pollen types and all six time periods. Descriptive statistics were calculated for each date proboscidean locality for their respective time period. The second method used two regression models, a zero-inflated negative binomial regression and a linear regression. The regressions were calculated for one time period (~18 to 11.5 ka), two taxa (mammoth and mastodon), and two vegetation types (arboreal and nonarboreal).

CHAPTER FOUR: RESULTS

Objective 1: FAUNMAP Comparison

The first objective for this study was to compare the FAUNMAP database, with no additions or modifications, to the new modified database by creating geographic ranges of American mastodon (*Mammut americanum*) and mammoth species (*Mammuthus* spp.) in the Great Lakes region.

Record Comparison

First, a comparison of the original FAUNMAP database and the modified database was performed. FAUMAP database shows 180 documented proboscidean sites, with 98 of those records being *Mammut americanum* (American mastodon), 48 *Mammuthus jeffersonii* (Jefferson mammoth), 16 *Mammuthus primigenius* (woolly mammoth), and 9 *Mammuthus imperator* (imperial mammoth, earlier mentioned is be now considered as *M. columbi*; Table 4-1; FAUNMAP, 1996).

Table 4-1: The difference (number of records and percentage) between the FAUNMAP database and the modified database created in this study as shown by species. Using additional sources, 528 Proboscidean records were added to the original FAUNMAP database.

Taxa	FAUNMAP	Additional	Total
M.americanum	98	324	422
M.jeffersonii	48	47	95
M.primigenius	25	40	65
M.imperator	9	0	9
Mammuthus spp.	0	67	67
Proboscidean spp	0	50	50
TOTAL	180	528	708

While going through “gray literature” (documents of state historical societies, state academy of science journals, regional specific journals, etc.), other databases (NEOTOMA), and personal contacts (Dr. Richard Slaughter, University of Wisconsin Geology Museum), an additional 528 records were added to the original FAUNMAP database of 180 sites. This represents a significant contribution of data previously not available in electronic form. Within these records, 325 were American mastodon, 47 were Jefferson mammoth, 40 were woolly mammoth, 67 were an unidentified mammoth species, and 50 were an unidentified Proboscidean species (Table 4-1; Figure 4-1).

Overall, 708 Proboscidean sites were documented. To compare the number of records between the original FAUNMAP database and the modified database (containing the additional records), the percentage of FAUNMAP records to the total records was calculated (Table 4-1). FAUNMAP records ranged from 100% of the total (*Mammuthus imperator*), so no additional imperal mammoth sites were discovered in my research, to 0% (*Mammuthus* spp. and *Proboscidea* spp.), where these were not reported in the original FAUNMAP database. The percentages for the American mastodon, Jefferson mammoth, and woolly mammoth were 23.22%, 50.53%, and 38.46%, respectively (Table 4-1), indicating that my research identified a significant number of new proboscidean sites, most particularly those of the Jefferson mammoth.

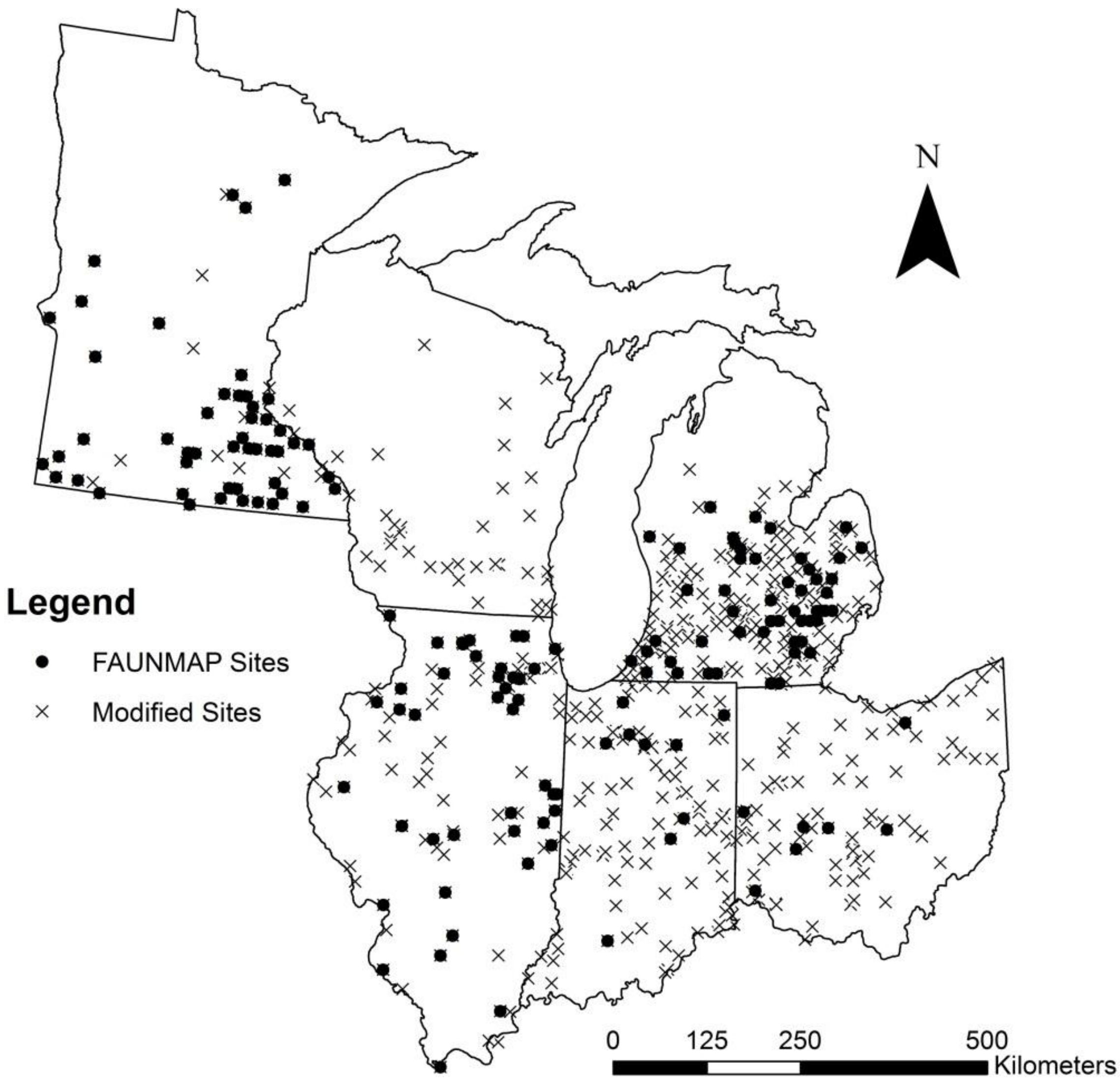

Figure 4-1: Map of the United States Great Lakes Region (Minnesota, Wisconsin, Illinois, Indiana, Michigan, and Ohio) showing the differences between proboscidean sites documented in the FAUNMAP database and the additional (modified) proboscidean sites discovered in this thesis research. FAUNMAP sites are shown as black circles while additional sites shown as black X's. Overall, an additional 528 site localities were found throughout this research.

In addition to comparing the number of records, the Directional Distribution (one standard deviation) method was used to produce polygons for which areas could be calculated, as described below.

*Directional Distribution Ellipses (one standard deviatio*n)

Larger differences existed between the FAUNMAP database and the Modified database when using the Directional Distribution ellipse (one standard deviation) to determine the geographic ranges (Table 4-2). Figure 4-2 (shown below) shows that there was a eastern/western divide between the ellipses created from the FAUNMAP and modified databases, with the FAUNMAP data covering further west and the Modified data covering further east. The areas of the geographic ranges for the FAUNMAP database and Modified database were 380,293 square kilometers and 325,501 square kilometers, respectively. The overlap between the two geographic ranges was 253,877 square kilometers, which was approximately 66.26% of the FAUNMAP geographic range and approximately 42.23% of the Modified geographic range. The distance between the mean centers for the two Directional Distribution-derived geographic ranges was approximately 205.29 kilometers, with the Modified center being east-southeast of the FAUNMAP center (Figure 4-2).

Table 4-2: Areas (square kilometers) of the polygons, and overlap, produced from the FAUNMAP and Modified databases using the Directional Distribution ellipse (one standard deviation) method. Areas were rounded to the nearest whole number.

	FAUNMAP	Modified	Overlap
All Species	380,293	325,501	253,877
Mammoth	248,373	389,701	186,083
Mastodon	261,436	201,489	164,572

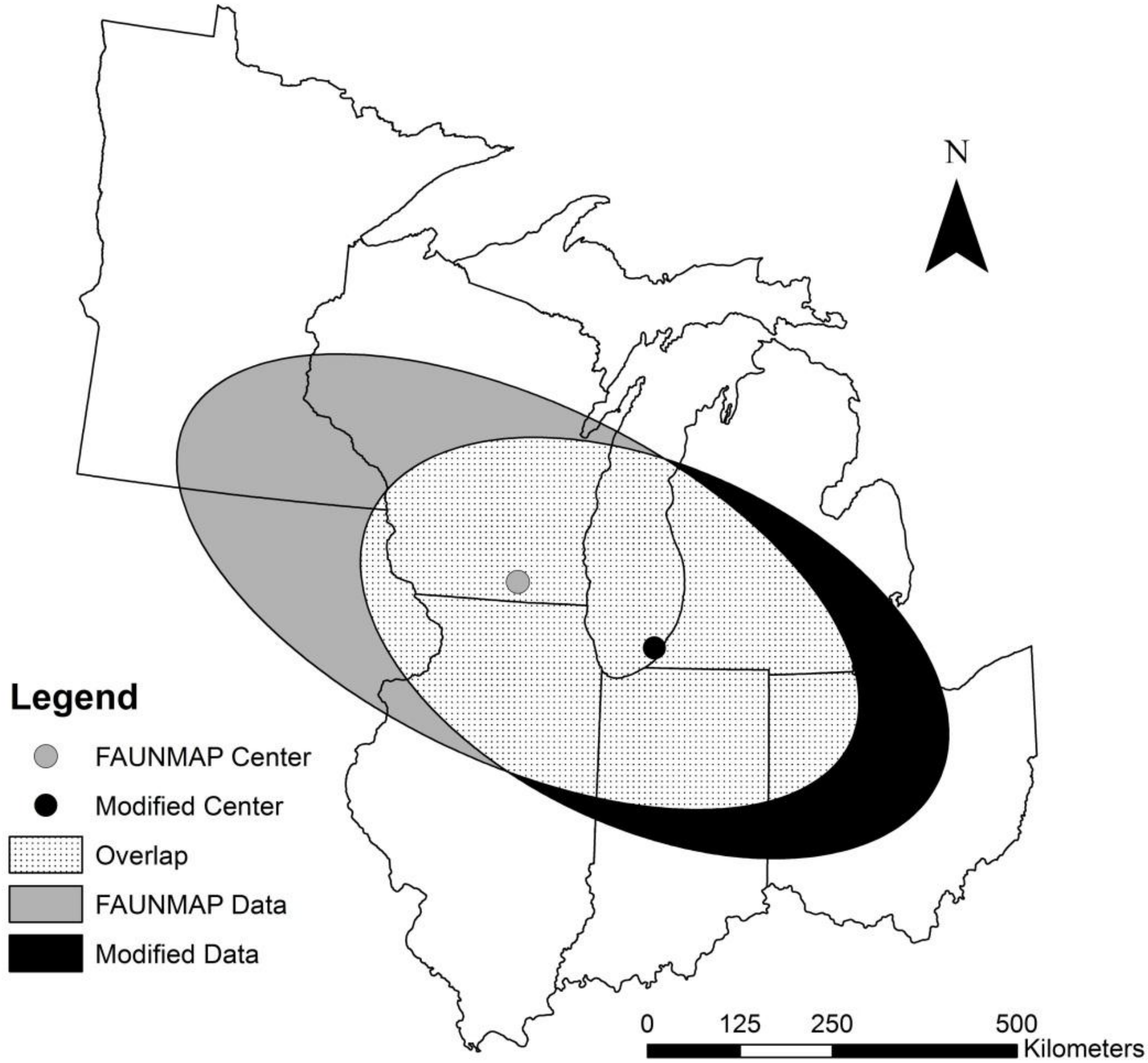

Figure 4-2: Map showing the geographic ranges determined using the FAUNMAP and Modified databases and the Directional Distribution ellipse (one standard deviation) method. The black ellipse represents the geographic range determined from the Modified database. The dot ellipse represents the overlap between the geographic ranges of the two databases. The gray ellipse represents the geographic range of the FAUNMAP database.

Due to the limited data, statistical analyses were not performed. However, using the large distances between the FAUNMAP database and Modified database mean centers (approximately 205 kilometers), the differences between the two databases became apparent.

Analysis

For Objective 1, the purpose was discuss the differences between the FAUNMAP database, with no additions or modifications, and the new modified database, using mammoth and mastodon data from the southern Great Lakes region.

The FAUNMAP database originally had 180 documented proboscidean sites, but an additional 528 sites were added after going through other databases, published literature, and personal contacts, nearly three times the original number. Using the Directional Distribution ellipse (one standard deviation) method, the ellipses created using the two datasets were similar in size (380,293 square kilometers versus 325,502 square kilometers), but the shift in mean center was over 205 km to the east-southeast.

Overall, even though the polygons were similar in size and had much overlap, the distances between mean centers and extreme lack of site data show the necessity of using as much data as possible for biogeography studies.

Objective 2: Geographic Ranges of Mammoth and Mastodon

The purpose of Objective 2 was to determine the sizes of the mammoth and mastodon geographic ranges and identify whether any overlap occurred between their geographic ranges within the southern Great Lakes region. Using the Modified database as determined in Objective 1, geographic ranges for *Mammut americanum* (American mastodon), *Mammuthus spp.* (mammoth species), *Mammuthus jeffersonii* (Jefferson mammoth), and *Mammuthus* *primigenius* (woolly mammoth) were created using the Directional Distribution ellipse (one standard deviation) methods. Geographic ranges were compared within the same taxa and between taxa.

Geographic Ranges within Taxa

Mammut americanum

The Modified database had 422 site localities (Table 4-1) for *Mammut americanum* (American mastodon). The geographic range created using the Directional Distribution ellipse (one standard deviation) was 201,489 square kilometers (Table 4-2). In general, the geographic range produced by the Directional Distribution ellipse centered over southern Michigan and northern Indiana and Ohio (Figure 4-3).

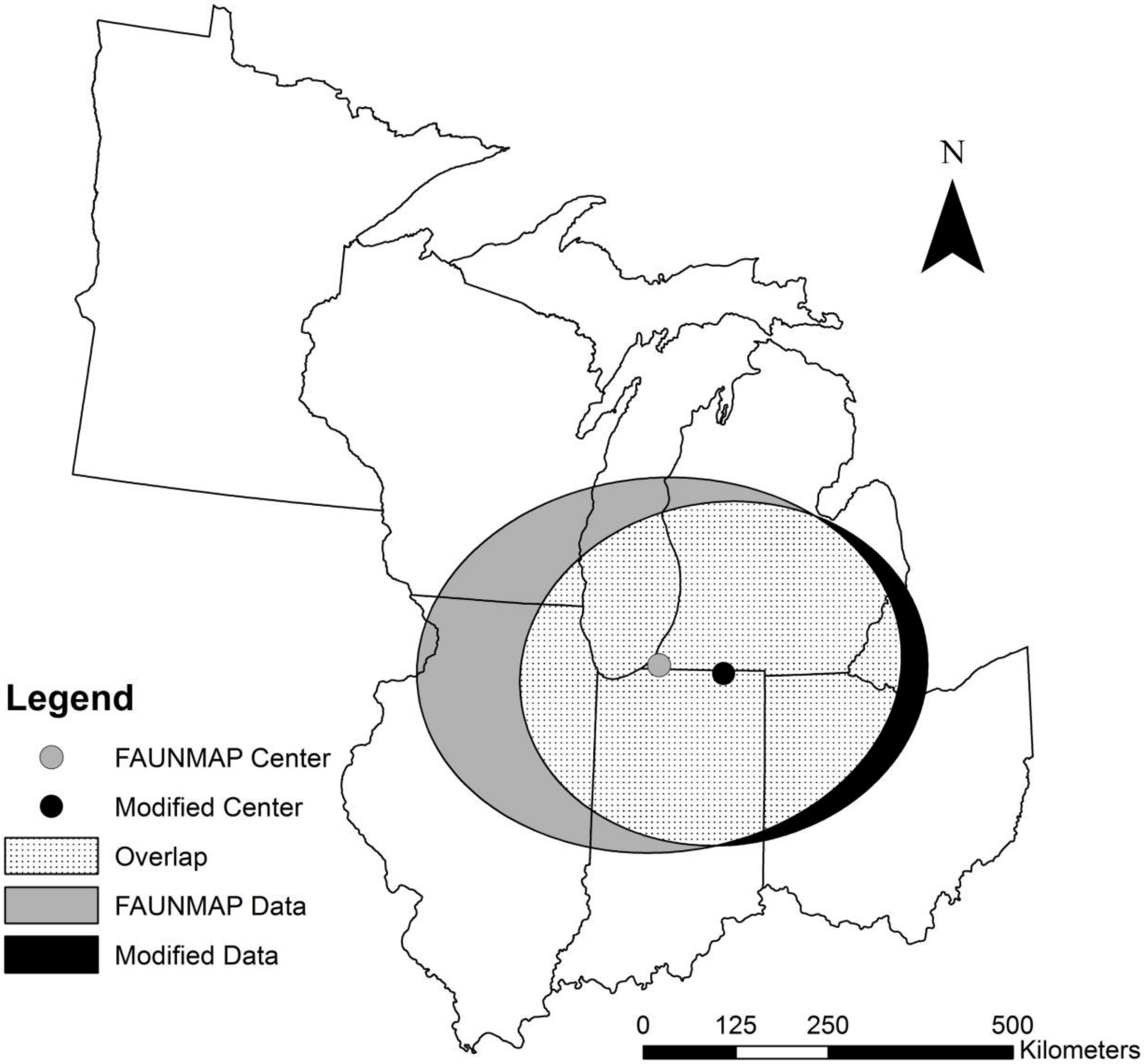

Figure 4-3: American mastodon geographic ranges produced by the Directional Distribution ellipse (on standard deviation) method. Figure shows the ellipses determined by the FAUNMAP only data (grey) and the modified data (black), as well as the overlap.

Mammuthus species

The Modified database consisted of 236 site localities (Table 4-1) of mammoth species (*Mammuthus jeffersonii*, *Mammuthus primigenius*, *Mammuthus imperator*, and unidentified mammoth species). The reason these species were initially combined into one category was to enable a comparison between mammoth and mastodon taxa. The geographic range produced by the Directional Distribution ellipse (one standard deviation) was a 389,701 square kilometers (Table 4-2). In general, the geographic range produced by Directional Distribution ellipse (one standard deviation) method was centered over southern Lake Michigan, covering southern Wisconsin, southwestern Michigan, northern Illinois, northern Indiana, and western Ohio (Figure 4-4).

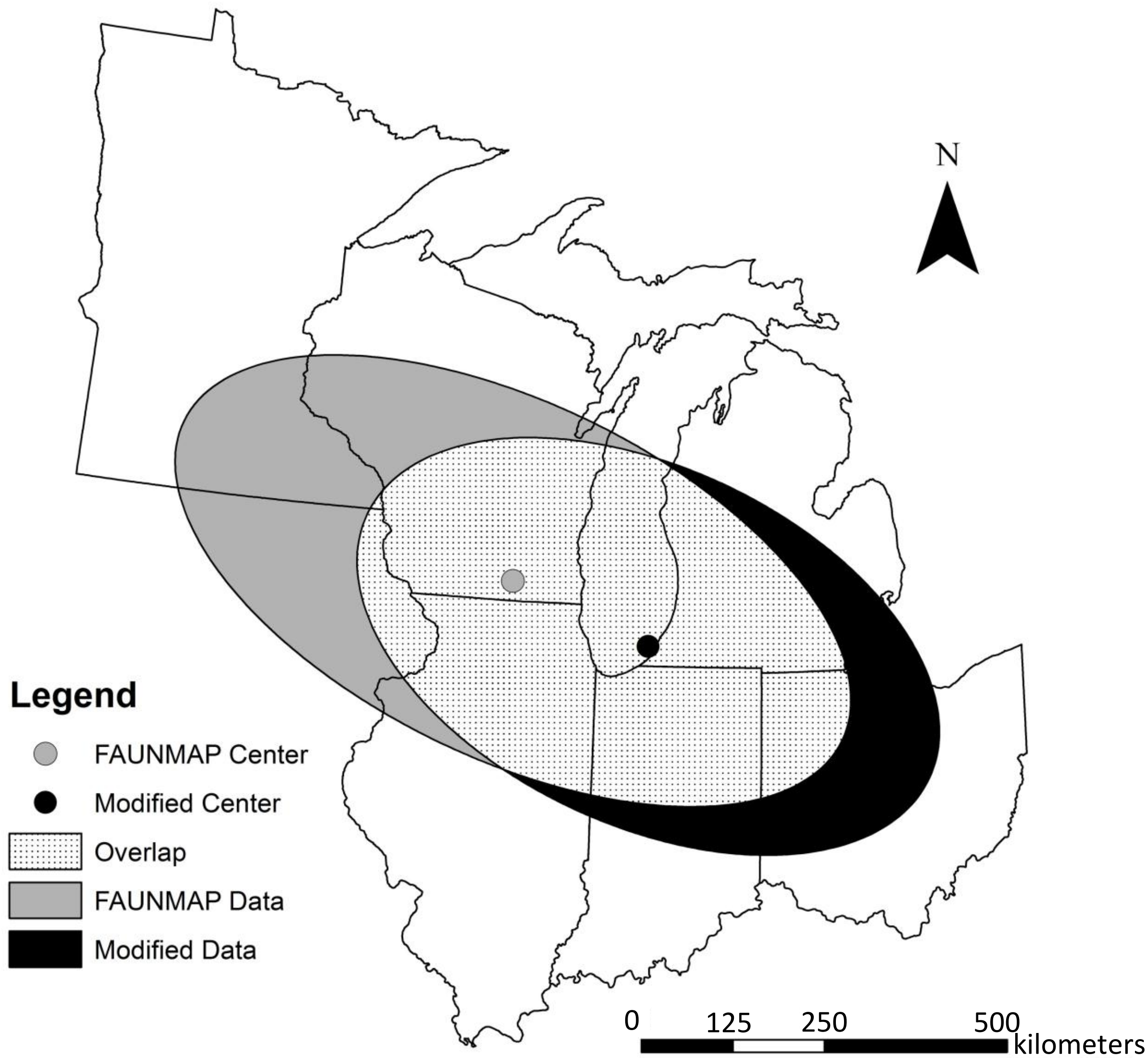

Figure 4-4: Mammoth species geographic ranges produced by the Directional Distribution ellipse (one standard deviation) techniques. Figure shows the ellipses determined by the FAUNMAP only data (grey) and the modified data (black), as well as the overlap.

M. jeffersonii and M. primigenius

The Modified database recorded 95 *Mammuthus jeffersonii* (Jefferson mammoth) and 65 *Mammuthus primigenius* (woolly mammoth) site localities (Table 4-1). The geographic range produced by the Directional Distribution ellipse (one standard deviation) method was 318,806 kilometers for the Jefferson mammoth and 339,165 square kilometers for the woolly mammoth (Table 4-3). Expectedly, the both the Jefferson mammoth and woolly mammoth had smaller geographic ranges than the one created for all mammoth taxa. For the Jefferson mammoth, the Directional Distribution ellipse geographic range was centered on southern Lake Michigan and southern Wisconsin, covering south-eastern Minnesota, northern Illinois, northern Indiana, southwestern Ohio, southwestern Michigan, and most of Wisconsin (Figure 4-5). For the woolly mammoth, the Directional Distribution ellipse geographic range was centered on northern Illinois and Indiana, covering southeastern Minnesota, southern Wisconsin, northern Illinois, southwestern Michigan, western Ohio, and most of Indiana (Figure 4-5).

Geographic Ranges Between Taxa

The Directional Distribution ellipse (one standard deviation) method of producing geographic ranges showed much variation in the sizes and locations of the taxa's geographic ranges. The American mastodon had 13.3% of its entire geographic range to itself. As shown in Table 4-3, 36.3% of the Jefferson mammoth geographic range was independent of any other taxa. Approximately 3.71% of the woolly mammoth geographic range was void of any other taxa (Table 4-3).

Table 4-3: Geographic ranges (square kilometers) of the four taxa (American mastodon, Jefferson mammoth, woolly mammoth, and unidentified mammoth species) produced by the Directional Distribution ellipse method. The size of the ranges completely independent of all other taxa are also shown, as with the percentage of that area compared to the total area of each taxon's respective geographic range.

Taxa	Range (Sq. km)	Only (Sq. km)	Percentage of total
Unidentified Mammoths	374,156.00	122,521.16	32.75%
Wooly Mammoth	339,164.82	12,574.88	3.71%
Jefferson mammoth	318,806.10	115,741.00	36.30%
American mastodon	201,489.00	26,797.27	13.30%

The geographic overlap of all four taxa (American mastodon, Jefferson mammoth, woolly mammoth, and unidentified mammoth species) was approximately 78,413 square kilometers (Table 4-7), which was 24.6% of the Jefferson mammoth's, 23.12% of the woolly mammoth's, and 38.92% of the American mastodon's total geographic range (Table 4-4).

Table 4-4: Size of the geographic range (square kilometers) for the four taxa (American mastodon, Jefferson mammoth, woolly mammoth, and unidentified mammoth species) produced by the Directional Distribution ellipse (one standard deviation) method, as well as the sizes of areas of overlap.

Taxa	Range (Sq. km)	Taxa	Range (Sq. km)
Unidentified Mammoths	374,156.00	Unidentified + Wooly + Jefferson	168,183.65
Wooly Mammoth	339,164.82	Mastodon + Unidentified	146,882.67
Jefferson mammoth	318,806.10	Mastodon + Wooly	137,363.51
Unidentified + Wooly	316,254.34	Mastodon + Unidentified + Wooly	135,677.76
American mastodon	201,489.00	Mastodon + Jefferson	115,786.40
Unidentified + Jefferson	194,370.53	Mastodon + Jefferson + Unidentified	89,618.35
Jefferson + Wooly	176,878.23	All Taxa	78,413.45

The area where the geographic ranges of all the taxa overlapped was centered around the southern end of Lake Michigan. As shown in Figure 4-5, the mammoth species (unidentified, Jefferson mammoth, and woolly mammoth) appear to be further west and south of the American mastodon geographic range. The American mastodon geographic range was centered on southern Michigan while most of the mammoth taxa were centered around southern Wisconsin or northern Illinois (Figure 4-5).

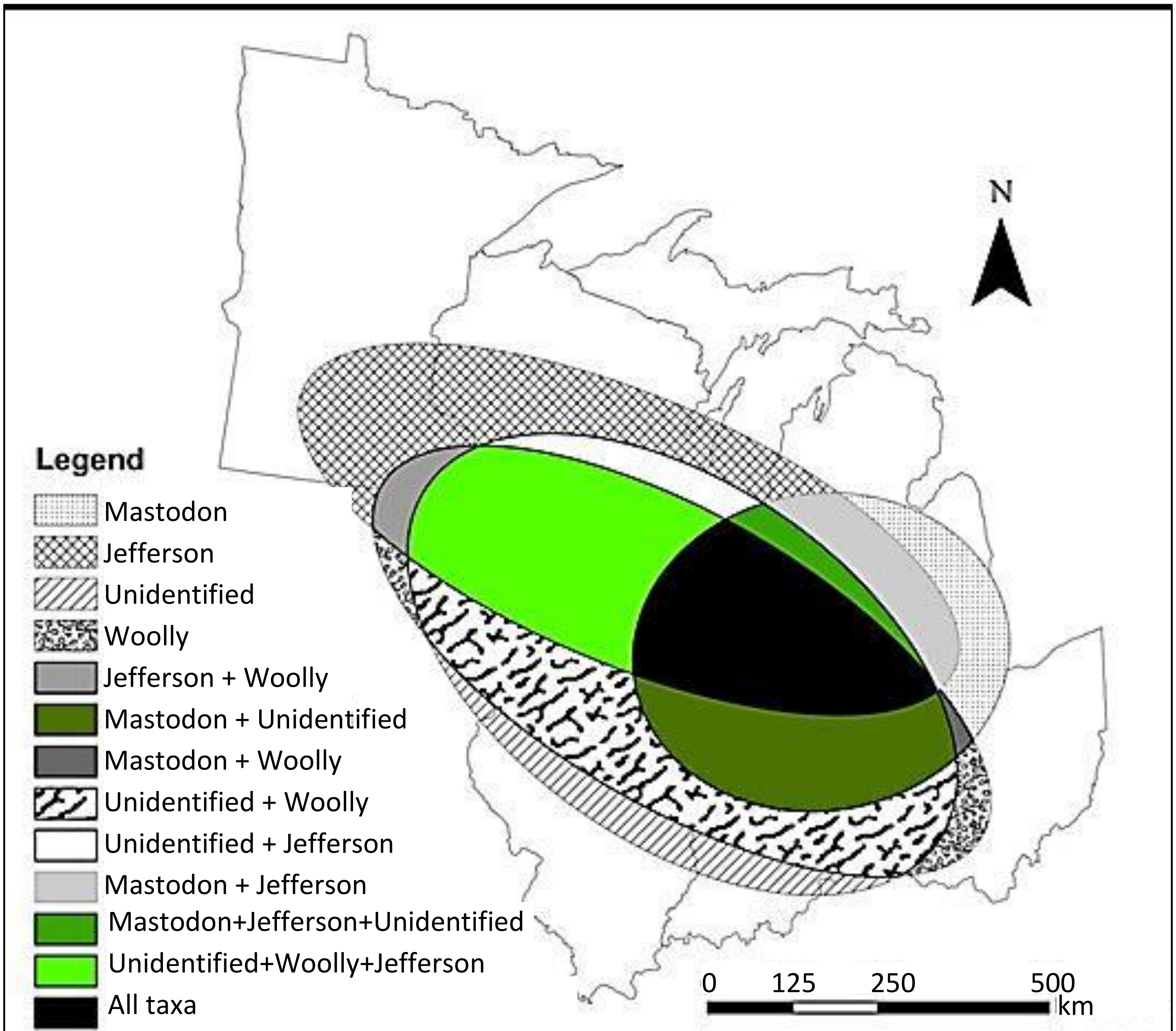

Figure4-5: Geographic ranges, and overlap, produced by the Directional Distribution technique for the four taxa (American mastodon, Jefferson mammoth, woolly mammoth, and unidentified mammoth species). As shown, very little area exists where only one taxon is present. Only 0.38% of the American mastodon's, 2.51% of the woolly mammoth's, and 10.57% of the Jefferson mammoth's geographic range is independent of any other taxa. <u>For interpretation of the references to color in this and all other figures, the reader is referred to the electronic version of this thesis.</u>

Kernel Density

In addition to the Minimum Convex Polygon and Directional Distribution ellipse (one standard deviation), Kernel Density rasters were created (Figures 4-6A-D). The Kernel Density raster for the American mastodon site localities shows a cluster in the southern half of Michigan. Additionally, high density clusters can be seen in northern Indiana and northeastern Illinois (Figure 4-6A). In comparison, the Kernel Density raster for mammoth species shows the highest density in southeastern Minnesota. Density clusters can also be seen in Michigan, southern Ohio, northern Illinois, southeastern Wisconsin, and Indiana (Figure 4-6B).

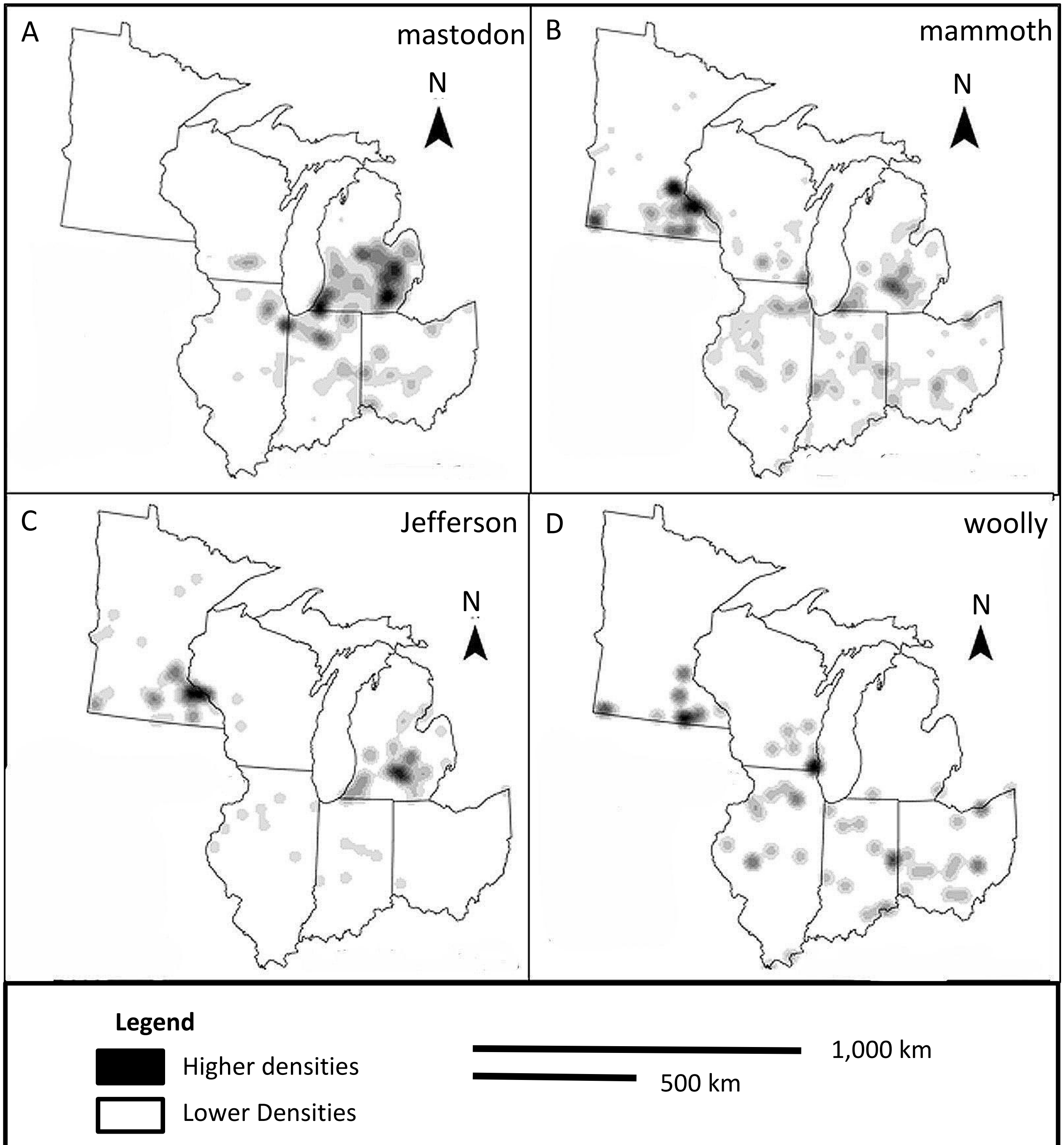

Figure 4-6: Kernel Density rasters of mastodon (A), mammoth (B), Jefferson mammoth (C), and woolly mammoth (D) site localities. Mastodons have a higher density in the southern half of Michigan and the southern tip of Lake Michigan. Mammoths appear to be more spread out, with heaviest density in southeastern Minnesota, and other clusters in Michigan, Indiana, Illinois, Ohio, and southern Wisconsin.

Analysis

For Objective 2, the purpose was to determine the geographic ranges of each (American mastodon, Jefferson mammoth, and woolly mammoth) and identify if an overlap existed between taxa. When looking at the geographic ranges produced from the Directional Distribution ellipse (one standard deviation) and Kernel Density rasters, the conclusion is that the null hypothesis, which stated that there would be no overlap between taxa, must be rejected.

The Directional Distribution ellipse (one standard deviation) geographic ranges also had overlap between the taxa. However, there was much more independent range area, with approximately 13.3% of the American mastodon's, 36.3% of the Jefferson mammoth's, and 3.71% of the woolly mammoth's geographic ranges being independent of one another (Table 4-3). A qualitative analysis of the Kernel Density rasters also show overlap between the taxa, even if the highest density clusters were found in different locations. According to the Kernel Density rasters, the mastodons had the highest density in southern Michigan while the mammoths had the highest density in southeastern Minnesota (Figures 4-6A-B). In particular, the Jefferson and woolly mammoths' areas of higher density were similar, but the woolly mammoth had lower density clusters across the study area while the Jefferson mammoth only two higher, and larger, density clusters (Figures 4-6C-D). Overlap between mammoths and mastodons exists in Michigan, Indiana, Illinois, and Ohio. Minnesota is the only state in the region where only mammoths were found.

Objective 3: Geographic Range Shifts

The purpose of objective three was to determine whether a geographic range shift for mammoths and mastodons can be detected using the Directional Distribution ellipse (one standard deviation) for the available data. The null hypothesis was that range shifts can be detected. Due to the limited number of site localities for 24-18 ka, the only taxa used for this analysis was *Mammut americanum* (American mastodon) and *Mammuthus* spp. (lumping all mammoth species together).

Mammut americanum (American mastodon)

According to the Directional Distribution ellipse (one standard deviation) method, the 24-18 ka geographic range for the American mastodon was 264,000 square kilometers and the geographic range for 18-11.5 ka was 145,000 square kilometers, approximately 119,000 square kilometers smaller (Table 4-5). The overlap between the two time periods was about 37,132 square kilometers, approximately 14% of the 24-18 ka geographic range and 26% of the 18-11.5 ka geographic range (Table 4-5; Figure 4-7).

Table 4-5: 24-18 ka and 18-11.5 ka Directional Distribution ellipse areas and overlap. Table shows the area (square kilometers) of the geographic ranges determined by the Directional Distribution ellipse (one standard deviation) method, as well as the area, and percentage, of overlap.

	24-18 ka	18-11.5 ka	Overlap	Percentage overlap of 24-18 ka	Percentage overlap of 18-11.5 ka
Mastodon	264,084.76	144,797.33	37,132.04	14.06%	25.64%
Mammoth	326,301.12	312,002.84	100,057.70	30.66%	32.07%

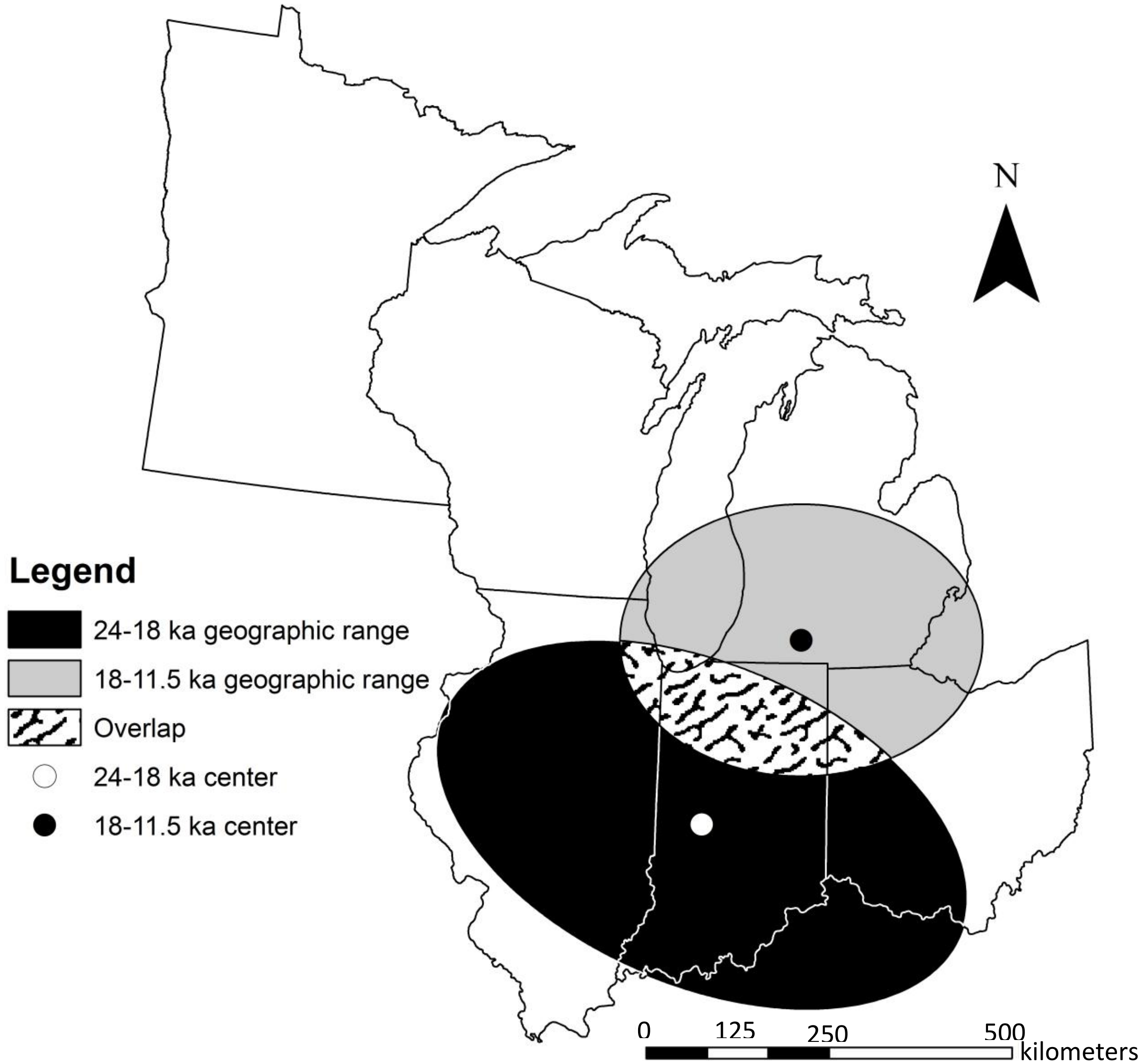

Figure 4-7: Directional Distribution ellipses of Mastodons for 24-18 ka and 18-11.5 ka. The black polygon represents the 24-18 ka geographic range and the gray polygon represents the 18-11.5 ka geographic range. The overlap is shown in between.

Mammuthus spp. (Mammoth species)

The 24-18 ka mammoth geographic ranges produced by the Directional Distribution ellipse (one standard deviation) method was approximately 326,300 square kilometers. The Directional Distribution ellipse produced 18-11.5 ka geographic range for mammoths was approximately

312,000 square kilometers, about 14,300 square kilometers smaller than the 24-18 ka geographic range. The overlap between the two time periods was approximately 100,000 square kilometers, about 31% of the 24-18 ka geographic range and 32% of the 18-11.5 ka geographic range (Table 4-5; Figure 4-8).

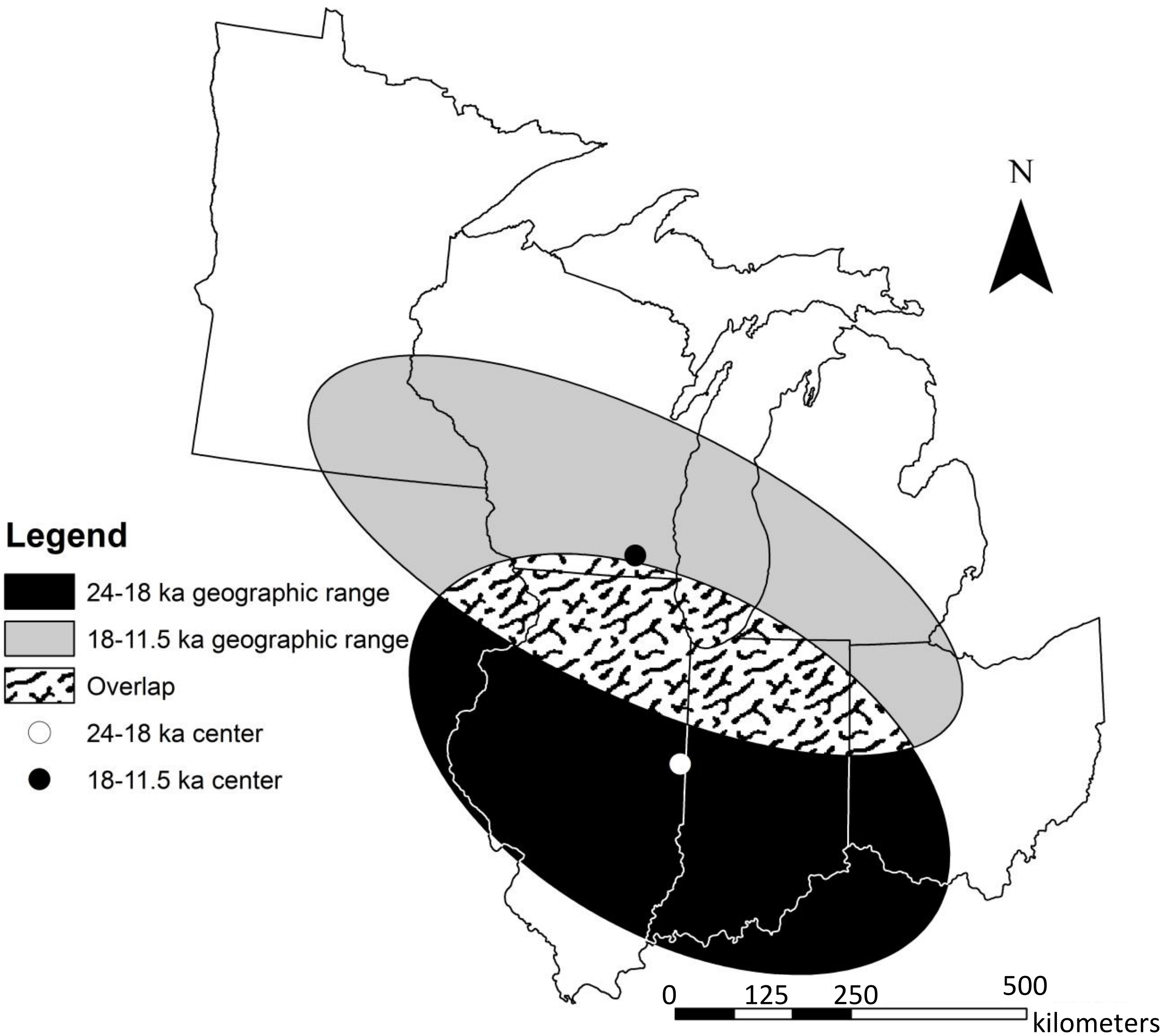

Figure 4-8: Directional Distribution ellipses of Mammoths for 24-18 ka and 18-11.5 ka. The black polygon represents the 24-18 ka geographic range and the gray polygon represents the 18-11.5 ka geographic range. The overlap is shown in between.

Range shift was determined by measuring the distance between the mean center points created for each time period. The mean center of the mastodon geographic range shifted approximately 286 kilometers to the northeast between time periods (Table 4-6; Figure 4-7). Mammoth geographic range mean centers shifted approximately 304 kilometers to the north-northwest (Table 4-6; Figure 4-8).

Table 4-6: Range shift of Directional Distribution ellipses for mammoths and mastodons. Table shows the distance and direction of the range shift of the mean centers of mammoth and mastodon geographic ranges between 24-18 ka and 18-11.5 ka.

	Distance	**Direction**
Mastodon	286.1 km	NE
Mammoth	303.5 km	N/NW

Analysis

For Objective 3, the Directional Distribution ellipse (one standard deviation) method was used to determine whether a geographic range shift occurred between 24-18 ka and 18-11.5 ka. Both the mammoth and mastodon taxa showed similar results. Mammoths had a geographic range of approximately 326,000 square kilometers at 24-18ka and approximately 312,000 square kilometers at 18-11.5 ka (Table 4-5). Mastodons showed smaller geographic ranges, with approximately 264,000 square kilometers at 24-18 ka and 145,000 at 18-11.5 ka (Table 4-5). Both taxa also showed a northern shift in geographic ranges between the two time periods, with mammoths shifting towards the north-northwest (by ~304km) and mastodons shifting towards the northeast (by 286 km; Table 4-6). With both methods showing a range shift, the null hypothesis for Objective 3, that range shifts for the two taxa could be detected, was accepted.

Objective 4: Habitat Partitioning (Vegetation)

With both methods of producing geographic ranges showing a similar, yet taxa independent, shift in direction (mastodons towards the north and northeast; mammoths towards the north-northwest), vegetation data were analyzed to determine whether this variable explained these results. The null hypotheses related to the vegetation data were that (1) the American mastodon (*Mammut americanum*) would be found in environments with higher percentages of arboreal vegetation, including *Picea*, *Betula*, Cupressaceae, *Fraxinus*, (2) while the mammoth taxa would be found in environments with higher percentages of non-arboreal vegetation, such as Cyperaceae, Poaceae, and *Artemisia*. Using pollen data derived from the NOAA Paleoclimatology Program's Top 15 Pollen Types (http://www.ncdc.noaa.gov/paleo/pollen.html), rasters were created for six time periods (18+ ka, 18-17 ka, 17-15.7 ka, 15.7-13.9 ka, 13.9-12.9 ka, and 12.9-11.5 ka). The pollen data were shown in percentage format. In total, for all time periods, there were 83 vegetation sites, most covering more than one time period (Table 4-7).

Table 4-7: Totals for radiocarbon dated mammoth and mastodon localities and vegetation sites divided between the six time periods (18+ ka, 18-17 ka, 17-15.7 ka, 15.7-13.9 ka, 13.9-12.9 ka, 12.9-11.5 ka). There were 60 dated sites (22 mammoth, 38 mastodon) and when divided between the time periods, 258 vegetation sites.

	Sites (Total)	Mammoth	Mastodon	Vegetation
18+ ka	6	6	0	14
18-17 ka	0	0	0	21
17-15.7 ka	4	3	1	35
15.7-13.9 ka	12	4	8	44
13.9-12.9 ka	15	3	12	62
12.9-11.5 ka	23	6	17	82
Total	60	22	38	258

Descriptive Statistics

The plant taxa associated with mastodons and mammoths were determined by comparing all proboscidean site locality data (Table 4-1) to pollen percentages for all pollen sites for six time periods (Table 4-7) to determine if there was a relationship between particular proboscidean species and specific vegetation types. For undated proboscidean localities, vegetation percentages were calculated for each time period. Images of the relative abundance of key plant taxa (*Artemisia*, *Betula*, Cupressaceae, Cyperaceae, *Picea*, *Pinus*, Poaceae, *Fraxinus*, and *Ostrya*-type) over time are shown in Appendix A.

Mammut americanum (American mastodon)

When using all site localities (Tables 4-1, 4-7), meaning that each locality was counted multiple times, once for each time period, the pollen percentages related to the American mastodon are 2.04% *Artemisia*, 1.24% *Betula*, 0.66% Cupressaceae, 6.20% Cyperaceae, 9.67% *Fraxinus*, 3.12% *Ostrya*-type, 35.83% *Picea*, 12.67% *Pinus*, and 3.17% Poaceae, totaling 74.62% of the pollen associated with the site localities. The average arboreal percentage (AP, of total) was 83.88%, and the average non-arboreal percentage (NAP, of total) was 16.12%.

Table 4-8: Descriptive statistics for American mastodon for nine vegetation type percentages (*Artemisia*, *Betula*, *Cupressaceae*, *Fraxinus*, *Ostrya-t*, *Picea*, *Pinus*, and *Poaceae*) and six time periods. Grey shaded columns were considered arboreal taxa and white shaded columns were considered non-arboreal taxa. Total percentages and arboreal and non-arboreal pollen percentages (of total) were also calculated.

	Artemisia	*Betula*	*Cupressaceae*	*Cyperaceae*	*Fraxinus*	*Ostrya-t*	*Picea*	*Pinus*	*Poaceae*	***Total***	***AP %***	***NAP %***
18+ka	2.3999	0.5594	0.0000	11.1530	3.7216	0.8675	51.5733	3.9369	3.7203	77.9318	77.8355	22.1645
18-17 ka	2.5823	0.8939	2.5493	5.8907	9.3530	1.8210	44.7771	4.2671	2.7319	74.8662	81.6283	18.3717
17-15.7 ka	2.3129	0.2794	0.6018	4.8338	17.3436	3.1549	44.9310	1.3933	3.0183	77.8690	86.1731	13.8269
15.7-13.9 ka	2.1590	1.3582	0.4003	7.7108	12.9895	4.6559	31.1289	5.8683	5.7168	71.9877	77.7921	22.2079
13.9-12.9 ka	1.9885	1.7022	0.2731	4.7814	9.4012	3.9549	29.3861	20.0764	2.3235	73.8873	87.3233	12.6767
12.9-11.5 ka	0.8221	2.6618	0.1489	2.8344	5.1996	4.2764	13.2100	40.4956	1.5132	71.1619	92.5260	7.4740
Average	2.0441	1.2425	0.6622	6.2007	9.6681	3.1218	35.8344	12.6729	3.1707	74.6173	83.8797	16.1203
Maximum	2.5823	2.6618	2.5493	11.1530	17.3436	4.6559	51.5733	40.4956	5.7168	77.9318	92.5260	22.2079
Minimum	0.8221	0.2794	0.0000	2.8344	3.7216	0.8675	13.2100	1.3933	1.5132	71.1619	77.7921	7.4740
Range	1.7602	2.3824	2.5493	8.3186	13.6220	3.7884	38.3633	39.1023	4.2036	6.7699	14.7339	14.7339
Median	2.2359	1.1261	0.3367	5.3623	9.3771	3.5549	37.9530	5.0677	2.8751	74.3768	83.9007	16.0993
Standard Dev.	0.6322	0.8666	0.9473	2.9023	5.0089	1.4937	14.0429	15.1619	1.4468	2.8639	5.8401	5.8401
Standard Error	0.2581	0.3538	0.3867	1.1849	2.0449	0.6098	5.7330	6.1898	0.5906	1.1692	2.3842	2.3842
Variance	0.3996	0.7509	0.8973	8.4233	25.0887	2.2311	197.2038	229.8844	2.0931	8.2019	34.1072	34.1072

Patterns can be seen between the different time periods, such as between *Picea* and *Pinus*. The *Picea* pollen percentages decrease through time, starting at 51.57% for 18+ ka and ending at 13.21% for 12.9-11.5 ka; Figure 4-9).

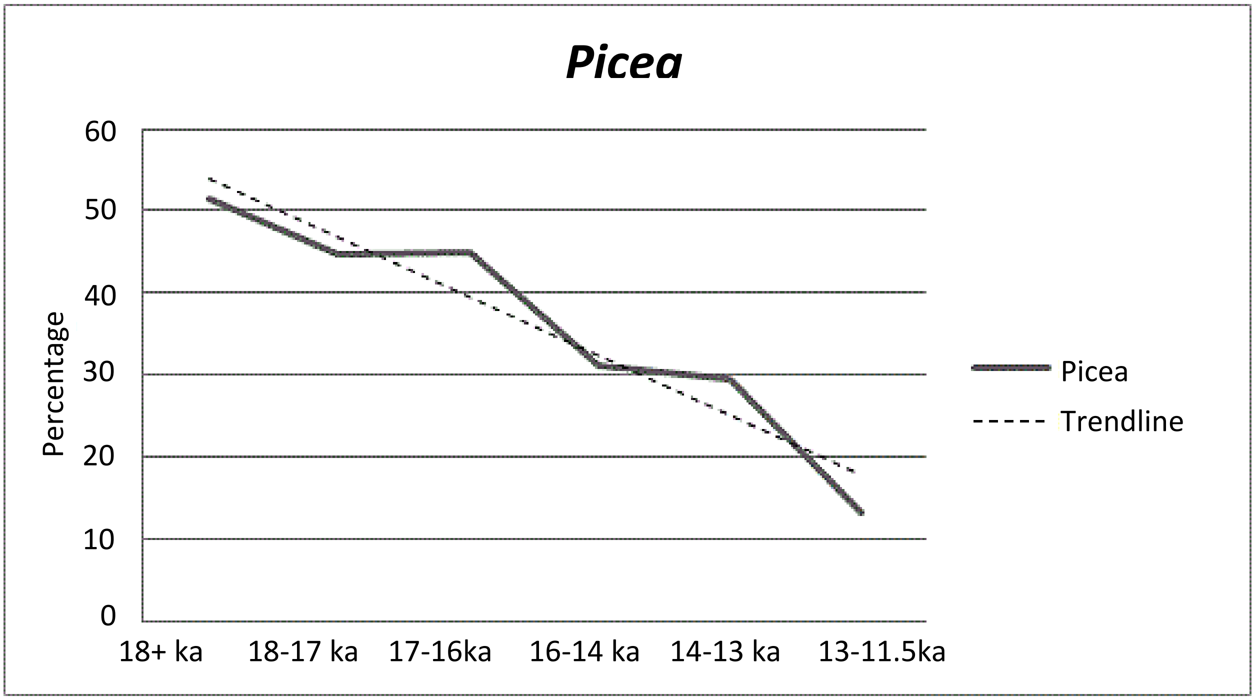

Figure 4-9: Line graph showing the almost linear trend of decreasing *Picea* pollen percentages through time. *Picea* pollen percentages started at 51.57% for 18+ ka and ended at 13.21% for 12.9-11.5 ka.

The opposite is observed for *Pinus* pollen percentages, starting at 3.94% for 18+ ka and ending at 40.5% for12.9-11.5 ka. However, while the *Picea* pollen percentages decrease linearly through time, the *Pinus* pollen percentages increase exponentially through time (Figure 4-10).

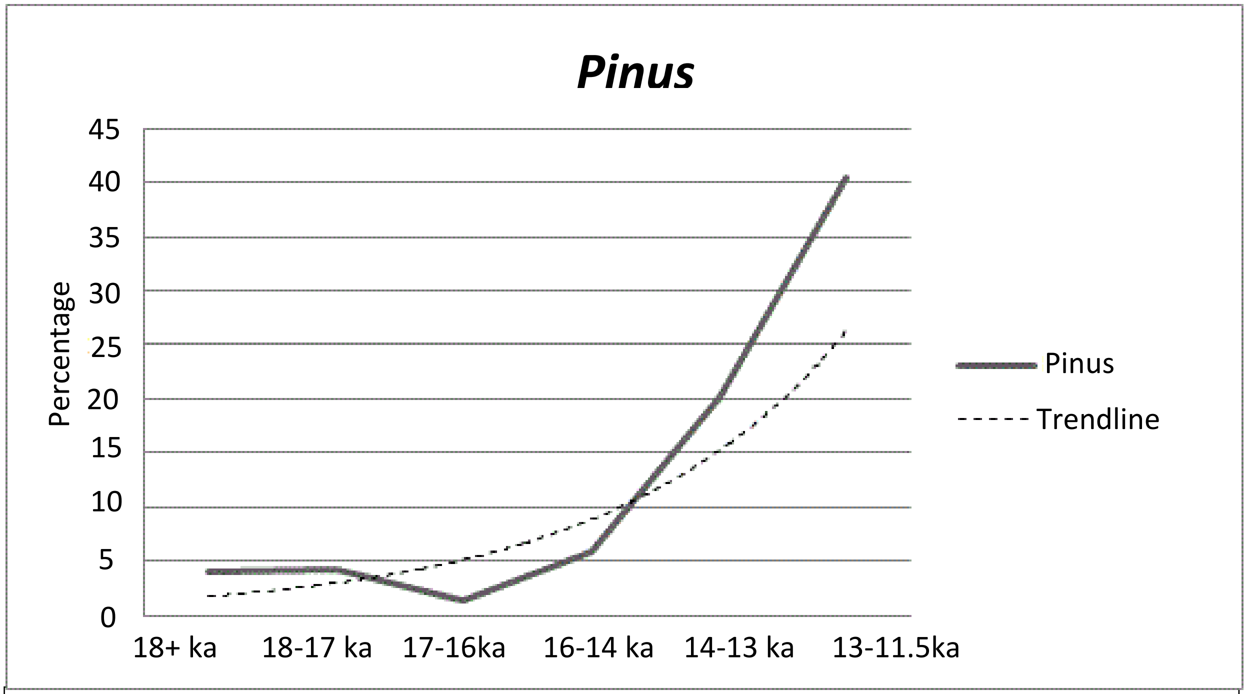

Figure 4-10: Line graph showing the exponential trend of increasing *Pinus* pollen percentages through time for the American mastodon. *Pinus* pollen percentages were 3.94% for 18+ ka and at 40.5% for 12.9-11.5 ka.

None of the other vegetation taxa show noticeable trends through time (Table 4-8). After calculating the totals for each time period, arboreal pollen (AP) and non-arboreal pollen (NAP) percentages were calculated from the total. A general increase can be seen with the AP percentages, 77.84% to 92.53%, indicating expanding forest cover, with the only time period not following the pattern being 15.7-13.9 ka Correspondingly, a general decrease could be seen with the NAP values, 22.16% to 7.47%, suggesting the shrinking of open habitats over time (Figure 4-11).

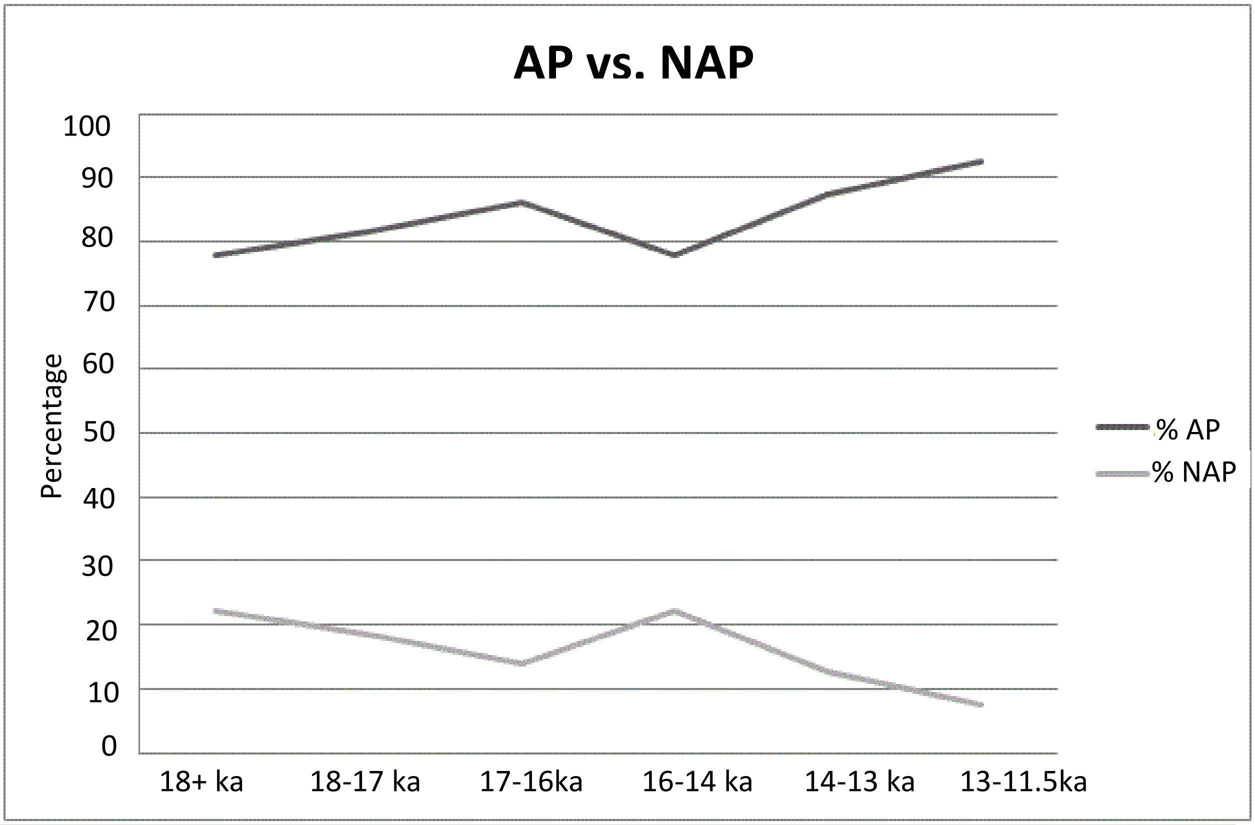

Figure 4-11: Line graph showing the linear trends seen for arboreal pollen (AP) and non-arboreal pollen (NAP) percentages associated with the American mastodon. AP percentages appear to increase with time (77.84% to 92.53%) and NAP percentages decrease with time (22.16% to 7.47%).

In addition to looking at all of the American mastodon sites, descriptive statistics were also determined for the site localities that were associated with dates. There were 38 dated American mastodon site localities (one from 17-15.7 ka, eight from 15.7-13.9 ka, twelve from 13.9-12.9 ka, and seventeen from 12.9-11.5ka). Using these site data, the average pollen percentages for the nine vegetation taxa were 1.14% *Artemisia*, 1.38% *Betula*, 0.24% Cupressaceae, 5.79% Cyperaceae, 8.66% *Fraxinus*, 3.95% *Ostrya*-type, 33.56% *Picea*, 14.93% *Pinus,* and 4.08% Poaceae, with a sum of 73.72% of the total pollen data analyzed. The average AP percentage of the total was 84.79% and the average NAP percentage was 15.21%. Table 4-9 shows the calculated statistics dealing with the radiocarbon dated mastodon localities.

Table 4-9: Descriptive statistics for American mastodon for nine vegetation type percentages (*Artemisia*, *Betula*, *Cupressaceae*, *Fraxinus*, *Ostrya-t*, *Picea*, *Pinus*, and *Poaceae*) and four time periods. Grey shaded columns were considered arboreal taxa and white shaded columns were considered non-arboreal taxa. Total percentages and arboreal and non-arboreal pollen percentages (of total) were also calculated. Statistics for the two other time periods discussed (18+ ka and 18-17 ka) were not calculated due to the absence of dated site localities.

	Artemisia	*Betula*	*Cupressaceae*	*Cyperaceae*	*Fraxinus*	*Ostrya-t*	*Picea*	*Pinus*	*Poaceae*	***Total***	***AP %***	***NAP %***
17-15.7 ka	0.3324	0.3367	0.0000	6.2886	5.0958	2.6278	59.1511	3.2530	3.9667	81.0521	86.9372	13.0628
15.7-13.9 ka	1.6808	0.7164	0.5506	8.6528	14.3400	4.7644	30.7644	2.9230	8.3551	72.7476	73.5533	26.4467
13.9-12.9 ka	1.9007	1.6807	0.2709	4.8067	9.6134	3.8469	30.6326	17.3334	2.2452	72.3305	87.2481	12.7519
12.9-11.5 ka	0.6275	2.7793	0.1297	3.4024	5.6039	4.5691	13.6780	36.2212	1.7487	68.7598	91.4073	8.5927
Average	1.1353	1.3783	0.2378	5.7876	8.6633	3.9521	33.5565	14.9326	4.0789	73.7225	84.7865	15.2135
Maximum	1.9007	2.7793	0.5506	8.6528	14.3400	4.7644	59.1511	36.2212	8.3551	81.0521	91.4073	26.4467
Minimum	0.3324	0.3367	0.0000	3.4024	5.0958	2.6278	13.6780	2.9230	1.7487	68.7598	73.5533	8.5927
Range	1.5683	2.4427	0.5506	5.2504	9.2442	2.1367	45.4731	33.2982	6.6065	12.2922	17.8540	17.8540
Median	1.1541	1.1986	0.2003	5.5477	7.6087	4.2080	30.6985	10.2932	3.1059	72.5391	87.0926	12.9074
Standard Dev.	0.7716	1.0920	0.2361	2.2444	4.2901	0.9670	18.8554	15.7015	3.0051	5.2038	7.7611	7.7611
Standard Error	0.3858	0.5460	0.1180	1.1222	2.1450	0.4835	9.4277	7.8507	1.5025	2.6019	3.8806	3.8806
Variance	0.5953	1.1925	0.0557	5.0372	18.4047	0.9352	355.5274	246.5369	9.0304	27.0795	60.2351	60.2351

For these statistics, instead of calculating statistics for each locality in every time period, the statistics were only calculated for the time period in which the locality was dated. For example, for Table 4-8, an individual locality's statistics would be calculated for each of the six time periods, (e.g., site one would have statistics calculated for 18+ ka, 18-17 ka, 17-15.7 ka, 15.7-13.9 ka, 13.9-12.9 ka, 12.9-11.5 ka, no matter if the locality's radiocarbon date) while Table 4-9 shows statistics for one site locality and one time period (e.g., site two is dated at 18-17 ka, and therefore, statistics are only calculated for pollen percentages between 18 ka and 17 ka). The reason for calculating statistics these two different ways is due to the large quantities of undated proboscidean localities.

Similar patterns can be seen with statistics derived from the dated American mastodon site localities as evident when all site localities of this taxon were calculated. Once again, the pollen percentages for *Picea* decreased through time and *Pinus* percentages increased through time (Figure 4-12).

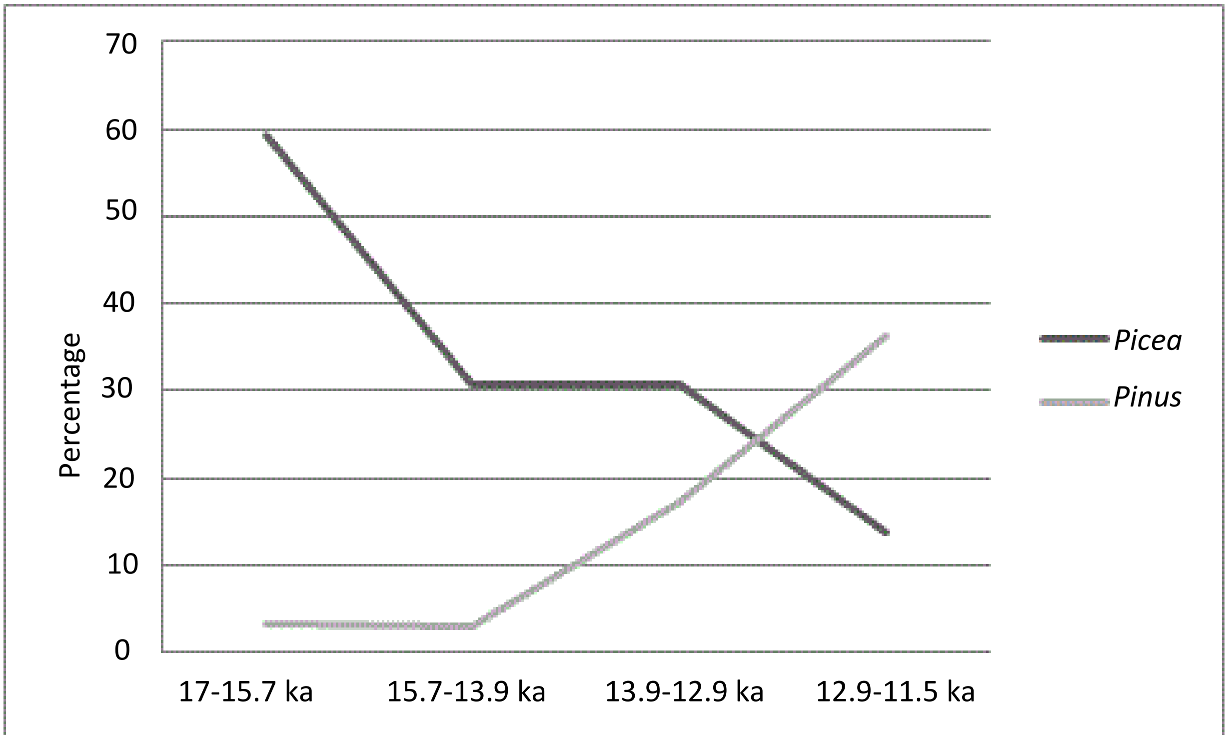

Figure 4-12: Line graph showing the general linear decrease of *Picea* pollen and the general linear increase of *Pinus* through time for the dated site localities of the American mastodon. *Picea* pollen percentages started at 59.15% 17-15.7 ka and ended at 13.68% 12.9-11.5 ka. *Pinus* pollen percentages shifted from 3.25% 17-15.7 ka to 36.2212.9-11.5 ka

Additionally, positive trends can be seen with *Artemisia* (excluding 12.9-11.65 ka) and *Betula*. Negative trends can be seen with Cupressaceae, Cyperaceae (excluding 15.7-13.9 ka) and Poaceae (excluding 15.7-13.9 ka). No patterns were observed for the AP and NAP percentages calculated from the total.

When comparing the statistics calculated using all American mastodon site localities to those calculated using only the dated site localities, the difference between most vegetation taxa were within one percent. The vegetation taxa showing higher percentages for the statistics calculated using all American mastodon sites, as described in the first set of statistics (Table 4-8), were *Artemisia,* Cupressaceae*,* Cyperaceae*, Fraxinus*, and *Picea,* while those showing lower percentages were *Betula, Ostrya*-type*, Pinus,* and Poaceae. *Picea*, with a difference of 2.78%, and *Pinus*, with a difference of 2.56%, were the only two taxa showing a difference higher than one percent. The first set of statistics used each site for each time period, creating duplicate records, and therefore could increase the total percentages for each vegetation type.

Mammuthus (Mammoth species)

Vegetation statistics for mammoth species (*Mammuthus* spp.) were calculated with similar methods as for the American mastodon. Statistics were first calculated on all site localities, for all six time periods 18+ka, 18-17 ka, 17-15.7 ka, 15.7-13.9 ka, 13.9-12.9 ka, 12.9-11.5 ka), and secondly, statistics were calculated for those mammoth site localities that had an associated date.

When using all site localities, the average pollen percentages are 3.91% *Artemisia*, 2.85% *Betula*, 1.09% Cupressaceae, 16.01% Cyperaceae, 7.43% *Fraxinus*, 2.21% *Ostrya*-type, 33.0% *Picea*, 8.78% *Pinus*, and 3.74% Poaceae, totaling 79.03%. After calculating the percent AP and NAP taxa from the totals, the results show 69.81% of the key taxa were arboreal, whereas 30.19% were non-arboreal (Table 4-10).

Few trends were observed between the vegetation taxa. However, after calculating the percentage of AP or NAP taxa from the totals, a positive trend was observed for the arboreal taxa through time, and correspondingly, a negative trend was observed for non-arboreal taxa (Figure 4-13).

Table 4-10: Descriptive statistics for *Mammuthus* for nine vegetation type percentages (*Artemisia*, *Betula*, *Cupressaceae*, *Fraxinus*, *Ostrya-t*, *Picea*, *Pinus*, and *Poaceae*) and six time periods Grey shaded columns were considered arboreal taxa and white shaded columns were considered non-arboreal taxa. Total percentages and arboreal and non-arboreal pollen percentages (of total) were also calculated.

	Artemisia	*Betula*	*Cupressaceae*	*Cyperaceae*	*Fraxinus*	*Ostrya-t*	*Picea*	*Pinus*	*Poaceae*	***Total***	***AP %***	***NAP %***
18+ ka	5.5563	0.7638	1.3147	35.7999	4.3625	2.3625	23.0250	5.6397	5.0283	83.8526	43.1155	56.8845
18-17 ka	6.6850	2.2495	3.6606	27.6709	3.4129	1.7121	37.2298	3.3318	2.4055	88.3580	54.2520	45.7480
17-15.7 ka	2.9739	0.7952	0.5491	13.9488	9.4447	1.0750	48.9612	4.0973	2.6933	84.5385	76.1469	23.8531
15.7-13.9 ka	3.7299	4.0901	0.2666	6.1589	12.8559	2.4680	39.3058	3.4907	5.1269	77.4928	80.2791	19.7209
13.9-12.9 ka	3.0261	5.6176	0.4196	8.7488	8.6433	2.1155	32.9884	7.3132	5.3302	74.2027	76.3826	23.6174
12.9-11.5 ka	1.5012	3.5978	0.3260	3.7593	5.8658	3.5512	16.4862	28.7674	1.8526	65.7075	88.6785	11.3215
Average	3.9121	2.8523	1.0894	16.0144	7.4309	2.2140	32.9994	8.7733	3.7395	79.0254	69.8091	30.1909
Maximum	6.6850	5.6176	3.6606	35.7999	12.8559	3.5512	48.9612	28.7674	5.3302	88.3580	88.6785	56.8845
Minimum	1.5012	0.7638	0.2666	3.7593	3.4129	1.0750	16.4862	3.3318	1.8526	65.7075	43.1155	11.3215
Range	5.1838	4.8538	3.3940	32.0406	9.4430	2.4762	32.4750	25.4357	3.4776	22.6505	45.5630	45.5630
Median	3.3780	2.9237	0.4844	11.3488	7.2546	2.2390	35.1091	4.8685	3.8608	80.6727	76.2648	23.7352
Standard Dev.	1.8923	1.9335	1.3162	12.8974	3.5487	0.8287	11.7015	9.9106	1.5843	8.2918	17.3414	17.3414
Standard Error	0.7725	0.7893	0.5373	5.2653	1.4487	0.3383	4.7771	4.0460	0.6468	3.3851	7.0796	7.0796
Variance	3.5807	3.7383	1.7324	166.3430	12.5931	0.6867	136.9239	98.2195	2.5101	68.7532	300.7250	300.7250

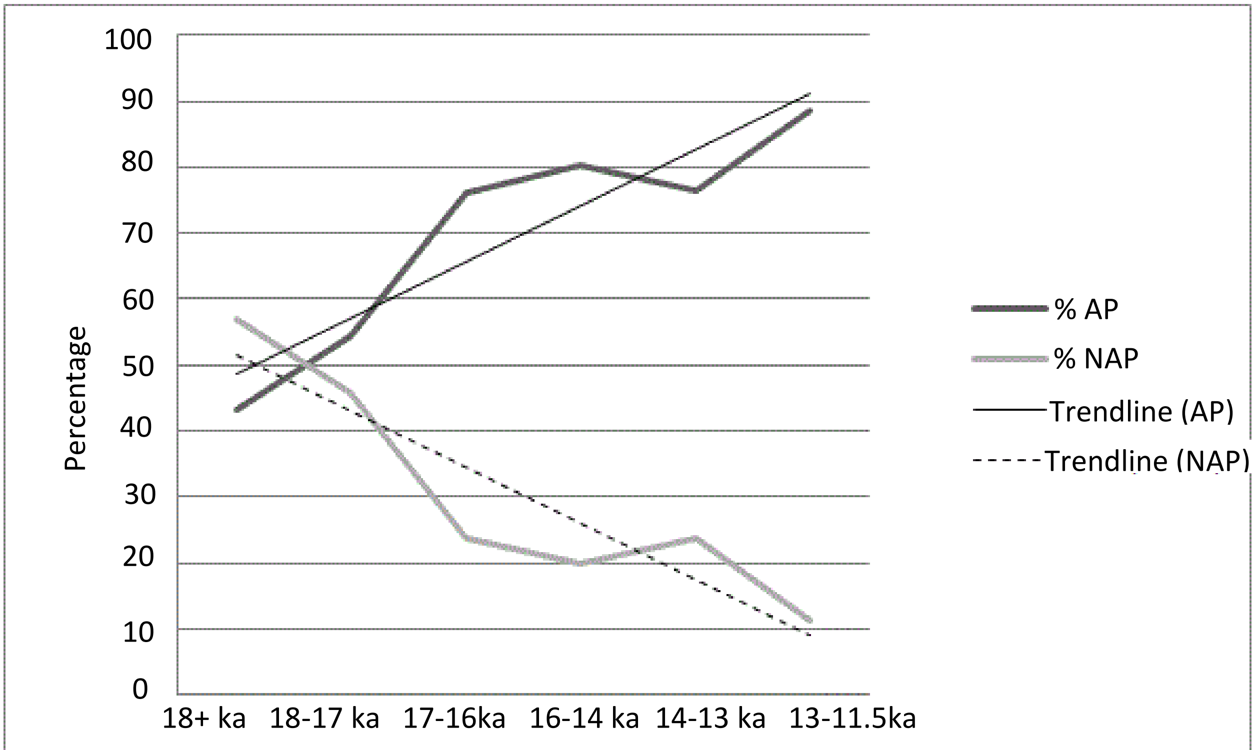

Figure 4-13: Line graph showing the observed trends of arboreal and non-arboreal percentages related to mammoth species. The arboreal percent from total started at 43.12% and ended at 88.68% while the non-arboreal percent from total started at 56.88% and ended at 11.32%.

Positive trends were also observed for *Betula*, *Fraxinus*, *Ostrya*-type, and *Pinus* and negative trends were observed for *Artemisia*, Cupressaceae, and Cyperaceae. The two remaining vegetation classes (*Picea* and Poaceae) showed very little change through time according to their trendlines.

In addition to the statistics calculated for all mammoth site localities, statistics were also calculated for the 22 dated site localities (six from18+ ka, three from 17-15.7 ka, four from15.7-13.9 ka, three from 13.9-12.9 ka, and six from12.9-11.5 ka). The average pollen percentages for these site localities are 2.38% *Artemisia*, 1.73% *Betula*, 0.30% Cupressaceae, 6.57% Cyperaceae, 8.86% *Fraxinus*, 3.0% *Ostrya*-type, 34.73% *Picea*, 15.02% *Pinus*, and 3.18% Poaceae, totaling 75.77% of the pollen total. AP and NAP percentages were calculated from the total, resulting in the site localities associated with 83.65% arboreal taxa and 16.35% non-arboreal taxa (Table 4-11).

Positive and negative trends were observed for the pollen data associated with the dated mammoth site localities. Positive trends were seen for *Betula* (1.41% to 3.74%), *Ostrya*-type (2.39% to 4.0%), and *Pinus* (11.43% to 26.48%). Negative trends were seen for *Artemisia* (2.44% to 1.13%), Cyperaceae (9.46% to 4.73%), *Picea* (36.80% to 17.79%), and Poaceae (3.97% to 1.75%). Very little change was observed for Cupressaceae or *Fraxinus* according to their trendlines. The best observed trends, however, were seen after the AP and NAP percentages were calculated. As shown in Figures 4-14 and 15, the percentage of arboreal taxa increased through time and the percentage of non-arboreal taxa decreased; again indicating an increase in forest cover over time.

Table 4-11: Descriptive statistics for mammoth species for nine vegetation type percentages (*Artemisia*, *Betula*, *Cupressaceae*, *Fraxinus*, *Ostrya*-type, *Picea*, *Pinus*, and *Poaceae*) and five time periods. Grey shaded columns were considered arboreal taxa and white shaded columns were considered non-arboreal taxa. Total percentages and arboreal and non-arboreal pollen percentages (of total) were also calculated. The sixth time period (18-17 ka) was not included due to the lack of dated mammoth site

	Artemisia	*Betula*	*Cupressaceae*	*Cyperaceae*	*Fraxinus*	*Ostrya-t*	*Picea*	*Pinus*	*Poaceae*	***Total***	**AP %**	**NAP %**
18+ ka	2.4431	1.4175	0.0000	9.4611	9.0875	2.3935	36.8012	11.4302	4.8627	77.8968	78.4756	21.5244
17-15.7 ka	2.4512	0.6262	0.5760	6.3677	7.5470	1.8959	54.2016	5.1248	3.0964	81.8867	84.7456	15.2544
15.7-13.9 ka	2.7687	0.9100	0.4644	7.3069	10.6523	4.1307	40.7500	3.9565	3.4524	74.3918	81.1908	18.8092
13.9-12.9 ka	3.1121	2.2449	0.0953	4.9734	11.0303	2.5773	24.0899	28.0862	2.1833	78.3926	86.7793	13.2207
12.9-11.5 ka	1.1349	3.4744	0.3755	4.7386	5.9656	3.9993	17.7857	26.4802	2.3289	66.2832	87.0586	12.9414
Average	2.3820	1.7346	0.3023	6.5695	8.8565	2.9993	34.7257	15.0156	3.1847	75.7702	83.6500	16.3500
Maximum	3.1121	3.4744	0.5760	9.4611	11.0303	4.1307	54.2016	28.0862	4.8627	81.8867	87.0586	21.5244
Minimum	1.1349	0.6262	0.0000	4.7386	5.9656	1.8959	17.7857	3.9565	2.1833	66.2832	78.4756	12.9414
Range	1.9771	2.8481	0.5760	4.7224	5.0647	2.2348	36.4159	24.1298	2.6794	15.6035	8.5830	8.5830
Median	2.4512	1.4175	0.3755	6.3677	9.0875	2.5773	36.8012	11.4302	3.0964	77.8968	84.7456	15.2544
Standard Dev.	0.7494	1.1507	0.2454	1.9265	2.1258	1.0053	14.3178	11.5679	1.0759	5.9311	3.7227	3.7227
Standard Error	0.3351	0.5146	0.1097	0.8615	0.9507	0.4496	6.4031	5.1733	0.4812	2.6525	1.6648	1.6648
Variance	0.5616	1.3241	0.0602	3.7113	4.5189	1.0107	204.9984	133.8169	1.1576	35.1785	13.8585	13.8585

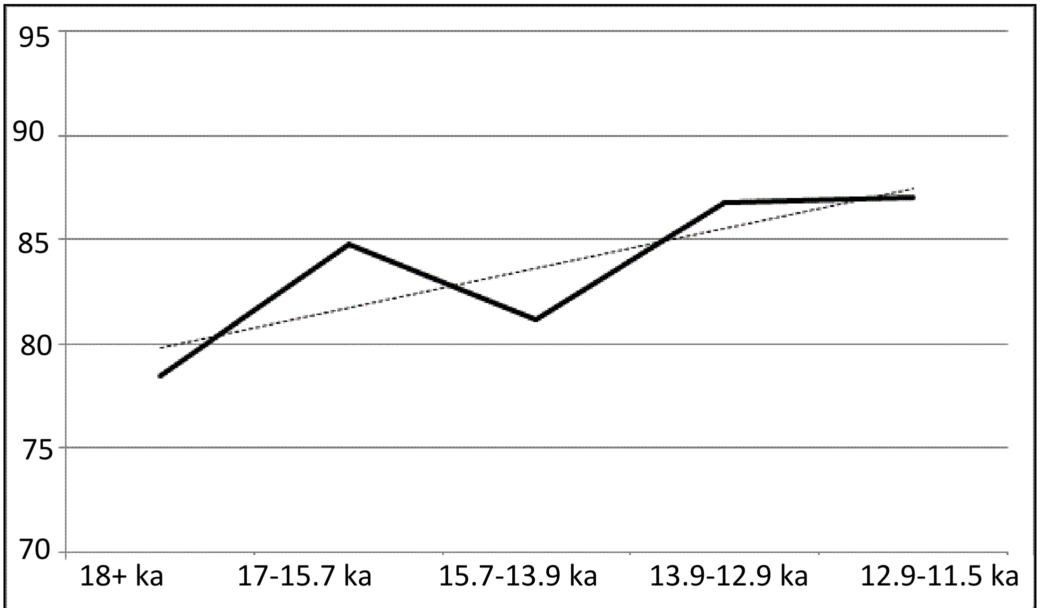

Figure 4-14: Line graph showing the positive trend observed for arboreal taxa's pollen percentage for mammoth species in the Great Lakes region. Arboreal pollen percentages were calculated from the sum of all individual vegetation taxa. The AP percentage started at 78.48% and ended at 87.06%, with the only decrease being for the 15.7-13.9 ka time period (73.55%).

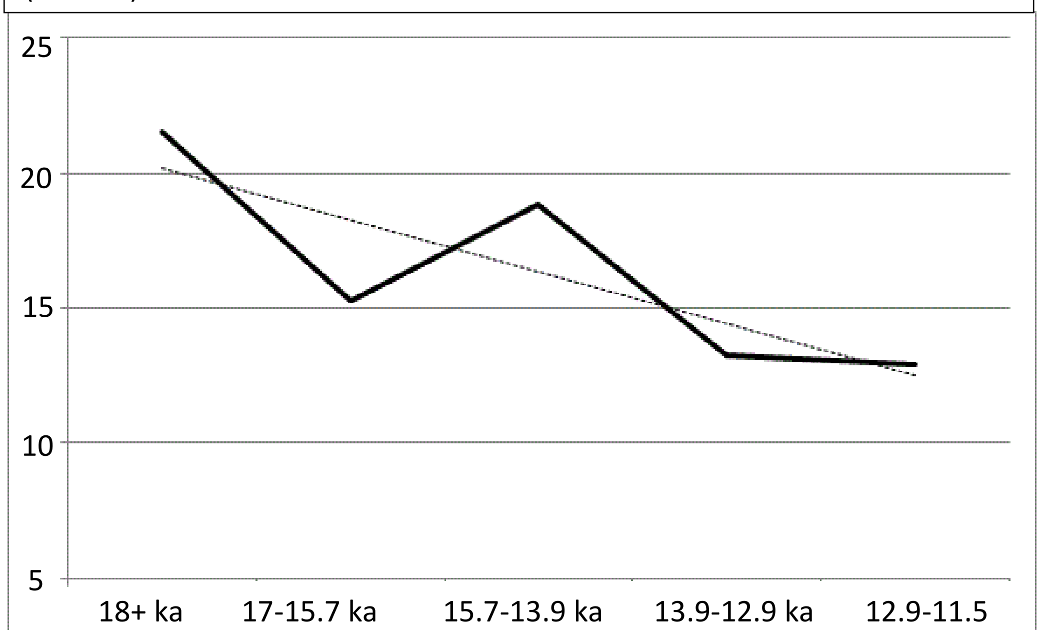

Figure 4-15: Line graph showing the negative trend observed for non-arboreal taxa's pollen percentages in relation to mammoth species in the Great Lakes region. NAP percentages were calculated from the sum of all individual vegetation taxa. The NAP percentage started at 21.52% and ended at 12.94%.

When comparing the descriptive statistics calculated using all the mammoth site localities and those calculated only from the dated mammoth site localities, it was observed that the differences were greater than those between the mastodon statistics. The differences for the mammoth statistics were rarely within one percent (only three taxa). The taxon with the lowest difference was Poaceae (0.55%); the taxon with the greatest difference was Cyperaceae (9.44%). The pollen percentages that were higher for the statistics calculated from all the site localities were *Artemisia*, *Betula*, Cupressaceae, Cyperaceae, and Poaceae, and those showing lower percentages for the statistics on the dated mammoth site localities were *Fraxinus*, *Ostrya*-type, *Picea*, and *Pinus*. The AP and NAP percentage differences were very large. The average AP percentage was much larger, 13.84%, for the dated mammoth site localities than when using all localities. Of course, the opposite was seen for the average NAP percentage. There were only two vegetation taxa, Cupressaceae and *Fraxinus*, that showed changes in pollen percentage trends between the two methods of calculating the statistics. Cupressaceae showed a negative trend when using all mammoth site localities and a horizontal trend when only using the dated site localities. *Fraxinus* changed from a positive trend (all site localities) to a horizontal trend (dated site localities).

Comparison between Vegetation Reconstructions for Mammoth vs. Mastodon

Differences between the American mastodon- and mammoth-associated vegetation were determined by subtracting the percentages of pollen types found at mammoth sites from those identified at mastodon localities. When using all the site data, the general observation is that for most taxa, and time periods, the pollen percentages associated with mastodon sites were less than the percentages associated with mammoth localities. Mastodon habitats had greater amounts of *Fraxinus*, *Ostrya*-type, *Pinus*, and, in general, higher values for arboreal taxa, indicative of a forested environment. Mammoths existed in areas that had higher percentages for *Artemisia* and Cyperaceae, suggestive of a more open environment. Of the arboreal taxa, Cupressaceae, *Betula*, and *Picea* were more common at mammoth sites than mastodon ones.

Based on comparison of pollen data associated with mammoth vs. mastodon sites, the greatest difference were found in the percentages of Cyperaceae and *Picea*. The average Cyperaceae percentage was 16.01% in mammoth habitats, while the average for mastodon localities was 6.20%, almost a 10% difference. Specifically, during the 18+ ka, 18-17 ka, and 17-15.7 ka time periods, with the differences in Cyperaceae pollen abundance were 24.65%, 21.78%, and 9.12%, respectively, in favor of mammoths. The difference in average *Picea* percentages for mammoths and mastodons for these same time intervals was only 2.835%. However, when looking at the individual time periods, mastodons were associated with much greater percentages of *Picea* for the 18+ ka and 18-17 ka intervals, with differences of 28.55% and 7.54%, respectively. Additionally, it was observed that the American mastodons were more likely to be associated with arboreal taxa (83.88%), compared to the mammoths (AP average of 69.81%). Correspondingly, the percentage of non-arboreal taxa found at mammoth sites (30.19%) was nearly doubled the percentage in mastodon habitats (16.12%).

When looking at the line graphs comparing plant taxa associated with mammoths and mastodons, similar trends were observed through time (Figures B1-11; C1-11). However, the steeper slopes of some trend lines, such as for *Betula,* Cyperaceae, or *Ostrya*-type, were observed. The trendlines calculated for the vegetation percentages associated with mammoth localities showed steeper slopes for *Betula* and Cyperaceae percent data are evident for the mammoth-reconstructed habitat, while steeper trendlines are noted for *Ostrya*-type in the mastodon-inferred vegetation.

When comparing the vegetation data related to the dated mammoth and mastodon site localities, only four time periods could be compared (17-15.7 ka, 15.7-13.9 ka, 13.9-12.9 ka, and 12.9-11.5 ka). Dated mastodon site localities were absent from the 18+ ka interval and dated mammoth site localities were absent from the 18-17 ka time period.

When comparing mammoth- and mastodon-associated vegetation data, all taxa, except for *Artemisia,* had averaged differences within one percent. The most significant difference was during 17-15.7 ka, which was approximately 2.1% higher for mammoth species. However, the average pollen percentages for each pollen type associated with dated mammoth sites were consistently higher than for mastodon localities. There were only two vegetation taxa with higher percentages at mammoth sites across all time periods, *Artemisia* and *Betula*; whereas *Ostrya*-type and Poaceae were the only taxa with higher average percentages at mastodon localities,. Arboreal and non-arboreal percentages between mammoth and mastodon habitats were also similar.

The two most abundant plant taxa in the terminal Pleistocene were *Picea* and *Pinus*, as indicated by having the highest pollen percentage averages (Tables 4-8 to 4-11). *Picea* pollen percentages were variable between time periods, with mammoths associated with higher percentages for the 15.7-13.9 ka and 12.9-11.5 ka intervals and lower percentages for the 17-

15.7 ka and 13.9-12.9 ka time spans. *Pinus* percentage differences between mammoth and mastodon localities were very different at 13.9-12.9 ka and 12.9-11.5 ka. Mammoth site localities had higher percentages 13.9-12.9 ka (10.75%) and mastodon site localities had higher percentages 12.9-11.5 ka (9.74%). *Pinus* pollen abundance needs to be interpreted with caution, however, as it's a notorious over-producer of pollen (Delcourt and Delcourt, 1991), and so it was less abundant in the landscape than was *Picea* during the terminal Pleistocene.

Unlike the line graphs based on all site localities (Figures B1-11), the line graphs using only the dated site localities showed differences between the vegetation associated with mammoths versus mastodons (Figures C1-C11). Mastodon localities showed a slight positive trend in *Artemisia* pollen percentages through time, while a negative trend through time was observed for *Artemisia* at mammoth sites (Figures B1; C1). The only other differences between the taxa were the trend line slopes, with the graphs showing the greatest slope differences for *Picea*, *Pinus*, and Poaceae (Figures B7-9, C-9). The other plant taxa (*Betula*, Cupressaceae, Cyperaceae, *Fraxinus*, and *Ostrya*-type) showed very similar slopes between the two proboscidean-reconstructed habitats (Figures B2-B6; C2-6). Even when comparing the arboreal and non-arboreal percentages, few differences were observed with the trend lines (Figures B10-11; C10-11).

Regression

Regression analyses were performed on a series of random points generated in ArcGIS 10 (ESRI, 2011). Originally, 2,532 random points were generated under the conditions that the number of points was ten percent of the total number of cells in the vegetation rasters and the minimum distance between the points was the width of the cell, approximately five kilometers. Two different types of regressions were performed on the data, both with slight modifications to the data.

Negative Binomial Regression

The first regression analysis executed was a Zero-inflated Negative Binomial regression (ZINB), which was performed in R with the pscl package. The random points not lining up with the vegetation rasters, essentially showing NO DATA, were deleted to minimize error. After the deletion, there were 2,251 points. The data were further transformed by multiplying the mammoth and mastodon kernel density values by 10^9 so the count regression could be performed.

Mastodon Localities

The Zero-inflated Negative Binomial Regression was performed to determine whether a relationship exists between mastodon localities and the four most significant vegetation classes identified (arboreal, non-arboreal, *Picea*, and Cyperaceae). According to the ZINB, mastodon sites were positively related to arboreal taxa percentages (coefficient= 0.02615) and the relationship was highly significant (P=7.41e-08) (Table 4-12). The coefficient for the zero-component was 0.026878 with a P value of 4.22e-08 (highly significant). These results indicate a positive relationship between pollen percentages of arboreal taxa and mastodon localities; however, the zero-component indicates that the higher the arboreal percentages, the more likely the location did not contain mastodons.

Table 4-12: Zero-inflated Binomial Regression analyses of mastodon site data show a highly significant positive relationship with arboreal pollen percentages (coefficient= 0.02615, P value= 7.41e-08) and a non-significant negative relationship with non-arboreal percentages (-0.0126; 0.165). Zero components indicate that the higher the arboreal percentage, the least likely the site would contain mastodons (0.0269; 4.22e-08), while the higher the non-arboreal percentage, the least likely the site would contain mastodons (0.1478; <2e-16).

	Estimate	Pr(>|z|)	Significance
Arboreal	0.02615	7.41E-08	High
Zero-inflation model coefficient	0.026878	4.22E-08	High
Nonarboreal	-0.0126	0.165	None
Zero-inflation model coefficient	0.14776	<2E-16	High

Mastodon localities showed a negative relationship to non-arboreal taxa percentages (coefficient= -0.01260) and a P value of 0.165 (not significant) (Table 4-12). The zero component of the regression was 0.14776, with a P value of <2e-16 (highly significant). According to the results, mastodon sites may show a negative relationship to non-arboreal pollen percentages, but since the results were not significant, this relationship is not definite. The zero-component indicates the higher the non-arboreal percentage, the less likely the site contains mastodons (Table 4-12), which corresponds to the hypothesis that mastodons are more likely associated with arboreal taxa than non-arboreal.

ZINB results showed a somewhat significant (P value= 0.001) negative relationship between mastodon localities and Cyperaceae pollen percentages. The highly significant zero-component indicates the higher the Cyperaceae percentage, the least likely the site would contain mastodons (coefficient= 0.06892; P= 1.18e-06). The ZINB results between mastodons and *Picea* show a highly significant negative relationship (coefficient=-0.054778; P=<2e-16). The zero-component indicates that the higher the *Picea* percentage, the less likely the site would contain mastodons (coefficient=0.052355; P=<2e-16; Table 4-13).

Table 4-13: Zero-inflated Binomial Regression analyses of mastodon localities show a somewhat significant negative relationship with *Cyperaceae* pollen percentages (coefficient= -0.0553, P= 0.001) and a highly significant negative relationship with *Picea* pollen percentages (-0.0548; <2e-16). Zero components indicate that the higher the *Cyperaceae* and *Picea* percentages, the less likely the site would contain mastodons.

	Estimate	Pr(>|z|)	Significance
Cyperaceae	-0.05534	1.00E-03	Somewhat
Zero-inflation model coefficient	0.06892	1.18E-06	High
Picea	-0.054778	<2e-16	High
Zero-inflation model coefficient	0.052355	<2e-16	High

Mammoth localities

According to the ZINB results, mammoths are positively related to arboreal pollen percentages (coefficient=0.003429), but the relationship was not significant (P=0.434). The zero-component of the model was 0.02324 (highly significant), indicating that the higher the arboreal percentage, the more likely the site did not contain mammoths. ZINB results showed a positive relationship for mammoths and non-arboreal taxa (coefficient=0.00349); however, this was not significant (P=0.484). The zero-component was highly significant (coefficient=0.053192), which indicates that the higher non-arboreal percentages decreased the probability of the site containing any mammoths (Table 4-14).

Table 4-14: Zero-inflated Binomial Regression analyses of mammoth site localities show a non-significant positive relationship with AP percentages (coefficient= 0.00349, P value= 0.484) and a non-significant negative relationship with NAP percentages (-0.0004165; 0.962). Zero components indicate that the higher the arboreal percentage, the more likely the site did not contain mammoths (0.02324; 1.65E-06), and the higher the non-arboreal percentage, the more likely the site did not contain mammoths (0.053192; <2.32E-11).

	Estimate	Pr(>|z|)	Significance
Arboreal	0.003429	4.84E-01	None
Zero-inflation model coefficient	0.02324	1.65E-06	High
Nonarboreal	-0.0004165	0.962	None
Zero-inflation model coefficient	0.053192	2.32E-11	High

When analyzing Cyperaceae and *Picea* taxa, ZINB results show Cyperaceae had a very significant (P=7.4E-08) negative relationship with mammoth site localities (coefficient=-0.07494) and a highly significant zero-component (coefficient=0.04591). The positive zero-component indicates that the higher the Cyperaceae percentage, the more likely the site did not contain mammoths. The analysis also showed mammoths had a highly significant (P=1.05-06) negative relationship to *Picea* (coefficient=-0.22666). The zero-component (coefficient=0.030236) indicates that the higher the *Picea* percentage, the least likely the site contained any mammoths (Table 4-15).

Table 4-15: Zero-inflated Binomial Regression analyses of mammoth sites show highly significant negative relationships with *Cyperaceae* percentages (coefficient= -0.0553, P= 0.001) and *Picea* percentages (coefficient= -0.0548; P= <2e-16). The highly significant positive zero-component coefficients indicate that the higher the *Cyperaceae* and *Picea* percentages, the more likely the site did not contain mammoths, similar to the result for mastodons (Table 4-14).

	Estimate	Pr(>|z|)	Significance
Cyperaceae	-0.07494	7.40E-08	High
Zero-inflation model coefficient	0.04591	8.36E-04	High
Picea	-0.22666	1.05-06	High
Zero-inflation model coefficient	0.030236	7.24E-10	High

Summary of Zero-inflated Binomial Regression

Using the Zero-Inflated Binomial Regression analysis, the results were inconsistent. Mastodon sites show a negative relationship to non-arboreal vegetation and a positive relationship to arboreal vegetation, which supports my hypothesis, but only the arboreal vegetation analysis showed a statistical significance. In contrast, the ZINB results for mammoth localities rejected the hypothesis that they would be correlated to non-arboreal vegetation. Specifically, mammoth sites showed a negative relationship to non-arboreal vegetation and a positive relationship to arboreal vegetation; however, neither of these results were statistically significant.

The zero-components were highly contradictory, with all of the coefficients being positive and highly significant. The results indicated that the higher the non-arboreal and arboreal percentages, the more likely the location did not contain any mastodons. Zero-components for mammoths showed similar results, indicating that the higher the non-arboreal and arboreal percentages, the more likely the location did not contain any mammoths.

Analyses of individual vegetation taxa, Cyperaceae and *Picea*, also showed contradictory results. According to the ZINB analysis of mastodon sites, they had a negative relationship with both Cyperaceae and *Picea*, and both showed a level of significance. Mammoths also showed significant negative relationships to Cyperaceae and *Picea.* Zero-components for all four analyses were all significant and positive, indicating the higher the Cyperaceae or *Picea*, the more likely the site localities did not contain either mammoths or mastodons.

Since the hypothesis related to this objective stated that mammoths would be related to non-arboreal vegetation dominated by Cyperaceae, these results would reject the hypothesis. For mastodons, the results of the ZINB analyses show a possibility of accepting the hypothesis that mastodons would be related to arboreal vegetation dominated by *Picea*; however, the arboreal results were not statistically significant and the *Picea* results were contradictory. Due to the lack of statistical significance and the existence of contradictions, the hypothesis was ultimately rejected.

However, these results are contradictory to plant fossil analyses at and near proboscidean sites which report high pollen and macrofossil abundances of sedges and other members of Cyperaceae and spruce associated with mammoth and mastodon skeletons (e.g., Fredlund et al., 1996; Holman, 2001; Bearss and Kapp, 2003; Saunders et al., 2010). Therefore, an attempt to further decrease error must occur before further analyses can be performed.

Linear Regression

The second regression model run was a Linear Regression, also performed in R. The random points were split into two different categories, one without zeroes from the mammoth Kernel Density raster and one without zeroes from the mastodon Kernel Density raster. Duplication existed between the two categories if both mammoths and mastodons had non-zero entries for the random points. Once divided, the mammoth and mastodon Kernel Densities were data transformed by multiplying them by the natural log. After the modifications, there were 1,020 records for mastodons and 1,088 records for mammoths.

Mastodon Localities

The Linear Regression analyses were only performed for arboreal and non-arboreal vegetation, because much of the Cyperaceae and *Picea* results from previous analyses showed little significance. According to the Linear Regression, mastodon sites were positively related to arboreal vegetation (coefficient=0.33406), which was statistically significant (P=1.63E-06). The ANOVA shows a significant difference of the means, indicating that the relationship seen is not due to chance. The analysis for non-arboreal vegetation showed a negative relationship (coefficient=-0.01858), but the results were not significant (P=0.249). The ANOVA showed no significant difference between the means (Table 4-16).

Table 4-16: Linear regression of mastodon localities show a highly significant positive relationship with arboreal pollen percentages (coefficient=0.33406, P= 1.63E-06) and a non-significant negative relationship with non-arboreal pollen percentages (coefficient= -0.01858; P= 0.249). ANOVA results indicate the arboreal pollen results are not due to chance.

	Estimate	**Std. Error**	**t value**	**Pr(>|t|)**	**Significance**
(Intercept)	-9.669986	0.414151	-23.349	<2e-16	High
Arboreal	0.33406	0.6926	4.823	1.63E-06	High
				Adjusted R2	0.0214
(Intercept)	-7.48122	0.19254	-38.854	<2e-16	High
Nonarboreal	-0.01858	0.01612	-1.153	0.2490	None
				Adjusted R2	0.0003229
ANOVA	**Sum Sq**	**Mean Sq.**	**F Value**	**Pr(>F)**	**Significance**
Arboreal	81.2	81.237	23.265	1.63E-06	High
Nonarboreal	4.7	4.7399	1.3288	0.2493	None

Mammoth Localities

Results of the Linear Regression for mammoth sites show little statistical significance. According to the analysis, mammoths are positively related to arboreal percentages (coefficient=0.016517), but this was not very significant (P=0.0143). The relationship between mammoths and non-arboreal percentages was negative (coefficient= -0.2946), but was also not very significant (P=0.138). The ANOVA results for both analyses showed little significance (Table 4-17).

Table 4-17: Linear regression of mammoth localities show little statistical significance, revealing a positive relationship with arboreal pollen percentages (coefficient=0.016517; P=0.143) and a negative relationship with non-arboreal pollen percentages (coefficient=-0.2946; P=0.138). ANOVA results show no statistically significant differences between the means.

	Estimate	**Std. Error**	**t value**	**Pr(>|t|)**	**Significance**
(Intercept)	-9.37774	0.403137	-23.262	<2e-16	High
Arboreal	0.016517	0.006732	2.454	0.0143	Low
				Adjusted R2	0.004601
(Intercept)	-8.02616	0.15878	-50.55	<2e-16	High
Nonarboreal	-0.2946	0.01194	-2.468	0.138	Low
				Adjusted R2	0.004664
ANOVA	**Sum Sq**	**Mean Sq.**	**F Value**	**Pr(>F)**	**Significance**
Arboreal	17.4	17.3986	6.0202	0.0143	Low
Nonarboreal	17.6	17.5968	6.0891	0.01376	Low

Summary of Linear Regression

Overall, the Linear Regression analyses explained very little of the variability present in the data. The only analysis that showed significant results was the positive relationship revealed between mastodon sites and arboreal pollen percentages and the ANOVA results that showed this relationship was not due to chance. The other analyses show little or no significance either way. Therefore, the vegetation hypothesis was rejected.

Summary

The purpose of Objective 4 was to determine whether, if possible, a difference exists between mammoth and mastodon vegetation preference. With the general opinion as a basis, the null hypothesis for this objective was that the American mastodon (*Mammut americanum*) would be found in environments with higher percentages of arboreal vegetation and mammoths would be found in habitats dominated by non-arboreal vegetation. Four different methods were used to decide whether to accept or reject the null hypothesis. The first method, using descriptive statistics on all the sites, was informative but inconclusive. Mastodon sites were dominated by arboreal pollen taxa, showing higher pollen percentages of *Fraxinus*, *Ostrya*-type, and *Pinus*. Mammoth sites did not show a clear dominance between arboreal or non-arboreal vegetation, but have higher percentages of *Artemisia*, *Betula*, Cupressaceae, Cyperaceae, and *Picea*. Other than slight differences in trend line slope, such as for *Betula*, Cyperaceae, and *Ostrya*-type, similar trends were seen when looking at the changes of vegetation through time.

The second method, using descriptive statistics on the dated site localities, showed even similar results between the vegetation types reconstructed for mammoths and mastodons than using data from all the sites. Even though the average pollen percentages for dated site localities were consistently higher, the difference was rarely larger than one percent. The only taxon showing a greater difference between mammoth and mastodon sites was *Artemisia*. The dated localities, however, showed differences between taxa when looking at the changes of vegetation through time (*Artemisia*, *Picea*, *Pinus*, and Poaceae).

The third method, using a Zero-Inflated Negative Binomial Regression model, also showed inconsistencies. The only statistically significant results were the positive relationship between mastodons sites and arboreal vegetation and the contradictory zero components, which indicated that both the higher the non-arboreal or arboreal pollen percentages, the more likely the site did not contain either mammoths or mastodons.

The fourth, and final, method, using a Linear Regression model, showed even less statistical significance. Once again, the only statistically significant result was the positive relationship between mastodon sites and arboreal vegetation, and the ANOVA results indicating this relationship is most likely not due to chance.

Using these four methods, the only conclusive result would be to reject the null hypothesis stated for objective four. The only part of the hypothesis that can be accepted would be the relationship between mastodons and arboreal vegetation because both regression models show a statistically significant positive relationship between the two. However, neither of the models showed conclusive results for the other three relationships.

Conclusion

In summary, three objectives (1, 2, and 4) had null hypotheses that were rejected and one objective (3) that had a null hypothesis that was accepted. Objective one's purpose was to compare the FAUNMAP database to a database created by myself which, in addition to the data published in the FAUNMAP database, contained mammoth and mastodon site locality data unpublished in the database. The differences in the number of proboscidean localities found in addition to the FAUNMAP database and the large difference in geographic range mean centers showed the need to use all data available when attempting to do biogeography studies. Objective two's null hypothesis stated that there would be no overlap between the taxa's geographic ranges, and it was rejected due to the massive overlap observed using both Directional Distribution ellipses and Kernel Density rasters. Objective three's null hypothesis stated that a range shift between the two time periods (24-18 ka and 18-11.5 ka) would be observed for mammoths and mastodons, based on the radiocarbon dates of fossil sites. This hypothesis was accepted due to the large shifts in their geographic range mean centers between the two time periods. Using the Directional Distribution method, mammoths showed a range shift of up to 304 km towards the north-northwest, and mastodons had an average range shift of 286 km towards the northeast. Objective four's null hypothesis stated that American mastodons would be associated with arboreal, primarily *Picea*, vegetation and mammoths would be associated with non-arboreal, mainly Cyperaceae, vegetation. This hypothesis was ultimately rejected because of the lack of conclusive results. Mastodons did show dominance in arboreal vegetation using both the Zero-Inflated Negative Binomial Regression model and the Linear Regression model; however, the results were inconclusive regarding the mastodons' relationship with non-arboreal vegetation as well as the mammoths' relationship with any type of vegetation.

CHAPTER FIVE: DISCUSSION

Analysis of Research Objectives

The ultimate purpose of this thesis research was to serve as a preliminary step to determining geographic ranges and range shifts of individual mammal taxa during the terminal Pleistocene. However, when looking at individual taxa, Riddle (1996) suggested that FAUNMAP, the most popular database available for extinct and extant animal population studies may not be effective on a species resolution. One could argue that the FAUNMAP database is incomplete, and this is true. For the southern Great Lakes region the FAUNMAP databases reports 180 proboscidean (mammoth or mastodon) sites and I added to a modified database an addition 528 site reports from the “gray literature” (documents of state historical societies, state academy of science journals, regional specific journals, etc.). Therefore, using an expanded and improved database, and comparing it to the publically available FAUNMAP database, the focus of this research was to determine whether geographic range data could be produced for two of the most studied taxa during this period, the American mastodon and mammoth species. To do this, this research had four objectives:

1) Compare the FAUNMAP database, with no additions or modifications, to a modified database consisting of both the original site locality data and additional data that were previously unpublished, as well as those published in sources looked over by the FAUNMAP collaborators.

2) Determine geographic range sizes of mammoths and mastodons and whether any geographic range overlap existed between the individual species in this region by using the more comprehensive "modified" database.

3) Determine whether geographic range shifts for mammoths and mastodons could be detected, and if so, distance and direction of the shifts using the modified database. And by comparison of my expanded database to the North American Pollen Database (NAPD),

4) Determine whether vegetation could explain the variability in distance and direction between mammoth and mastodon geographic range shifts (if detected) and whether the different proboscidean taxa were more closely related to different vegetation types.

Each objective, since they built up on one another, had different null hypotheses, if possible. Ultimately, not all of the hypotheses were entirely rejected, nor were all accepted. Objective one, which was the original comparison between the FAUNMAP database and the modified one that was created during this research, did not have a null hypothesis. Since the modified database would contain many more site localities, it was automatically assumed the geographic ranges would be different, and since larger population sizes are better for statistical studies, the modified database would therefore, be better for biogeographic studies. Due to this assumption, the modified database created during this investigation was used for objectives two through four. The hypothesis for objective two was also rejected because overlap did exist between the individual species of mammoths and mastodons in the Great Lakes region. Objective three's hypothesis, which stated that geographic ranges could be detected, was accepted. Distances of ~286 km (mastodons) and ~304 km (mammoths) were observed using the Directional Distribution ellipse method. Objective four's hypothesis, which entailed that the American mastodon would be more closely related to arboreal vegetation in this model and mammoth species would be more closely associated with non-arboreal vegetation, was also rejected. Rejection of two of the three hypotheses can be partly explained by error in the fossil proboscidean and pollen datasets.

Data Error

All studies have introduced error; however, studies utilizing fossil data pertaining to extinct animals introduce more error than studies that observe animal behavior and habitat interactions. The first problem with studies utilizing extinct animals rather than observable, or modern, animals is due to the nature of fossils. Fossils are defined as "any trace, impression, or remains of a once-living organism" (Shipman, 1993:1). Therefore, not all individual mammoths and mastodons were fossilized upon death, for example, and the biology and ecology of these extinct megaherbivores are reconstructed based on fragmentary remains, bones and teeth. Therefore, studies of fossil animals can only indirectly identify their preferred habitats. Investigations concerning such fossils can only infer behavior, such as reproduction and social interaction (Fisher, 2009), and this behavior may, or may not, be correct (Shipman, 1993). Shipman (1993) points out that it is incorrect to assume the fossils represent a living community frozen in time.

With studies trying to determine populations of extinct animals, one must understand that not all living organisms become fossils. Shipman (1993) recognized five causes of death: predation, disease, senility, accident, and starvation, and identified that each of these causes has different probabilities of the bones becoming fossils. Predation, senility, and starvation decrease the likelihood of preservation. For example, death by senility reduces the chances of fossil preservation, because of the loss of minerals from bones with age, prior to death. In contrast, accidents increase the likelihood of fossilization, especially those resulting in immediate burial by sediment (Shipman, 1993). Size, position in the food chain (herbivores vs carnivores), speed, environment, and body structure are other characteristics that can increase or decrease the probability of dead animals becoming fossils. Typically, small, slow, hard-bodied, aquatic (or maritime), herbivores are the most numerous fossils on the planet (Virtual Fossil Museum, 2011).

Paul (1998) estimated that anywhere between five and 14 percent of skeletized specimens became fossilized. This percentage is lower for mammoths and mastodons, which are big, vertebrate, herbivorous and terrestrial, and therefore, did not occur within the best environmental conditions for fossilization (Skeels, 1962; Holman, 2001). Skeels (1962) stated that most of the fossilized remains of Michigan proboscideans were found in swamps and bogs, and the abundance of these wetlands is due to their glacial origins. With the understanding of what specimens and environments have increased likelihoods of fossilization, it may be correct to assume that the documented proboscideans' site distribution may be more due to the distribution of glacial kettles in Michigan, and much of the Great Lakes region, than the actual paleoecology associated with the living animals. This idea of a relationship between glacial features and distribution of proboscidean localities was explored in Yansa and Adams (2012), which identified that mammoth and mastodon sites were more numerous in the formerly glaciated (northern) portion of the Great Lakes region than south of the LGM margin. This is also a good topic for future research.

Another source of error may have been introduced due to postmortem processes that moved fossil remains from where they were originally deposited, i.e., taphonomy. The two dominant postmortem taphonomic processes are predation and hydraulic transport. Flesh-bearing bones, especially the larger ones, are often carried away by predators to their dens, or even away from other predators to be fed upon in isolation. In contrast, ribs and smaller bones typically travel only short distances away from the site of death (Shipman, 1993). Bones and teeth carried by water, such as by glacial meltwater streams, can result in much larger distances travelled. The distances traveled relate to the hydraulic behavior of bones, which based on the bone's composition, shape, and size. Bones with high surface area to volume ratios, such as scapulae, can travel greater distances than bones with low surface area to volume ratios, like the mandible (Table 5-1). Therefore, the bones in Group I may not accurately represent the sites of initial deposition if they were fluvially transported (Voorhies, 1969; Shipman, 1993).

Table 5-1: The hydraulic behavior of mammal bones classified in three groups. Group I bones, such as ribs or vertebrae, can travel long distances, while Group III bones, e.g., the skull, do no travel very far from where they were first deposited. Modified from Voorhies (1969: 69).

GROUP 1	I & II	GROUP II	II & III	GROUP III
immediately moved, may float or bounce along bottom		gradually removed, stay in contact with the bottom		lag deposit
Far --> Close				
rib	scapula	femur	ramus of	skull
vertebra	phalange	tibia	mandibl	mandible
sacrum	ulna	humerus		
sternum		metapodial		
		pelvis		
		radius		

Despite Shipman's (1993) statement that it is incorrect to assume fossil locations represent a living community frozen in time and Voorhies (1969) study on the fluvial transport of bones, Behrensmeyer et al.'s (1979) study of death assemblages at the Amboseli National Park, Kenya, concluded that some animals do die where they had lived. Therefore, while errors exist when using fossilized specimens to reconstruct paleoenvironments, many paleoecologists are doing just that (e.g., Shunk et al., 2009; Bobe, 2011).

With an awareness of the errors mentioned above, I used all documented proboscidean site data for this M.S. research. Others, such as Abraczinkas (1992) and FAUNMAP (1996a), only used proboscidean localities that had accurate location descriptions. Abraczinkas (1992) eliminated 46 proboscidean records due to the inability to be accurately assigned to sections. FAUNMAP (1994) further limited their specimens by only including sites with known geographic locations, chronologies, and voucher specimens in a public institution. While creating my own database, I used all documented specimens, even if they did not have a definite location, associated to ^{14}C dates or were deposited in museums or universities. When accurate locations were not given, I estimated geographic coordinates based on the given descriptions. Even though using all documented sites introduced error, I believed that increasing the number of proboscidean sites was more important than their exact locations within quarter-sections.

Objective 1: FAUNMAP Comparison

The purpose of objective one was to compare the FAUNMAP database to the modified database containing all site locality data found throughout this research. Due to the knowing the statistical studies encouraged larger population sizes, it was assumed that the modified database would be better; however, the errors must also be known. Most of the errors introduced in this objective are attributed to site locations and fossilization processes. In particular, the FAUNMAP working group decided to limit the Pleistocene mammal sites to those with definite locations, chronologies, and known voucher specimens (FAUNMAP Working Group, 1994). I cannot say whether some of sites I added to the original FAUNMAP database were indeed found and rejected by the FAUNMAP Working Group (1994), instead I assumed that they had been ignored due to type of bone found, age (or lack thereof), not stored in public institutions, or having been documented only in the “gray literature.”

After all the additional sources were added to the original FAUNMAP database, there was a total of 708 proboscidean sites, only 180 of which were included in FAUNMAP. Another error that may have been introduced would be the one of duplication. Abraczinkas (1992, 1993) noted much duplication in proboscidean site localities while creating her database. Many publications list previously documented proboscidean site localities (e.g., Anderson, 1905; MacAlpin, 1940; Skeels, 1962; Abraczinkas 1992, 1993), and while these may be helpful, it can introduce error if these authors duplicated sites by assigning different names to proboscidean localities than were previously documented. While I tried to limit site duplication, there is no assurance that duplication was eliminated.

Despite the errors, I did notice the same issues mentioned by Riddle (1996) and Walker (2000). Much of the older publications (e.g., Anderson, 1905; MacAlpin, 1940) were not included in the FAUNMAP database unless they were reported in more recent publications. Significantly, the FAUNMAP database had no sites documented in Wisconsin prior to my research, and although the sites I added to the modified database from this state are not numerous, they do fill an important spatial gap. With the help of contacts from the Wisconsin Geological Museum (Slaughter, personal communication 2011; Dallman, J., n.d.) and local newspapers (e.g., Devitt, 1985; Hopkins, 1989; Associated Press, 1998, 1998a) 47 new sites were added from Wisconsin, most of them identified as *Mammuthus* spp.

While the geographic range areas for both mammoths and mastodons were similar between the two databases, there was a large distance between centroids (60 km and 205 km), both towards the east-southeast. This result is most likely due to the significant number of additional proboscidean sites from the southern and eastern states of the lower Great Lakes region in my modified database; 55 additional sites for Illinois, 101 sites in Indiana, 93 in Ohio, and 204 sites added for Michigan. In contrast, only 24 sites for Minnesota were added to the original FAUNMAP database in research.

Objective 2: Geographic Ranges of Mammoth and Mastodon

The purpose of objective two was to determine geographic range areas of mammoths and mastodons and whether overlap existed between them in the Great Lakes region. The null hypothesis stated that there would not be any overlap between the geographic ranges of these two different types of proboscideans. The basis for this hypothesis was the general assumption that the different taxa occupied two different habitats, with mammoths inhabiting more grassland (steppe) or tundra environments while mastodons favored more forested areas (e.g., Kurten and Anderson, 1980; Holman, 1995b).   However, the hypothesis of no overlap was rejected.   Since this M.S. research was looking at the entire southern Great Lakes region, this result could most likely be due to the relative small spatial resolution of this study; therefore, while overlap existed, it does not invalidate the assumption. Kernel Density rasters showed less overlap, but due to the limited sample size, exact geographic ranges could not be determined using this method.

While the geographic ranges for the taxa overlapped, there were some interesting patterns observed when looking at the locations inhabited by only one taxon. For example, the Directional Distribution ellipse technique showed the Jefferson mammoth occupied the most northern habitats; a location previously thought to be occupied by the woolly mammoth (Kurten and Anderson, 1980; Harington and Ashworth, 1986; Holman, 1991; Saunders et al., 2010). Woolly mammoths and American mastodons occupied the central regions of the study area, where there was much overlap, while the unidentified mammoths generally occupied the southern extent of the study area. The distributions of these proboscidean species probably changed over time with the shifting of plant communities in response to climatic warming during the terminal Pleistocene, but the resolution of these changes cannot be ascertained given the limited ^{14}C dating of plant and animal fossils recovered from the region.

The areas of the geographic ranges for all proboscideans were similar. The geographic range areas based on the Directional Distribution Ellipse method produced, from largest to smallest, were unidentified mammoth species (374 sq. km), woolly mammoth (339 sq. km), Jefferson mammoth (319 sq. km), and the American mastodon (201 sq. km).

In addition to the errors previously discussed, when looking at individual species, especially with mammoth species, much error could have been introduced into fossil databases due to the misidentification of species. Much debate exists when differentiating between mammoth species (e.g., Osborn, 1942; Kurten and Anderson, 1980; Madden, 1981a; Holman, 1995b; Pasenko and Schubert, 2004). Due to this controversy, it is impossible to determine whether many of the mammoth specimens from the Great Lakes region were accurately identified. The possibility exists that the more northern Jefferson mammoths were misidentified as woolly mammoths. Additionally, it is impossible to accurately produce geographic ranges due to the abundance of specimens labeled as “unidentified mammoth.” The unidentified mammoths could be either woolly or Jefferson mammoths; either way, they would, if eventually classified, would affect the estimated geographic ranges of their respective taxon.

Objective 3: Geographic Range Shifts

The purpose of objective three was to determine whether mammoth and/or mastodon geographic range shifts could be detected. The null hypothesis for this objective was that range shifts could be detected, which was ultimately accepted. However, this objective, more than the others, was the most error ridden due to the methods of determining ages for proboscidean localities. Out of the 708 sites collected, both from FAUNMAP and additional sources, only 60 localities, 8%, had associated ^{14}C dates. More than half of the dated site localities were younger than 12,000 ^{14}C yr BP. And many of these dates are erroneously too young, because of the incorporation of younger humic acids in bones from overlying soils; an finding only recently reported (Saunders et al., 2010). Only the purified collagen-dating method, where humic acids are removed from fossil bone and tooth (dentine) collagen in the laboratory, provides reliable ^{14}C ages, and these dates are limited to a very small number, and are mainly from recent discoveries in Illinois (Saunders et al., 2010). Hence, the chronological resolution of mammoth and mastodon sites in the Great Lakes region is very poor and it puts a constraint on the biogeographic analysis conducted for this study.

Due to the paucity of well-dated proboscidean localities, I decided to use the LGM limit of the Laurentide ice sheet as a basis for separating the older sites from the younger under the assumption of superposition. The sites north of the maximum glacial extent were dependent upon ice sheet recession before the land could be colonized by plants and animals, and thus had to be younger than those south of the LGM margin. This assumption alone would result in a northern range shift, because it would not account for the continued existence of proboscideans south of the LGM limit after the ice margin had retreated northwards.

Additionally, postmortem transportation could have affected the assumed ages of the site localities. During the time of glacial retreat, the hydrology of the region was much different than present. Glacial lakes were abundant and the large outwash plains indicate large quantities of water were discharged from the melting ice sheet (Andrews, 1987; Larson and Schaetzl, 2001). Fluvially transported bones could have crossed this perceived LGM boundary, and therefore be considered much older than actuality.

Despite the introduced errors, my study reconstructed northern range shifts of both mammoths and mastodons over time, which agrees with the findings of previous studies (FAUNMAP Working Group, 1996b; Lyons, 2003, 2005; Stuart et al., 2004; Bradshaw and Holzapfel, 2010). Using the FAUNMAP database, the FAUNMAP Working Group (1996b) published a study assessing the community response to environmental change, focusing on community models instead of geographic range shifts of individual species. They concluded that Pleistocene mammals could be modeled by a Gleasonian community model, meaning that individual species responded to environmental changes independently according to their own environmental tolerances. They also noted many species dispersed northward upon glacier retreat, agreeing with the results of my study.

A unique finding in my study was the different dispersion directions between mammoths and mastodons in the Great Lakes region in spite of an overall northward migration. Mastodons showed a range shift towards the north and northeast, whereas mammoths had a range shift towards the north-northwest, for reasons described below.

Lyons (2003, 2005) also observed northern, but individualistic, range shifts, as well as increasing geographic range sizes from the terminal Pleistocene to Holocene. Range size median change was 1.705. In my study, the Directional Distribution ellipses produced from my dataset showed a decrease in geographic range sizes of mammoths and mastodons in the region from the terminal Pleistocene to Holocene (median= 1.43; Table 4-5). The average distance of mammalian shifts as published by Lyons (2003) was between 1,200 and 1,400 km. The range shifts observed in this thesis research were significantly smaller. Mastodons had a range shift of approximately 286 km north-northeast and mammoths had an approximate range shift of about 304 km to the north-northwest. The discrepancies for sizes and range shift distances between this research and Lyons (2003, 2005) is most likely due to their focus on multiple species and community structures, whereas my study targeted two mammalian taxa within one region.

The causes behind the northern geographic range shift are commonly attributed to the increasing temperatures and the opening up of habitable land as the ice sheets retreated (Davis and Shaw, 2001; Graham and Grimm, 2003; Bradshaw and Holzapfel, 2010). However, another cause behind the geographic range shifts could be changes in vegetation. Many studies (e.g., Jackson et al., 2000; Williams et al., 2000; Davis and Shaw, 2001; Williams et al., 2002; Yansa, 2006) show northward shifts in vegetation as glaciers melted. This shift in vegetation may be the cause of the diverted range shifts between mammoths and mastodons. If the assumption is correct that mammoth habitats were primarily grasslands/tundras and mastodon habitats were primarily forest lands, then individualistic shifts in vegetation would result in the two different dispersal directions. Specifically, American mastodons showed a range shift towards the north and northeast, which suggested that they tracked the expansion of forested habitats with the melting of the Laurentide ice sheet. Mammoths showed a range shift towards the north-northwest, towards the more open habitats of the northern Great Plains.

Objective 4: Habitat Partitioning (Vegetation)

How animals choose their habitats depends on a combination of many abiotic and biotic characteristics. Objective three showed a diverted dispersal pattern between mammoths and mastodons, with mammoths dispersing towards the north-northeast and mastodons dispersing towards the north-northwest within the Great Lakes region. Most of these characteristics are difficult to isolate due to their dependence on one another; however, vegetation differences across this portion of North America are easily discerned through pollen analysis. The purpose of objective four was to determine whether, if possible, a difference exists between mammoth and mastodon vegetation preferences. The null hypothesis stated that the vegetation most closely associated with the American mastodon would be arboreal (trees and shrubs, i.e., forested) and the vegetation most closely associated with mammoth species would be non-arboreal (grass- and herb-dominated). Ultimately, this hypothesis was rejected, but I offer here some explanations and note that some aspects of the results should be mentioned.

Like the previous objective, the main errors introduced in my analysis of the modified plant and proboscidean database dealt with location uncertainities, misidentifications of proboscidean remains, and the lack of accurate dates. However, since my work targeting this objective used another compiled database, that of pollen studies, another set of errors were introduced.

Vegetation Rasters

Pollen percentage data were obtained from the National Climatic Data Center (NCDC) Fossil and Surface Pollen database (Grimm et al. (eds.), 2008) and were then averaged and modeled, using Inverse Distance Weighted methods, to create raster files from which the associated vegetation data were derived. This method of gaining vegetation data was used because of the lack of pollen and macrofossil studies associated directly with proboscidean localities (e.g., Dreimanis, 1968). Out of the 708 proboscidean localities in the study area, only 32 sites had some type of associated plant fossil analysis, and many of these paleobotanical studies involved only qualitative descriptions of the plant species identified. In order to perform statistical analyses, quantitative data were needed, and therefore, the NCDC Fossil and Surface Pollen database was used. However, even when using the database, only 60 pollen studies within the southern Great Lakes region met the time requirements (24-11.5 ka). Due to the limited number of pollen studies and their irregular spatial coverage (variable geographic representations), additional errors could have been introduced. A qualitative analysis comparing the modeled rasters and previous vegetation studies was a required task to determine the extent of the introduced error.

Overall, 11 sets of raster files were generated (arboreal species, non-arboreal species, *Artemisia*, *Betula*, Cupressaceae, Cyperaceae, *Picea*, *Pinus*, Poaceae, *Fraxinus*, and *Ostrya*-type), each containing six different time periods (18+ ka, 18-17 ka, 17-15.7 ka, 15.7-13.9 ka, 13.9-12.9 ka, 12.9-11.5 ka). A comparison of my time series, which showed the spread and timing of migration of these taxa and plant groupings (arboreal vs. non-arboreal), imaged in Appendix A (Figures A1-9), to other reconstructions is provided below. These maps of pollen abundance are called isopoll maps, as the boundaries between polygons relate to cut-off percent values of pollen abundance

COHMAP Members' (1988) Isopoll Maps

COHMAP Members (1988) published an image showing changing isopolls of observed spruce (*Picea*) percentages during the late Pleistocene (Figure 5-1). The purpose of the isopolls was to compare observed spruce pollen percentages to the simulated percentages modeled by the Community Climate Model output. According to Figure 5-1, spruce composition shifted northwards as time progressed; however, the quality of the image could be better. This figure only had three different colors/patterns representing the isopolls, pollen percentages (dark striping for >20%, intermediate striping for five to 20%, and light striping for one to five percent) and could have provided finer resolution at other percentage ranges.

Spruce (Observed)

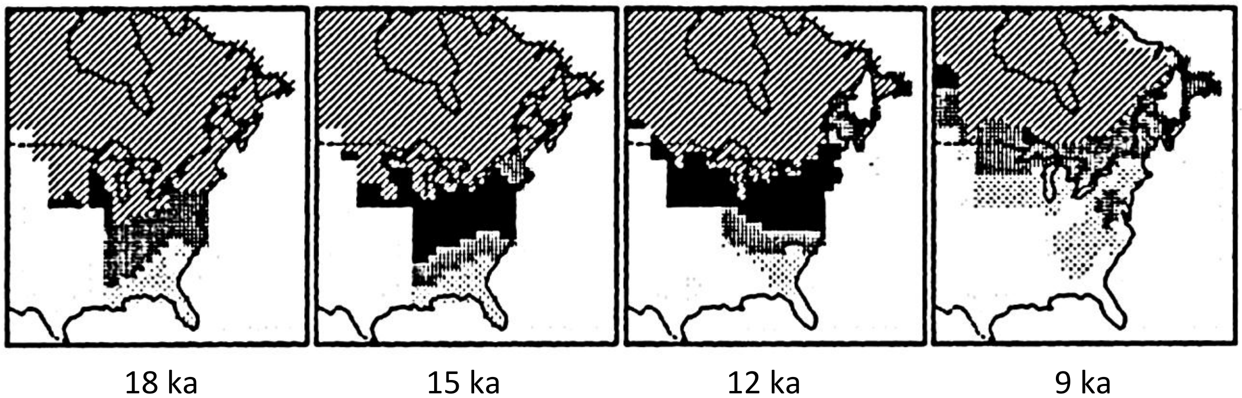

Figure 5-1: Spruce (*Picea*) pollen percentage observations for 3,000-year intervals from 18 ka to 9 ka. Areas of higher spruce percentage (>20%) are shown with dark striping, areas of lower percentages (1-5%) are shown with light striping, and the intermediate striping show areas of 5 to 20%. Image from COHMAP Members (1988).

the southern Great Lakes region was still covered by the Laurentide ice sheet, and what little area remained unglaciated during this time was covered in spruce (Figures A1-9). The raster file showed higher percentages of spruce pollen (40-100%) across the eastern half of the study area (present day Ohio, Indiana, Lower Michigan) (Figures A1-9) than shown in COHMAP Members' (1988) Figure 5-1. At 13,900 cal yr BP, the Laurentide ice sheet had retreated significantly, only remaining in the northern parts of the study area. The COHMAP Figure 5-1 still showed high percentages of spruce pollen throughout the Great Lakes region; however, some southern areas showed lower percentages. Similar results were observed for the created spruce raster time series (Figures A1-9), showing higher percentages (>50%) in the northern half of the study area (present day Minnesota and Wisconsin), while the southern half of the study area (present day Illinois and Indiana) showed lower percentages (<20%).

Webb et al.'s (1993, 1998) Maps

Webb et al. (1993) created a series of "modern" response surfaces for 12 pollen groups (prairie forbs, sedge (Cyperaceae), spruce (*Picea*), birch (*Betula*), alder (*Alnus*), fir (*Abies*), pine (*Pinus*), hemlock (*Tsuga*), beech (*Fagus*), oak (*Quercus*), hickory (*Carya*), and elm (*Ulmus*)) based on 951 surface samples depicted as isopolls. Webb et al. (1998) compared these response surfaces to simulated pollen maps created by using the Community Climate Model, Version 1, and concluded that the observed distributions matched the simulated for all taxa except birch, hemlock, pine, beech, oak, and elm. These inconsistencies are most likely due to an inaccurate climate simulation. Webb et al. (1998) states that the differences between simulated and observed distributions of oak, hickory, and elm were due to simulated temperatures being warmer than actual, and the differences of pine, beech, and hemlock were due to the region being drier than the simulations suggest.

Comparing the observed pollen distributions based on Webb et al. (1993, 1998) to my study, I identified that the important groups identified from pollen are the prairie forbs (Figure 5-2), birch (*Betula*), sedge (Cyperaceae), spruce (*Picea*), and pine (*Pinus*). Webb et al. (1998) reported very low pollen percentages for the prairie forbs (i.e., *Artemisia*), averaging between 5% and 20% for all time periods, with higher percentages appearing northwards as time progressed. For the rasters generated for my research, the study area generally had lower percentages of *Artemisia*, averaging less than 4%, than in Webb et al.'s (1993, 1998) research; however, a northward dispersal was also observed. I found that very little could be deduced due to the limited resolution and relatively stable composition of the vegetation (Figures 5-2; A1-3).

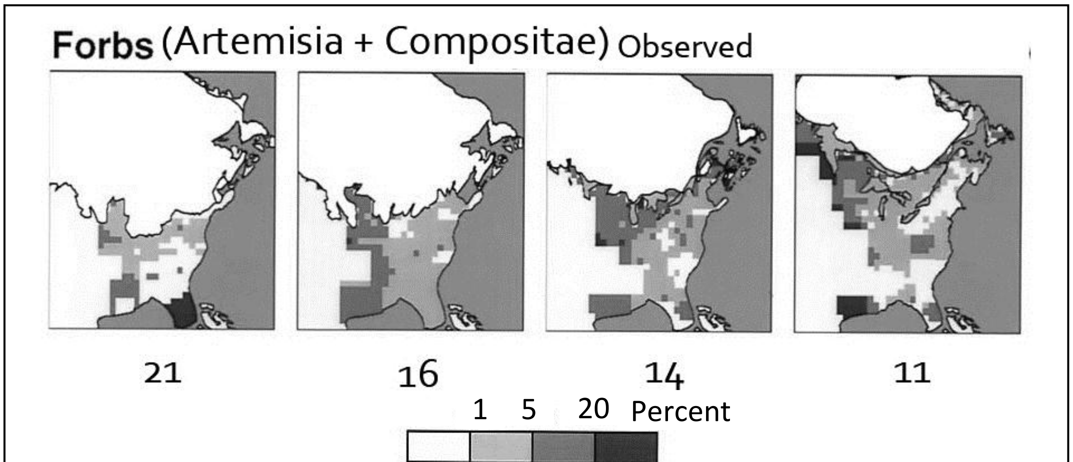

Figure 5-2: Map showing observed pollen percentages for prairie forbs (i.e., *Artemisia;* cal yr BP). Increasing percentages are indicated by darker colors, from white to dark grey. Image originally from Webb et al. (1998).

Very similar patterns are seen between the two series of figures for *Betula* composition. Webb et al. (1998) showed very low percentages of birch pollen at 21 ka and 16 ka that gradually increased through 14 ka and 11 ka. Additionally, the first areas showing increased percentages for were in the northern part of their study area (Figure 5-3). For the rasters generated for this research, similar trends are seen (Figures A1-4). Specifically, prior to 13,000 cal yr BP, the average percentage of birch pollen was less than 2%; however, beginning at 13,000 cal yr BP, the northern part of the southern Great Lakes showed gradually increasing percentages, increasing up to greater than 15% (Figures A1-4).

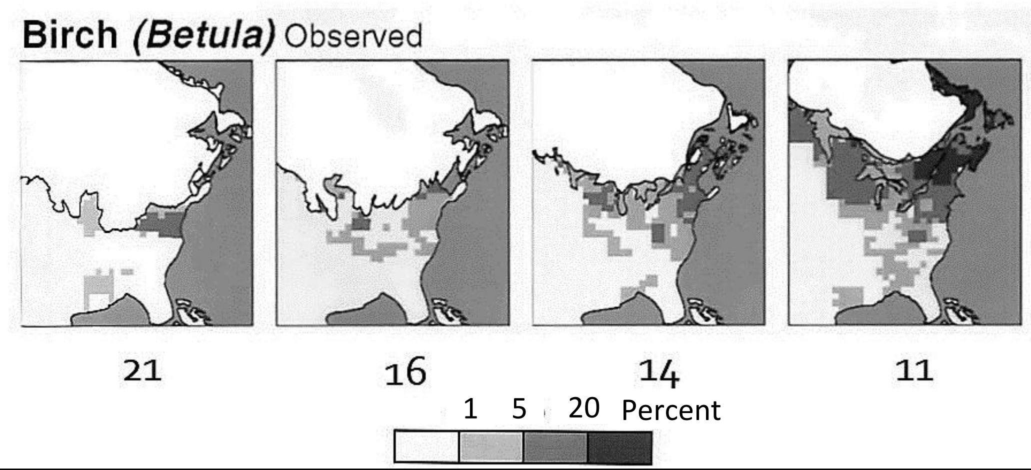

Figure 5-3: Map showing observed pollen percentages for birch (*Betula*; cal yr BP). Increasing percentages are indicated by darker colors, from white to dark grey. Image originally from Webb et al. (1998).

For Cyperaceae (i.e., sedges, bulrushes), Webb et al.'s (1998) isopoll plots also showed similar results when compared to the rasters created for this research. Both figures show a decreasing composition of sedges as time progresses (Figures 5-4, A1-6). For 16,000 cal yr BP, the figures published by Webb et al. (1998) showed a 1-5% sedge composition across the present-day state of Wisconsin and areas of greater than 20% in the southern half of the study area (modern states of Indiana and Illinois). Between 16 ka and 14 ka, the composition increased to 5-20% across eastern North America, with the areas of greater than 20% remaining consistent. By 11,000 cal yr BP, the percent of sedge pollen once again decreased to an average of 1-5% and compositions were no longer greater than 20% in any area (Figure 5-4). The rasters created for this research remained consistently lower than 10% (Figures A1-6). A similarity existed between the rasters and Webb et al.'s (1998) maps at approximately 15,000 cal yr BP, with both datasets showing higher sedge composition in the southern portions of the study area. At 17-15.7 ka, a stable sedge composition existed across the southern Great Lakes region, and by

12.9-11.5 ka, the percentages of sedge pollen decreased to less than 5% (Figures A1-6). An anomaly was present in the northwestern part of the study area (present day Minnesota); this location generally had a higher sedge composition (>15%). This anomaly disappeared around 12,900 cal yr BP (Figures A1-6).

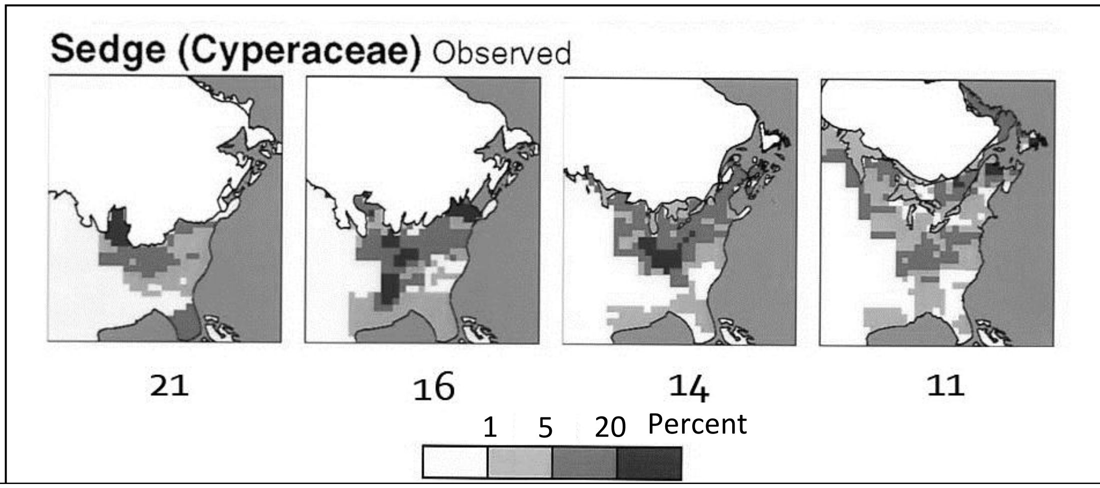

Figure 5-4: Map showing observed pollen percentages for sedge (Cyperaceae; cal yr BP). Increasing percentages are indicated by darker colors, from white to dark grey. Image originally from Webb et al. (1998).

Due to the different scales, it was difficult to compare *Picea* (spruce) composition between the two datasets. For Webb et al. (1998), the spruce composition was generally over 20%. They report that spruce in the entire Great Lakes region was greater than 20% at 16,000 cal yr BP, and by 14,000 cal yr BP, much of the region was still over 20%, with only southern portions (modern Indiana and Illinois) having compositions between 5% and 20%. At 11,000 cal yr BP, varying spruce percentages were observed throughout the region (Figure 5-5). Generally, the higher percentages were in the northern half of the study area, but the region is mostly fragmented, having a mixture of low and high percentage areas.

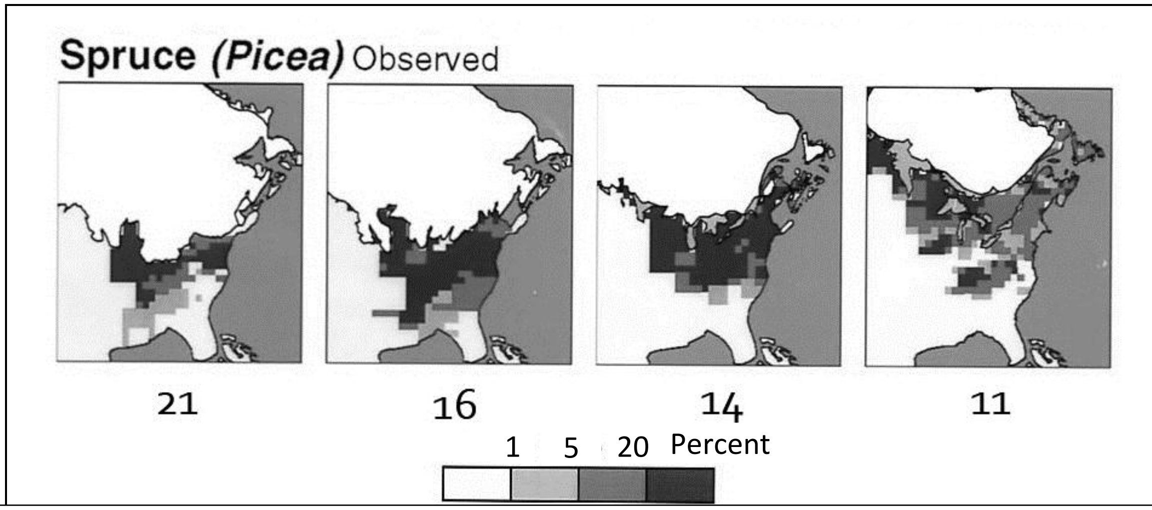

Figure 5-5: Map showing observed pollen percentages for spruce (*Picea*). Increasing percentages are indicated by darker colors, from white to dark grey. Image originally from Webb et al. (1998).

In contrast, the rasters created for this research showed similar patterns for *Picea* (spruce) (Figures A1-9). Generally, the spruce composition was greater than 30% for all time periods. At 18,000 cal yr BP, the southern half of the study area had spruce compositions greater than 50%. By 15,700 cal yr BP, almost all of the study area consisted of at least 50% spruce, with the southern half having a composition of greater than 60%. However, starting at 15.7-13.9 ka, a fragmented spruce composition appears. The northern half of the study area still contains greater than 40% spruce, but the lower half has patches of variable spruce composition. By 12,900 cal yr BP, the southern half of the study area has a composition of less than 20% spruce and the fragmentation has moved northward (Figures A1-9).

Webb et al. (1998)'s plots (Figure 5-6) and the rasters created for this research (Figures A1-10) were once again similar for another important tree species, *Pinus* (pine). At 16,000 cal yr BP, low percentages (0-5%) of pine pollen were observed for both sets of images. At 14,000 cal yr

BP, low percentages were still observed throughout the region, but areas of higher percent were located in the south (modern day Michigan, Indiana, Illinois). The plots of pine abundance over time produced for this masters research (Figures A1-10) showed uniform percentages across the region except for small areas of slightly higher pine composition in modern day Indiana, Illinois, and Michigan. At 11,000 cal yr BP, the figures published by Webb et al. (1998) showed increased pine composition in the northern half of the study area. The same pattern was observed by the raster images produced for this thesis research; however, fragmentation was also observed at 12.9-11.5 ka (Figures A1-10).

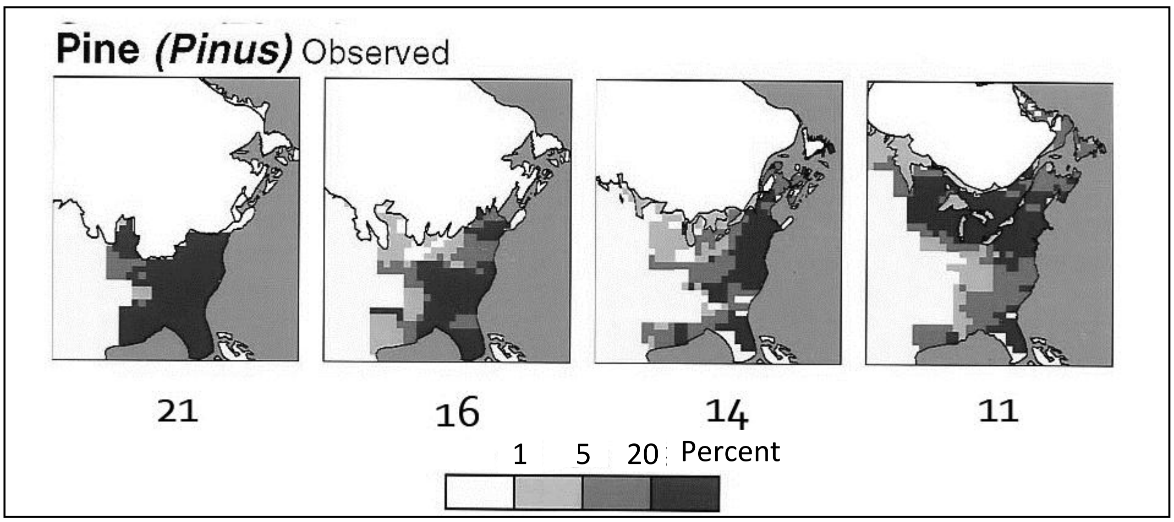

Figure 5-6: Map showing observed pollen percentages for pine (*Pinus*; cal yr BP). Increasing percentages are indicated by darker colors, from white to dark grey. Image originally from Webb et al. (1998).

Jackson et al. ‘s (2000) Isopoll Maps

Jackson et al. (2000) published a series of isopoll maps created by calculating the pollen percentages at the Last Glacial Maximum (LGM) and interpolating them across 100 km by 100 km grid. The purpose of the research was to determine the paleoecology of Eastern North America at the LGM, including vegetation composition, biomes, and inferred temperatures. Additionally, pollen groups were also compared to modern pollen assemblages to determine whether pollen-analogs could be detected. While Jackson et al. (2000) originally used 21 arboreal taxa and 8 non-arboreal taxa in their study, the only taxa important to this thesis research were *Artemisia*, *Betula*, Cupressaceae, Cyperaceae, *Picea*, *Pinus*, Poaceae, *Fraxinus*, and *Ostrya*-type.

At the LGM, the isopoll maps published by Jackson et al. (2000) showed low percentages (0-2%) of *Artemisia* (wormwood, sage) throughout the region. The figures produced for this M.S. research showed a similar, yet slightly higher (2-4%) pattern (Figures 5-7, A1-3). An anomaly, however, existed in the northwest portion of the study area (present day Minnesota), where much higher pollen percentages (>10%) for this taxon were observed. Both Jackson et al.’s (2000) maps and the rasters produced here showed similar trends for *Betula* (birch), with low percentages (0-2%) throughout the region (Figures 5-7, A1-4).

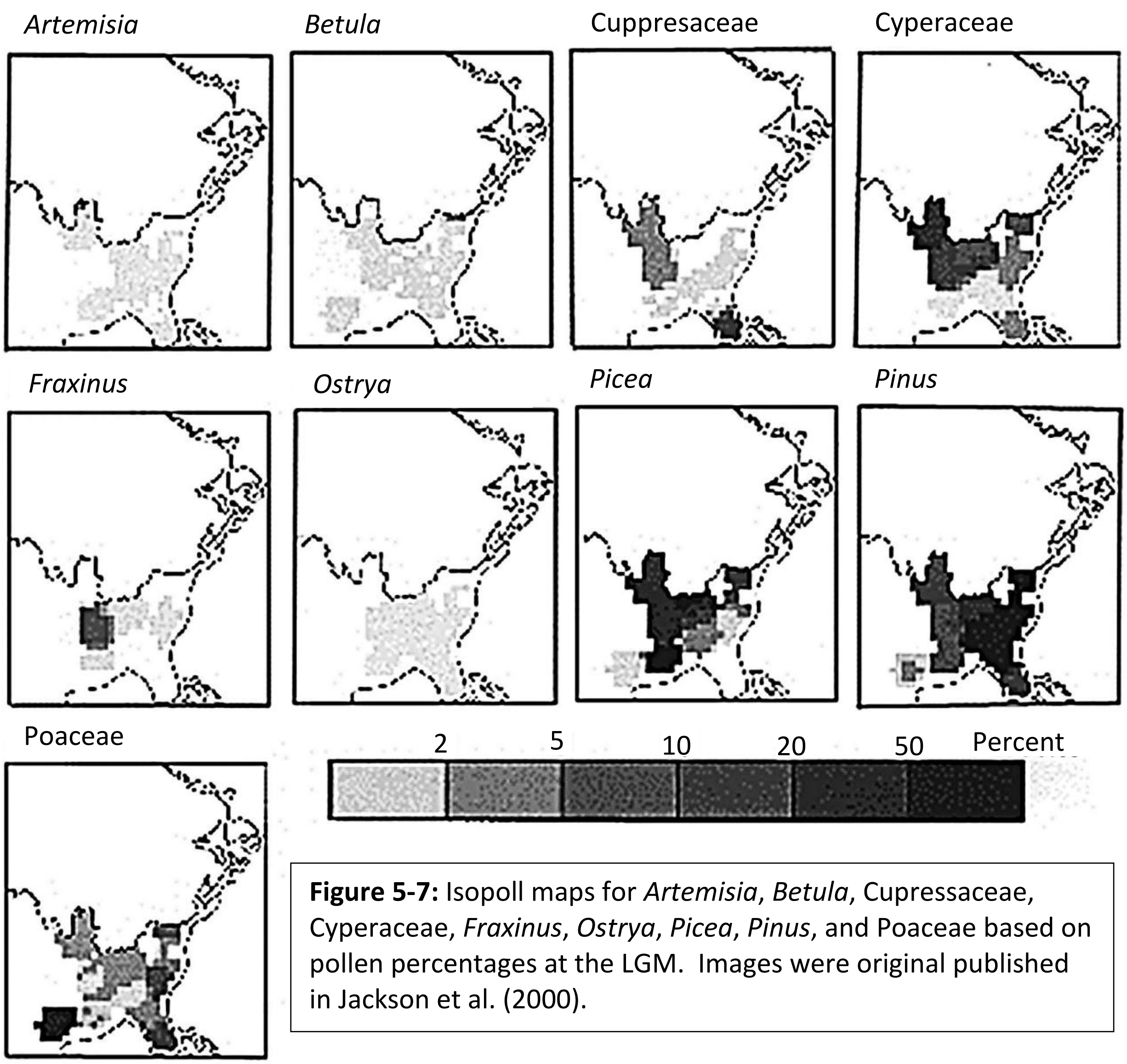

Figure 5-7: Isopoll maps for *Artemisia*, *Betula*, Cupressaceae, Cyperaceae, *Fraxinus*, *Ostrya*, *Picea*, *Pinus*, and Poaceae based on pollen percentages at the LGM. Images were original published in Jackson et al. (2000).

At the LGM, the composition of Cupressaceae (juniper and/or cedar) is observed to be around 5% for both sets of figures (Figures 5-7, A1-5). The only unglaciated areas at this time are in the western portions of present-day Wisconsin and Minnesota, and the rasters produced for this thesis research show percentages of 3-5% for Cupressaceae.

In contrast, differences between the two sets of figures are observed for Cyperaceae (sedge family) for the LGM. Jackson et al.'s (2000) maps, shown in Figure 5-7, indicate a Cyperaceae composition of about 20% (difficult to correctly assess to due to the color scheme of the scale) while the rasters produced for this thesis research (Figures A1-6) show much lower percentages of Cyperaceae, predominately less than 10%, during the height of the last glaciation. The differing scales of resolution, with my study having more percent classes, can explain the differing plots of Cyperaceae abundance between Jackson et al.'s (2000) study and mine. However, an area of higher Cyperaceae composition was located in modern day Minnesota, showing percentages up to 60%, in both Jackson et al.'s (2000) and my maps (Figures 5-7, A1-6).

Similar differences were observed for *Fraxinus* (ash, presumably *F. nigra*, black ash). In my research, a *Fraxinus* composition of around 15% was observed for the northern, unglaciated areas and much lower percentages of the sourthern portions of the study area during the LGM (Figures A1-7). In Jackson et al.'s (2000) analysis (Figure 5-7), the northern, unglaciated portion of the study area was devoid of *Fraxinus*, with only the southern portion (modern day Indiana and Illinois) showing the presence of *Fraxinus* (5-10%).

According to Jackson et al. (2000), *Ostrya*-type (pollen either of *Ostrya virginiana* (American hop hornbeam) or *Carpinus caroliniana* (American hornbeam or ironwood) was almost nonexistent in the study area, with low percentages only being observed in the southern half of the study area during the LGM (Figure 5-7). Similar results were observed for the rasters created for this thesis research (Figures A1-9).

Similar *Picea* (spruce) compositions were observed for both sets of isopoll maps (Figures 5-7, A1-9). Jackson et al.'s (2000) map showed uniform composition greater than 50% for spruce and the rasters produced for this masters research showed variable compositions greater than

40% for this taxon. The differences between the two figures could be due to the differences in scale.

For *Pinus* (pine), the different composition patterns were observed between the two figures. Jackson et al. (2000) showed a uniform composition of approximately 20-50% for this taxon (Figure 5-7), and the rasters produces for this thesis research showed a much lower amount of pine (0-5%) in the vegetation (Figures A1-10). However, similar trends are observed between the two figures for Poaceae composition, both showing low amounts (2-4%) of grasses. The only difference is that the composition of Poaceae in Jackson et al.'s (2000) plot (Figure 5-7) was uniform and my raster for this taxon during the LGM (Figures A1-11) was variable, probably again be due to the different resolutions of the plotted data.

Summary of Comparisons with Previous Pollen Studies

Overall, very few differences were observed between the isopoll figures published in previous studies (COHMAP Members, 1988; Webb et al., 1998; Jackson et al., 2000) and the rasters interpolated from the 82 pollen site data derived from the National Climatic Data Center (NCDC) Fossil and Surface Pollen database (Grimm et al. (eds.), 2008). Despite differences in the scales (breakdown of isopoll percentages), time periods and boundaries of study areas used, it was concluded that the rasters created for this thesis research were similar enough to previous studies that little additional error would be introduced. However, some studies did show differences that need to be mentioned. Webb et al.'s (1998) isopoll maps had consistently lower *Artemisia* percentages than the rasters produced for this thesis research. The figures produced by Jackson et al. (2000) also showed differences in vegetation abundance for Cyperaceae, *Fraxinus*, and *Pinus* compared to the rasters created for this study. These differences are most likely due to the methods of creating the vegetation maps. Webb et al. (1998) created isopolls dependent on their climate model output; therefore, the differences in *Artemisia* distribution and percentages are due to inaccurate climate simulations. Jackson et al. (2000) used plant macrofossil data to create their figures while this investigation used pollen data. Pollen data often introduces error due to the different quantities of pollen released as well as the method of dispersion.

Statistical studies must be very careful undertaken when such differences are discovered, because these various datasets could produce different results that may, or may not, affect the acceptation or rejection of a hypothesis.

Inconclusive Results for Proboscidean Habitat Preferences

The first set of methods dealt with descriptive statistics, primarily the median pollen percentages for each taxon. When looking at all the site localities and at five thousand year averages of pollen percentages, as a proxy for vegetation, mastodons appeared to be closely related to arboreal vegetation (Figure 4-12), but mammoths did not show a clear preference between arboreal and non-arboreal habitats (Figure 4-14). Statistics calculated from thousand year averaged vegetation associated with dated site localities showed very little difference between mammoth and mastodons for any vegetation type (Tables 4-9 and 4-11).

The second set of methods involved regression models. Zero-inflated binomial regression models were performed on random points containing data about the species kernel density estimation and the five thousand year averages of arboreal and non-arboreal vegetation groups. Mastodons showed a positive relationship to arboreal vegetation. However, the only other significant results were the contradictory zero-components, which indicated that the higher the arboreal or non-arboreal vegetation, the more likely the site contained neither proboscidean genera. Linear regression models were performed on the same dataset, except for the elimination of points associated with zeroes. The only significant result from these analyses was the positive relationship between mastodons and arboreal vegetation and the likelihood this relationship is not due to chance.

Explanation

Due to the inconsistencies, the null hypothesis for this objective was rejected; however, this does not mean that hypothesized vegetation relationships to mastodons and mammoths are invalidated. The only highly significant results do support the hypothesis, stating that American mastodons do have a positive relationship with arboreal vegetation. Previous studies concerning mastodon habitats show their preference for boreal forests (Osborn, 1942; Skeels, 1962; Drumm, 1963; Russell, 1965; Wittry, 1965, Dreimanis, 1967, 1968, Holman, 1995). Stomach content studies also agree with these results. Stomach contents of the Warren Mastodon of Orange County, New York, consisted of coniferous (hemlock) tree branches and needles (Drumm, 1963; Dreimanis, 1968). Pollen recovered from the mandible (mouth) of the Cole Mastodon of New Chambersburg, Ohio, assuming to be food, consisted of high percentages of spruce and pine, with some grass and composite (Ogden and Hay, 1957; Dreimanis, 1968). Plant remains associated with mastodon remains are consistently woody (Hay, 1923; Hatt, 1963; Oltaz and Kapp, 1963; Wittry, 1965; Ogden and Hay, 1967; Dreimanis, 1968; Holman et al., 1986; Woodman and Branstrator, 2008; Woodman and Athfield, 2009, Saunders et al., 2010). While there was not a clear relationship with *Picea* composition, despite popular assumption, it is clear that mastodons preferred arboreal habitats.

The results being "not significant" concerning mastodons' preference of *Picea* over other trees could be due to the methods of interpolating the pollen data. The time period of focus was 18,000-11,500 cal yr BP; a time of extreme environmental fluctuation with rapid recession and re-advance of the Laurentide Ice Sheet and attenuated climate changes. Averaging the pollen percentages for this five thousand year interval could have produced substantial error. As the Laurentide Ice Sheet retreated, spruce composition became more fragmented (Figures A1-9). By averaging the pollen percentages, these "refugiums" would have disappeared, showing an inaccurate, more uniform spruce composition on the maps produced. Since the majority of the mastodon localities found in the southern Great Lakes are attributed to this time of environmental fluctuation (Dreimanis, 1968), the results may indicate a shift away from spruce, resulting in an adaptation to new, possibly unsuitable, vegetation. A study by Lepper et al. (1991) supports this conclusion in that the stomach contents of a mastodon, inferred from pollen and plant macrofossils found between its ribs, consisted of sedges, grasses, weeds, mosses, aquatic plants, and a few leaves of deciduous trees that dated to 13,520 cal yr BP.

Mammoths had no highly significant association with vegetation, based on the results from both regression models. This is most likely due to the grouping of all mammoth species into one category. Studies have shown that woolly and Jefferson mammoths may have occupied different niches, with woolly mammoths occupying tundra biomes (Harington and Ashworth, 1986; Vereshchagin, 1995; Lister and Bahn, 2007) and Jefferson mammoths occupying parklands (Oltz and Kapp, 1963; Pasenko and Schubert, 2004; Saunders et al. 2010). According to preserved, intact woolly mammoths and dung from Siberia, 90% of their diets consisted of grasses and grass-like sedges (e.g., Vereshchagin, 1995; Lister and Bahn, 2007). While no preserved dung or intestinal contents of Jefferson mammoths has been found, plant macrofossil and pollen analyses at localities where they have been recovered may indicate some arboreal browsing by this species of mammoth (Oltz and Kapp, 1963; Pasenko and Schubert, 2004; Saunders et al. 2010; Yansa and Adams, 2012). Yansa and Adams (2012) proposed that the diet of the Jefferson mammoths consisted of sedges and other herbaceous plants around aquatic shorelines in the spruce-parkland biomes, and that they were also able to supplement their diet with the leaves of shrubs and trees. With the assumption that woolly and Jefferson mammoths occupy completely different niches, the non-significant results make sense.

The results for the vegetation associated with Great Lakes proboscideans, especially for the mammoths, were not significant, and may have been due to the environmental fluctuations, and fragmentation, that occurred during the time period of focus. Mammoths during this time period frequently showed signs of stress (i.e., increased enamel erosion, decreased age of sexual maturation) in their tusks and bones, which could have been the result of improper, or unaccustomed diet (Fisher, 1987; 2009; Saunders et al., 2010; Yansa and Adams, 2012). Pollen data for the Lincoln College woolly mammoth in Illinois, the youngest accurately dated mammoth for the Great Lakes region (13,500 cal yr BP), suggests it existed in a closed-canopy ash-spruce (*Fraxinus-Picea*) forest, and studies of its enamel show extensive wear, indicating a diet for which it was not adapted (Saunders et al., 2010). Harington and Ashworth (1986) also observed inconsistencies with the woolly mammoth skeletal remains, stating that the Emden mammoth of North Dakota was found in an area known for spruce forests at this time. The Schaefer mammoth of Kenosha County, Wisconsin, is also associated with a spruce-forest or spruce parkland environment (Joyce, 2006; Saunders et al., 2010). Yansa and Adams (2012) proposed that all proboscideans may have shifted their diets in an attempt to adapt to the fluctuating environments after about 13,500 cal yr BP, centuries before their extinction. The changing of diets may have, therefore, resulted in non-significant results.

The relationship between mammoths and Cyperaceae (sedge, bulrush and other members of this emergent plant family) was also inconclusive. This may have been due to the shifting diets, but it also may have occurred due to how the pollen percentages were interpolated. As mentioned before, there was a significant, qualitative difference between the Cyperaceae distribution as exhibited by Jackson et al. (2000) and the rasters produced for this thesis research. However, the distribution maps produced by Jackson et al. (2000) were only for the LGM, whereas my study created maps for the LGM and for the terminal Pleistocene (18,000-11,500 cal yr BP). No difference was observed for the isopoll maps of Cyperaceae produced by Webb et al. (1998) and those of this thesis.

Another reason for this lack of significance between proboscidean taxa and their respective vegetation could be that mammoths and mastodons did not partition their habitats as expected. Stable carbon isotope analyses of the dated proboscidean specimens from Illinois show no difference in $\delta^{13}C$ values (from bone collagen) between the three different taxa

(Saunders et al., 2010). Since $\delta^{13}C$ (collagen) values are commonly used to determine diet and are derived from the types of vegetation in their diet (Tieszen et al., 1983), similar $\delta^{13}C$ values would mean there was no different in the diets of proboscideans in Illinois (Saunders et al., 2010), or at least for the youngest ones, as they neared extinction.

However, Gill et al. (2009) stated that as the climate and vegetation changed near the end of the Pleistocene, the diets of megafauna had to adapt with these changes, possibly eliminating the habitat partitioning previously present between mammoths and mastodons. Using *Sporormiella*, a dung fungus common in the mammoth gut contents and coprolites, they attempted to track the decline of megafauna populations. *Sporormiella* was abundant until approximately 14,800 cal yr BP, when it began to decline, almost disappearing after 13,700 cal yr BP. Gill et al. (2009) attribute this decline to the population collapse and functional, not final, extinction of the species. During this time, there was an increase in hardwood taxa (*Fraxinus*, *Ostrya*), which may have decreased herbivory pressures because of the higher nutrient and water content of the newly available broadleaf vegetation. With the introduction of better nutrients, mammoths may have included the new vegetation into their diets, and therefore, brought them closer to mastodon habitats.

Mammoths and mastodons became functionally extinction in the Great Lakes region at about 13,000 cal yr BP, at the time when most American megafauna went extinct. However, proboscideans survived a bit longer in other regions. Agenbroad et al. (2002) have dated pygmy mammoth (*Mammuthus exilis*) remains from Santa Rosa Island, California, to 10,010±70 ^{14}C, or ~11,000 cal yr BP. Pygmy mammoths from the Channel Islands may have survived into the early Holocene, only becoming extinct 11,300-10,800 cal yr BP (Agenbroad, 2001). Additionally, mammoths persisted in Siberia even after they went extinct in North America. Many radiocarbon dates show the Siberian extinction of the woolly mammoth did not occur until approximately 9,500 cal yr BP (e.g., Lavrov and Sulerzhytsky, 1992; Vartanyan et al., 1995). However, radiocarbon dates from mammoth remains found on Wrangel Island, northeast of Russia, reveal another mammoth refugium that may have lasted until 3,000 cal yr BP (Vartanyan et al., 1995). While even the researchers question the validity of these dates, they could find no error. Even though mammoths and mastodons may have disappeared from the Great Lakes region by the end of the Pleistocene, their presence well into the Holocene shows how important it is to understand their biological and behavioral characteristics.

Possible Future Research

Many errors were introduced throughout this research: inaccurate locations of proboscidean sites, misidentification of mammoth and mastodon species, lack of all-encompassing FAUNMAP database, lack of radiocarbon dating of proboscideans (in most cases), and the paucity of plant fossil studies directly associated with proboscidean localities. While inaccurate locations cannot be fixed, the other three errors could be significantly reduced by future research endeavors.

First, an accepted reclassification of North American proboscideans must occur. Currently, very few mammoth specimens are identified at the species level, and the reason behind this is the controversy surrounding the validity of the Jefferson mammoth (Osborn, 1922, 1942; Skeels, 1962; Kurten and Anderson, 1980; Madden, 1981a; Holman, 1995b, 2001; Pasenko and Schubert, 2004; Saunders et al., 2010). In order to accurately deduce geographic ranges and associated habitats, as many mammoth skeletons as possible must be re-examined and their identifications confirmed or revised. According to Table 4-1, there are currently 117 unidentified mammoth and proboscidean specimens in the southern Great Lakes region. Of all mammoth sites in the modified database, ~28% of them are not identified to species, which comprises almost 9.5% of the total number of proboscidean localities.

Secondly, it has been established with this thesis research that the more fossil localities used in biogeography studies that reconstruct geographic ranges and habitats, the better. Over 500 site localities were added to the FAUNMAP database by my research, totaling 708 proboscidean records for the southern Great Lakes region. However, there are many more publications concerning proboscideans in this region that were not located (e.g., Baker, 1920; Hay, 1924; Forsyth, 1963) and would require an even more exhaustive gray-literature research. In order to accurately assess the geographic ranges of proboscideans in the southern Great Lakes region, as many of these sites must be known as possible; and therefore, a database must be established with the goal of accumulating all proboscidean site localities in the region. The database must also have the objective of establishing which of the documented site localities are duplicate records of the same fossil find.

Thirdly, an extensive undertaking must occur with the focus of obtaining radiocarbon (^{14}C) dates on proboscidean teeth or bone collagen, involving a substantial outlay of funds for such a task (at $600-1200 per ^{14}C date). Preferably tooth dentine and/or purified bone collagen would be selected for submission to ^{14}C-dating laboratories as these materials provide the most accurate radiocarbon dates for these materials (Saunders et al., 2010). For this thesis research, only 60 site localities, 8% of the total, had associated ^{14}C dates. Without accurate ^{14}C dates of proboscidean fossils, associated studies of range shifts of these extinct animals and reconstructions of their habitats, by comparison to local pollen records, will always be based on assumption and will therefore contain much error.

Lastly, a similar mission must take place regarding plant macrofossil and pollen analyses directly associated with proboscidean remains, to accurate assess their habitats and diets, instead of correlating separate pollen studies to mammoth and mastodon finds. While studies such as this thesis research can propose what habitats, or niches, proboscideans may have occupied, this proposal is based on interpolated pollen data from sites different, though somewhat close to, proboscidean localities, and is therefore not site specific.

The ultimate goal for my M.S. thesis research was to serve as a preliminary step towards contributing data useful for forecasting future biotic changes in response to climate change. I was able to assess mastodon and mammoth geographic ranges, range shifts, and habitat partitioning to some extent, limited by the errors inherent to the proboscidean and pollen datasets. My research highlighted how important it is to have datasets that minimize errors and have good temporal and spatial coverage in order to test biogeographic questions relevant to discussions about current and future animal responses to climate change. However, despite this realization, the dataset created for this research is still the most complete regarding mammoth and mastodon sites in the southern Great Lakes region.

CHAPTER SIX: CONCLUSIONS

Mammoths and mastodons are considered to be two of the "charismatic megafauna," that lived during the climate fluctuations of the Quaternary Period and became extinct shortly before the end of the Pleistocene (e.g., Kurten and Anderson, 1980; Holman 1995b). Many facts are known about these two genera, such as their evolutionary lineage (e.g., Shoshani et al., 1985, Lowenstein and Shoshani, 1996; Shoshani, 1998) and appearance (e.g., Osborn 1936, 1942; Skeels, 1962; Kurten and Anderson, 1980; Madden, 1981a; Holman, 1995b). However, there are also many debates concerning them, such as the reason(s) for their extinction (e.g., Marshall, 1984; Graham, 1990; Guthrie, 1990; Haynes, 2002; Firestone et al., 2007; Gill et al., 2009), and how they partitioned their habitats (e.g., Kapp, 1986, 1999; McAndrews and Jackson, 1988; McAndrews, 2003; Saunders et al., 2010; Yansa and Adams, 2012).

The ultimate goal of my thesis research was to contribute preliminary data from fossil sources useful for forecasting future biotic changes in response to climate change. My research involved compiling the most comprehensive database on mammoth and mastodon localities possible, by adding to the original FAUNMAP database an additional 528 records taken from museum and government reports and other gray literature sources. Performing statistical analysis of this modified database I tested the following research objections: 1) compare the FAUNMAP database, with no additions or modifications, to a modified database containing additional site localities; 2) To ascertain the general range areas of the different proboscideans in the southern Great Lakes and identify if range overlap existed; 3) To determine whether geographic range shifts occurred between 24-18 ka (the last glacial maximum, LGM) and 18-11.5 ka (the terminal

Pleistocene) in response to ice sheet recession and climate change; and 4) to identify whether, if possible, differences existed between mammoth and mastodon vegetation preference by comparison of mastodon sites and mastodon sites vis-à-vis plant communities, as reconstructed from independent pollen studies (from a fossil pollen database).

The reasoning behind the first objective was based on previous studies (Riddle, 1996; Walker, 2000) stating that FAUNMAP may not be effective for biogeography studies focused on individual species. The FAUNMAP database was originally created in 1994 with the goal of analyzing the evolution of mammal communities in the United States throughout the Pleistocene Epoch (FAUNMAP Working Group, 1994). Many studies have utilized the database in their studies (e.g., FAUNMAP Working Group, 1996b; Riddle, 1996; Burns et al., 2003; Lyons, 2003, 2005). However, Walker (2000) discovered the database lacked significant numbers of published sites, and therefore, could affect the results of biogeography studies. With the addition of over 500 sites, it was determined that the FAUNMAP database did, indeed, lack such data.

Objectives two, three, and four dealt with the geographic ranges and characteristics of proboscideans in the southern Great Lakes region. Objective two's hypothesis, which stated there would be no overlap between taxa, was rejected due to the presence of extensive overlap in mammoth and mastodon fossil localities. This result supports Yansa and Adam's (2012) earlier hypothesis that mammoths and mastodons were portioning habitats within the same (southern Great Lakes) region. The hypothesis for objective three, which declared that geographic range shifts could be detected between the two time periods, the LGM (24-18 ka) compared to the terminal Pleistocene (18-11.5 ka) was accepted. Finally, the fourth objective's hypothesis, which stated that mammoths would more closely related to non-arboreal (grass and herb) vegetation and mastodons would be more closely related to arboreal (tree and shrub) vegetation, was rejected.

While many of these hypotheses were rejected, it does not invalidate this thesis research. Prior to this M.S. research, an extensive analysis of the FAUNMAP database had not occurred. I compile in a comprehensive format the most complete database of proboscidean sites in the Great Lakes region, a database of significant value to future research endeavors. This is also the first study that tried to establish geographic ranges for proboscideans in the southern Great Lakes region, as well as the first attempt to quantitatively compare the habitat preferences of mammoth and mastodon populations rather than infer individual proboscidean habitats from single site investigations.

Throughout this thesis research, many errors were introduced, such as incomplete knowledge of proboscidean site locations, lack of radiocarbon dating of most sites, possibility of postmortem transportation, lack of vegetation studies directly associated the proboscidean sites, and errors inherent in the respective methods employed in analyzing fossil datasets. My research pushed the outer limits of these errors, and many of these errors must be addressed before future research with similar biogeographic goals can take place. Recommended future research includes compiling an extensive database containing all known proboscidean site localities, involving more gray literature research and in-depth scrutiny with a focus on detecting duplicate data and more accurately determining locations, obtaining radiocarbon dates for all possible proboscidean sites (an expensive undertaking), and conducting plant macrofossil and pollen analyses, when possible, for each proboscidean site. Until these corrections are made, accurate assessments of proboscidean response to climate change can never be reconstructed, and therefore, a valuable step to understanding how biotic changes respond to climate change will be missing. However, my compilation of data that now documents over 700 proboscidean sites in the southern Great Lakes is an important beginning of such research. Despite the errors in my dataset and that the results of my investigation were mainly inconclusive, there were several benefits of completing this thesis research, such as the (1) introduction of GIS modeling to determine geographic ranges and range shifts for extinct species, (2) comparing mammoth and mastodon ranges with the vegetation characteristics of their habitats, and (3) especially, compilation of the largest and most detailed database of mammoth and mastodon localities for any region of the world, in this case, of the southern Great Lakes region.

APPENDICES

APPENDIX A

Vegetation Reconstructions

The data used for vegetation reconstructions for the southern Great Lakes region for various time intervals are derived from pollen percentage data for 82 sites published in the NCDC Fossil and Surface Pollen database (Grimm et al. (eds.), 2008).

The pollen study sites used for this thesis research are shown below, with information on what millenniums each site could be used for and source information.

Table A1: Pollen sites derived from the NCDC Fossil and Surface Pollen database. In total, there were 82 sites for the southern Great Lakes region that fell within the desired time period (18-11.5 ka). Thousand year (radiocarbon) averages were calculated for the pollen percentages. There were 13 pollen sites averaged for 18+ ka, 18-17 ka, 17-15.7 ka, 15.7-13.9 ka, 13.9-12.9 ka, and 12.9-11.5 ka.

TABLE A1								
SITE NAME	ST	AUTHOR	18+	18-17	17-15.7	15.7-13.9	13.9-12.9	12.9-11.5
Almors Lake	MN	S Bjorck	-	-	-	-	X	X
Anderson Lake	MN	HE Wright, Jr	-	-	-	-	-	X
Andree Bog	MN	EG Cushing	-	-	-	-	X	X
Battaglia Bog	OH	LCK Shane	X	X	X	X	X	X
Beckman Lake	MN	PC Swain	-	-	-	-	-	X
Billy's Lake	MN	GL Jacobson, Jr	-	-	-	-	-	X
Blackhoof Site	MN	HE Wright Jr	-	-	-	-	-	X
Bluemounds Creek	WI	AM Davis	-	-	-	-	-	X
Bog D	MN	JH McAndrews	-	-	-	-	-	X
Brown Lake	OH	LCK Shane	X	-	-	-	X	X
Bucyrus Bog	OH	LCK Shane	-	X	X	X	X	X
Camp 11 Lake	MI	LB Brubaker	-	-	-	-	-	X
Canyon Lake	MI	MB Davis	-	-	-	-	-	X
Carter Site	OH	LCK Shane	X	X	X	X	X	-
Cedar Bog Lake	MN	EG Cushing	-	-	-	-	X	X

TABLE A1 (cont'd)								
SITE NAME	ST	AUTHOR	18+	18-17	17-15.7	15.7-13.9	13.9-12.9	12.9-11.5
Chatsworth Bog	IL	JE King	-	-	X	X	X	X
Clear Lake	IN	RE Bailey	X	X	X	X	X	X
Demont Lake	MI	RO Kapp	-	-	-	-	X	X
Devils Lake	WI	LJ Maher Jr	-	-	X	X	X	X
Disterhaft Farm Bog	WI	LJ Maher Jr	-	-	X	X	X	X
Disterhaft Farm Bog	WI	RG Baker	-	-	X	X	X	X
East Twin Lake	OH	LCK Shane	-	-	-	-	X	X
Ernst Brother's Pit	WI	LJ Maher Jr	-	-	X	X	X	X
Frains Lake	MI	WC Kerfoot	X	X	X	X	X	X
Fudger Lake	OH	LCK Shane	-	X	X	X	X	X
Gass Lake	WI	SL Webb	X	X	X	X	X	X
Green Lake	MI	RW Lawrenz	-	-	-	X	X	X
Hanson Marsh	WI	LJ Maher Jr	-	X	X	X	X	X
Horseshoe Lake	MN	EG Cushing	-	-	X	X	X	X
Hudson Lake	IN	RE Bailey	-	X	X	X	X	X
Irvin Lake	MN	EG Cushing	-	-	-	X	X	X
Jacobson Lake	MN	WA Watts	-	-	-	-	-	X
Kellners Lake	WI	LJ Maher Jr	-	X	X	X	X	X
Kellys Hollow	WI	KM Heide	-	-	-	-	-	X
Kellys Hollow	WI	KM Heide	-	-	-	-	-	X
Kirchner Marsh	MN	HE Wright Jr	-	-	-	X	X	X
Kirchner Marsh	MN	HE Wright Jr	-	-	-	-	X	X
Kotiranta Lake	MN	HE Wright Jr	-	X	X	X	X	X
Kylen Lake	MN	HJB Birks	X	X	X	X	X	X
Ladd Lake	OH	LCK Shane	-	-	X	X	X	X
Lake Ann	MN	LCK Shane	-	-	-	-	-	X
Lake Carlson	MN	HE Wright Jr	-	-	-	X	X	X
Lake Mary	WI	T Webb III	-	-	-	-	-	X
Lake Mendota	WI	MG Winkler	-	-	X	X	X	X
Lake Minnie	MN	JH McAndrews	-	-	-	-	X	X
Lake Sixteen	MI	RP Futyma	-	-	-	-	X	X

TABLE A1 (cont'd)								
SITE NAME	ST	AUTHOR	18+	18-17	17-15.7	15.7-13.9	13.9-12.9	12.9-11.5
Lily Lake	MN	NM Eyster-Smith	-	-	X	X	X	X
Little Bass Lake	MN	PC Swain	-	-	-	-	-	X
Martin Bog	MN	JH McAndrews	-	-	-	-	-	X
Myrtle Lake	MN	CR Janssen	-	-	-	-	-	X
Neville Marsh	OH	LCK Shane	X	X	X	X	X	X
Pogonia Bog Pond	MN	EG Cushing	-	-	-	-	X	X
Portage Lake	MN	JH McAndrews	-	-	-	-	X	X
Portage Marsh	IN	ST Jackson	-	-	X	X	X	X
Pretty Lake	IN	AS Jones	-	-	X	X	X	X
Quillin Site	OH	LCK Shane	-	-	X	X	X	X
Radtke Lake	WI	SL Webb	-	-	-	-	X	X
Reidel Lake	MN	H Almquist-Jacobson	-	-	-	-	X	X
Rhule Farm	IN	LCK Shane	-	-	X	X	X	X
Rossburg Bog	MN	HE Wright Jr	-	-	-	X	X	X
Rutz Lake	MN	JCB Waddington	-	-	-	-	X	-
Seidel	WI	JCB Waddington	-	-	-	X	X	X
Seidel	WI	LJ Maher Jr	-	-	-	-	X	X
Silver Lake	OH	JG Ogden III	X	X	X	X	X	X
Smoot Lake Bog	OH	LCK Shane	-	X	X	X	X	X
Spirit Lake	MI	MB Davis	-	-	-	-	X	X
Stewart's Dark Lake	WI	MA Peters	-	-	-	-	-	X
Stone Lake	MN	PC Swain	-	-	-	-	-	X
Stotzel-Leis Site	OH	LCK Shane	X	X	X	X	X	X
Terhell Pond	MN	JH McAndrews	-	-	-	-	-	X
Thompson	MN	JH McAndrews	-	-	-	-	-	X
Torren's Bog	OH	JG Ogden III	-	-	-	X	X	X

TABLE A1 (cont'd)								
SITE NAME	ST	AUTHOR	18+	18-17	17-15.7	15.7-13.9	13.9-12.9	12.9-11.5
Upper Graveen Lake	MN	H Almquist-Jacobson	-	-	-	-	X	X
Vestaburg Bog	MI	JA Gillam	X	X	-	X	X	X
Volo Bog	IL	JE King	-	-	-	-	X	X
Weber Lake	MN	M Fries	-	X	X	X	X	X
White Lily Lake	MN	EG Cushing	X	X	X	X	X	X
Wintergreen Lake	MI	RE Bailey	-	-	-	X	X	X
Wolf Creek	MN	HJB Birks	X	X	X	X	X	X
Wolsfeld Lake	MN	EC Grimm	-	-	-	X	X	X
Wolverine Lake	MI	RP Futyma	-	-	-	-	-	X
Wood Lake	WI	KM Heide	-	-	X	X	X	X
TOTAL (82)	-----	----------------	**13**	**20**	**33**	**43**	**61**	**83**

Interpolated vegetation data

This appendix also consists of a series of images created from pollen percentage data for the 82 sites from the database mentioned above (Grimm et al. (eds.), 2008). Specifically, these images show interpolate pollen percentages across the study area for the nine most significant plant taxa, the herbs *Artemisia* (sage), Cyperaceae (sedge family), Poaceae (grass family), and the trees and shrubs *Betula* (birch), Cupressaceae (cedar or juniper), *Fraxinus* (ash, presumably black ash), *Ostrya*-type (hop hornbeam or hornbeam), *Picea* (spruce), and *Pinus* (pine). Two additional groups were created by the clusterning of taxa, arboreal taxa of trees and shrubs (*Betula,* Cupressaceae, *Fraxinus, Ostrya*-type, *Picea,* and *Pinus*) and non-arboreal taxa, i.e., herbaceous plants (*Artemisia,* Cyperaceae, and Poaceae). The plant taxa and vegetation groups were interpolated across the study area by utilizing the Inverse Distance Weighted method from ArcGIS 10 (ESRI, 2010) with a maximum distance of 200 km on thousand year means for each pollen study site. Four additional images were created using five thousand year averages of the pollen sites (Figures A1 to A15) based on the abundance of arboreal, non-arboreal, Cyperaceae, and *Picea* in the vegetation over time. All 15 images are shown below:

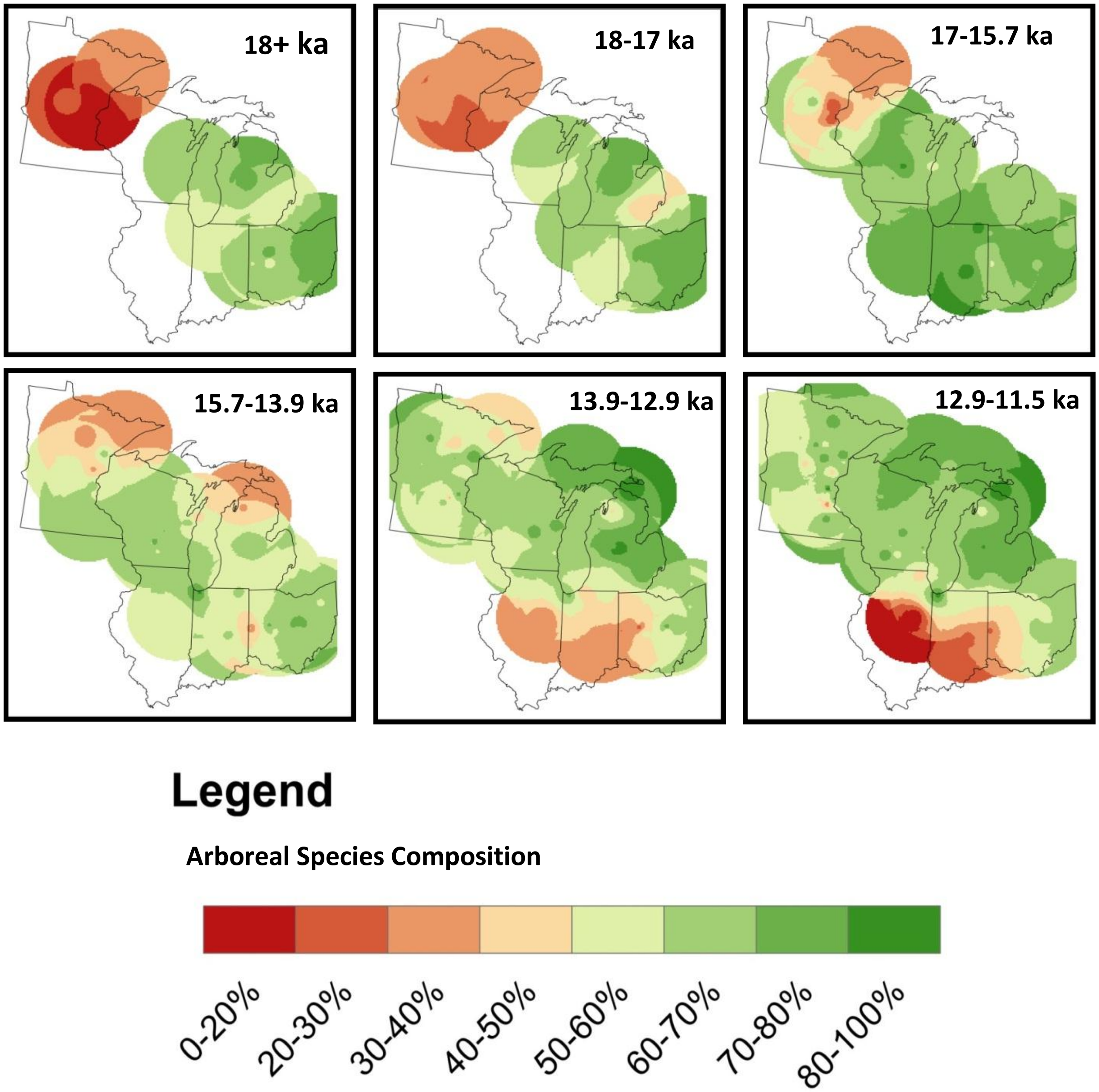

Figure A1: Arboreal (tree/shrub) species abundance. Based on the thousand year averages in radiocarbon years BP of the sum of *Betula,* Cupressaceae*, Fraxinus, Ostrya*-type*, Picea,* and *Pinus* pollen percentages, this series of images show how the arboreal abundance changed from 15 to 10 ka. At 18+ ka, higher percentages (>50%) of arboreal taxa were observed in the eastern half of the study area, with the western half showing NO DATA or low percentages (<20%). By 17-15.7 ka, most of the study area was covered by arboreal taxa, with lower percentages observed in the northwestern quadrant of the study area. Arboreal abundance can be observed shifting northward 13.9-12.9 ka through 12.9-11.5 ka. Lower percentages were replaced by higher percentages in the north, and the opposite was observed in the south.

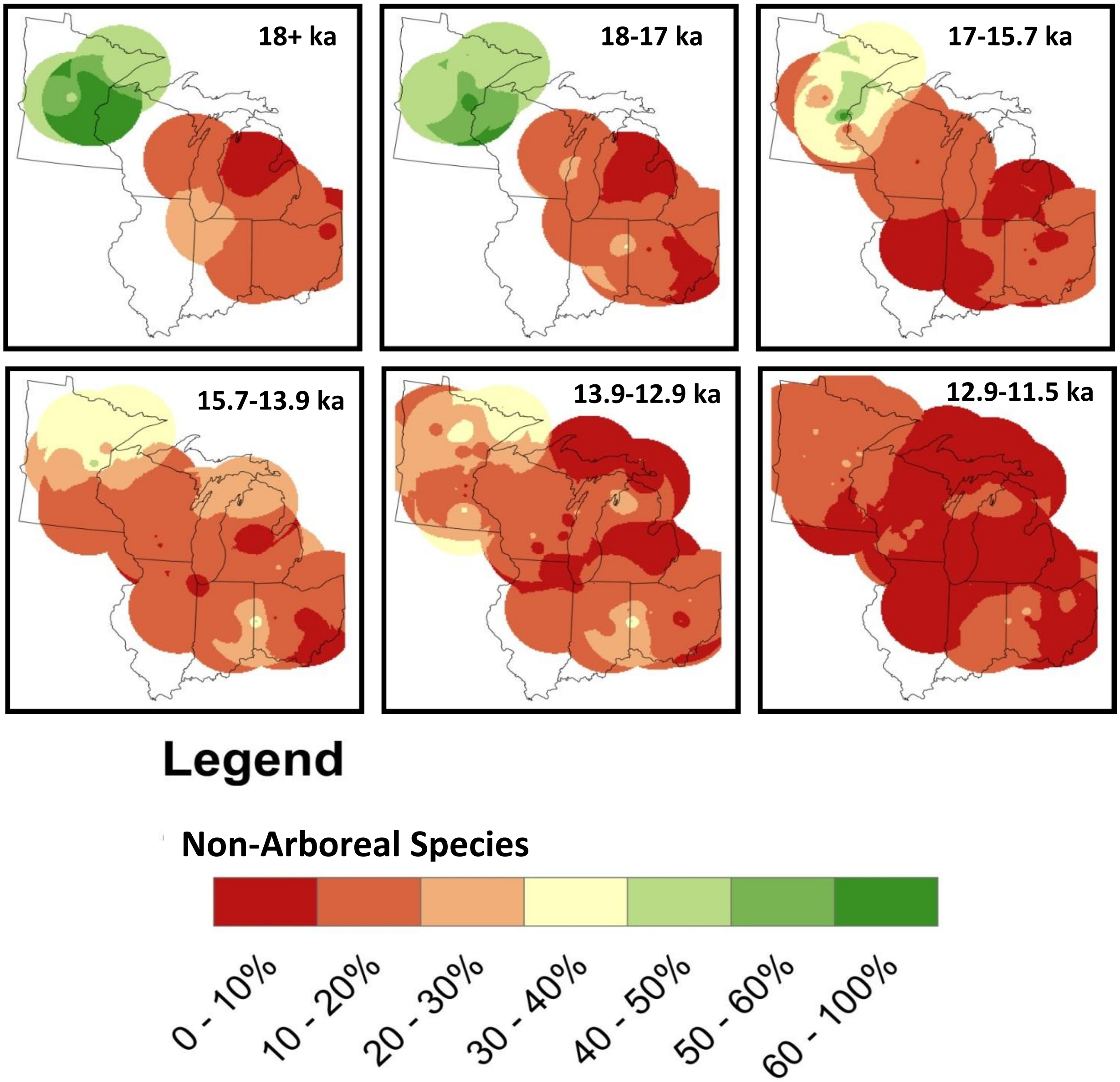

Figure A2: Non-arboreal (herbaceous) species abundance. Based on the thousand year averages of the sum of *Artemisia*, Cyperaceae, and Poaceae pollen percentages, this series of images show how the non-arboreal abundance changed from 18-11.5 ka. For all time periods, most of the study area had low percentages (<30%) of non-arboreal taxa. At 18+ ka, the only area of higher percentage was in the northwestern quadrant of the study area. The same pattern was observed for 18-17 ka and 17-15.7 ka ka. At 15.7-13.9 ka, most of the study area had an abundance of approximately 10-20% non-arboreal, with the northwestern quadrant showing a slightly higher 30-40%. The 13.9-12.9 ka time period non-arboreal abundance looked fragmented, and by 11-10 ka, most of the study area was <10% non-arboreal.

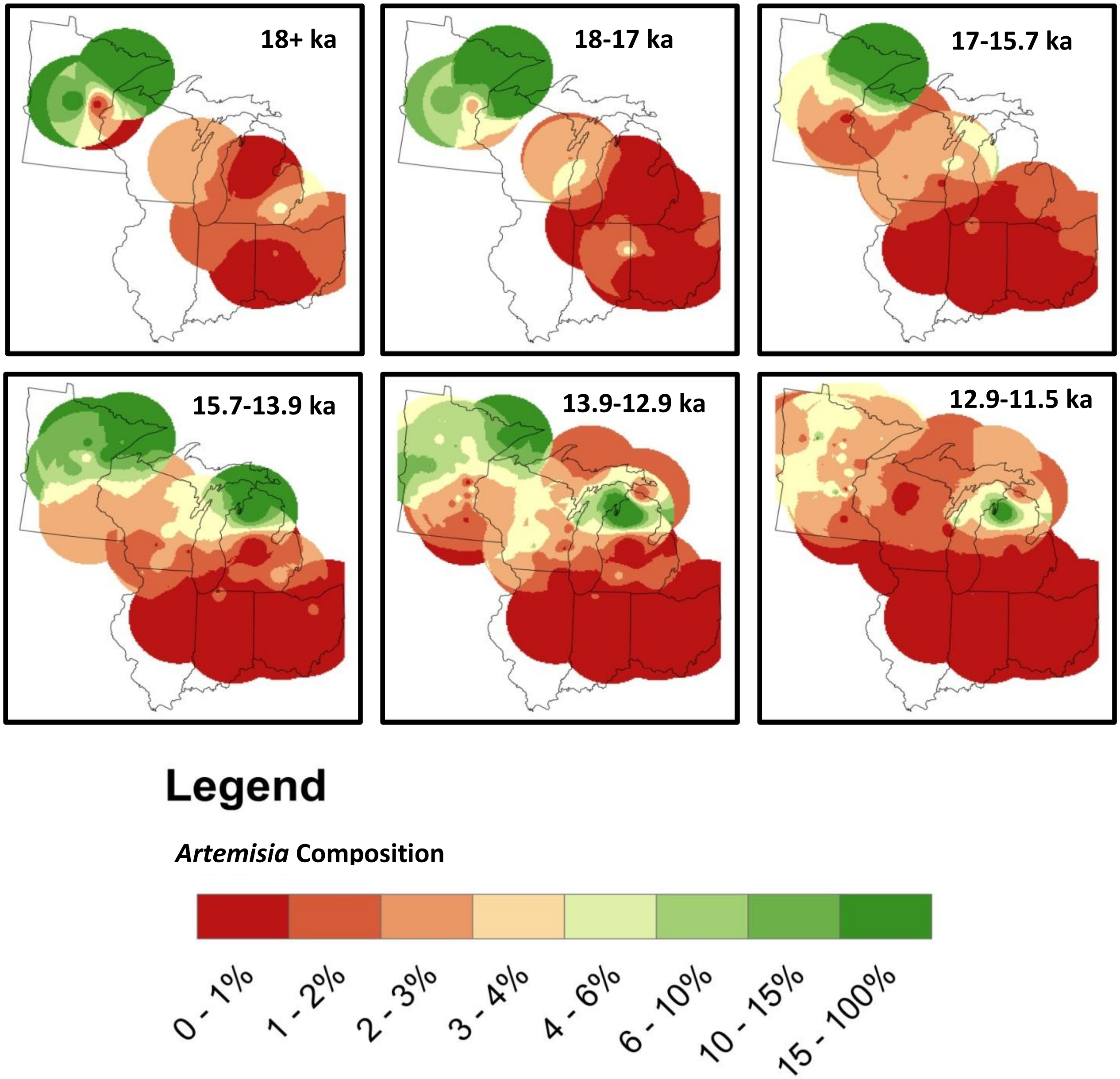

Figure A3: *Artemsia* (wormwood/sage) abundance. Based on the thousand year averages of *Artemisia*, this series of images show how the *Artemisia* abundance changed from 18 ka to 11.5 ka. At 18+ ka, the eastern half of the study area had an abundance of less than 6% and the northwestern quadrant had an abundance of greater than 12%. The same pattern is observed until 15.7-13.9 ka, where a clear north-south trend is observed, with higher percentages (>12%) is observed in the north and low percentages (<2%) in the south with a band of intermediate percentages between them. At 13.9-12.9 ka, the *Artemisia* abundance is highly fragmented. By 12.9-11.5 ka, most of the study area is less than 4% with small areas of higher percentages farther north.

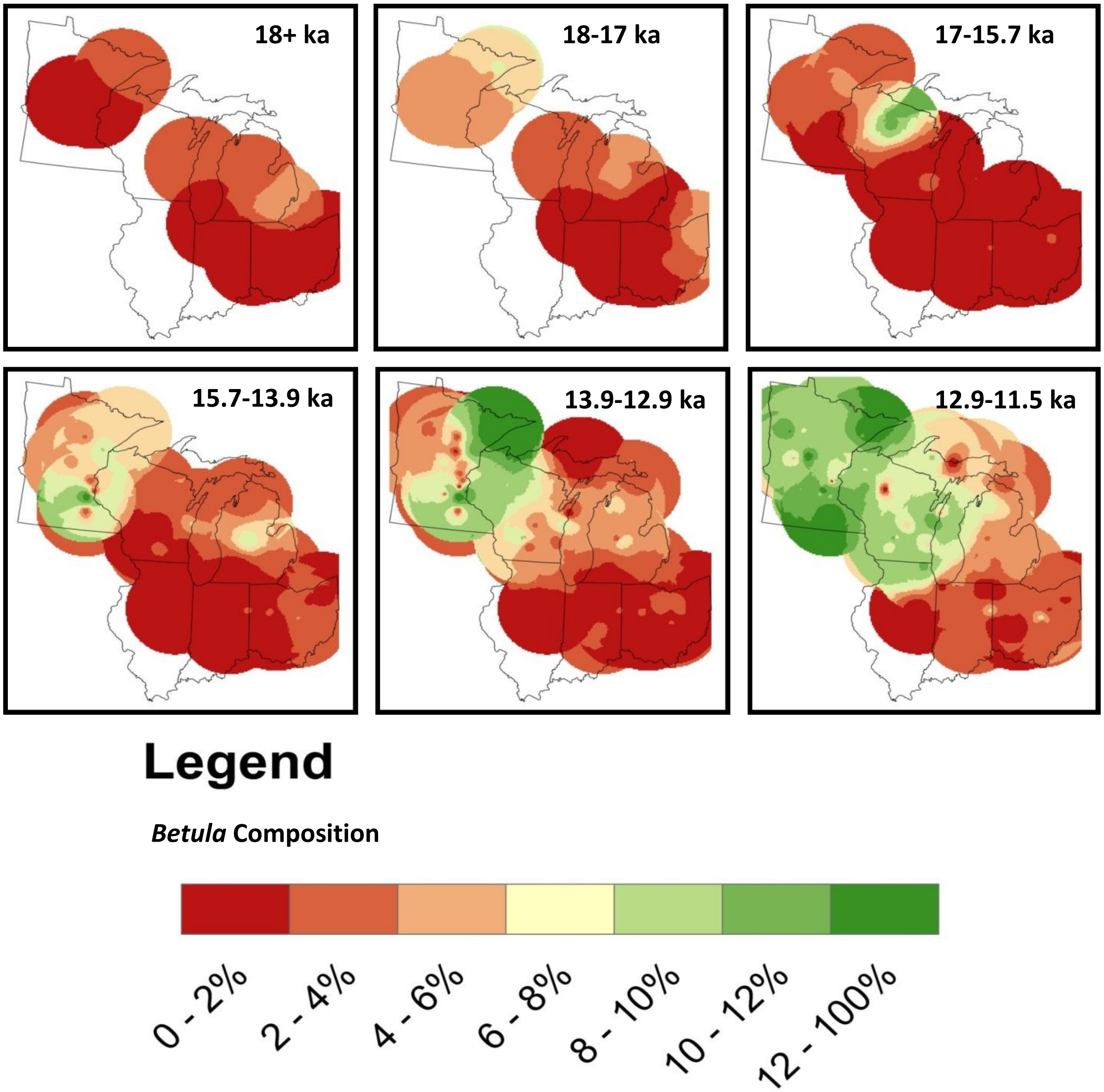

Figure A4: *Betula* (birch) abundance. Based on the thousand year averages of the sum of *Betula* pollen percentages, this series of images show how the *Betula* abundance changed from 18 ka to 11.5 ka. Initially, the *Betula* abundance was <2% across the study area (18+ ka). At 18-17 ka, slightly higher *Betula* percentages (3-4%) are observed in the northwest quadrant. Similar patterns are observed until 13.9-12.9 ka, where the *Betula* abundance becomes fragmented. The northwest quadrant has small areas of higher percentages (>15%). At 12.9-11.5 ka, fragmentation is still present but the higher percentages have shifted towards the south.

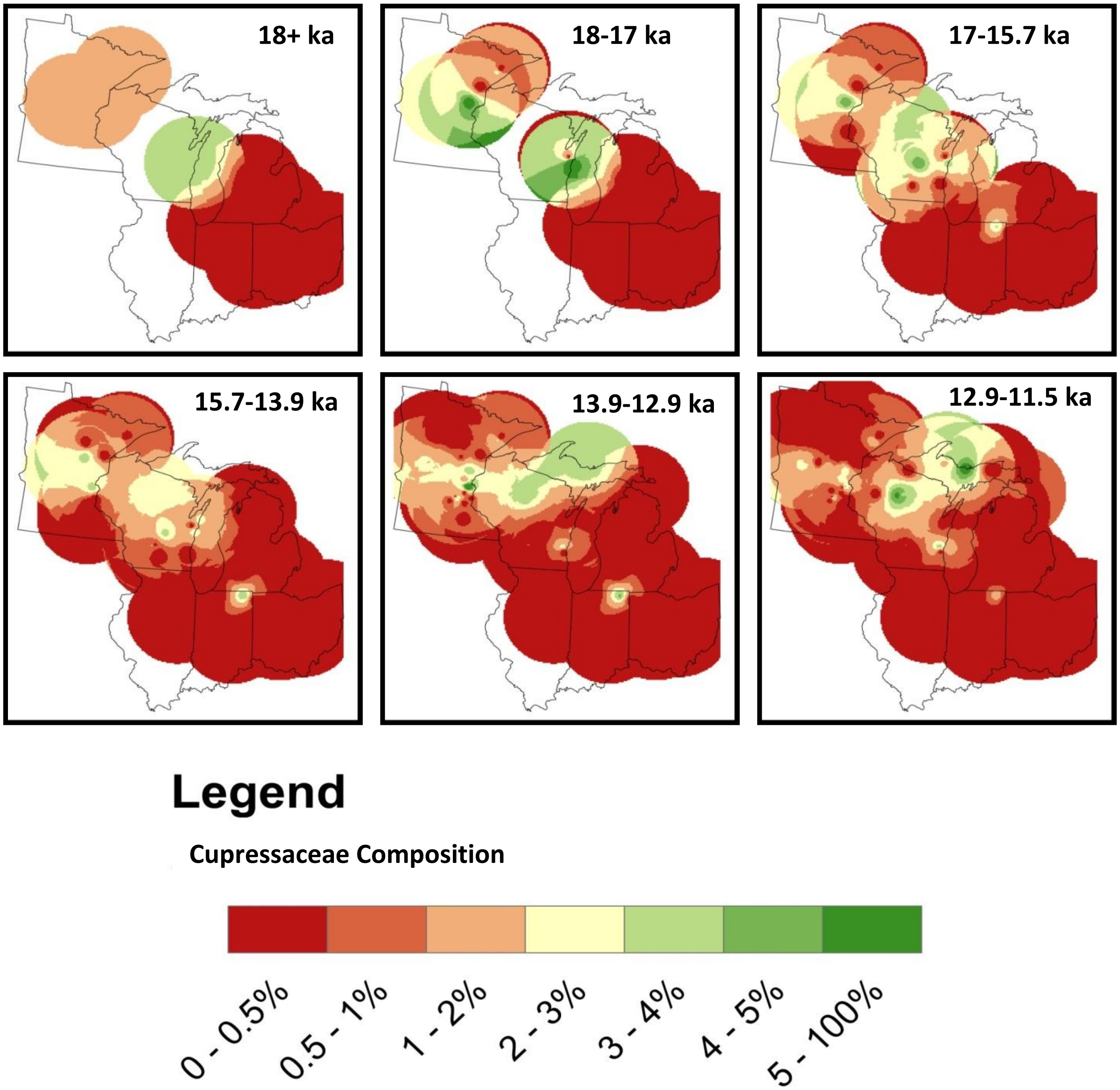

Figure A5: Cupressaceae (juniper or cedar) abundance. Based on the thousand year averages of the sum of Cupressaceae pollen percentages, this series of images show how the Cupressaceae abundance changed from 18 ka to 11.5 ka. The eastern half of the study area had low percentages (<0.5%) and the northwestern quadrant had slightly higher percentages (up to 4%) at 18+ ka. Fragmented Cupressaceae abundance was observed from 18 ka to 11.5 ka, with areas of higher percentages mostly in present day Wisconsin and Upper Peninsula Michigan.

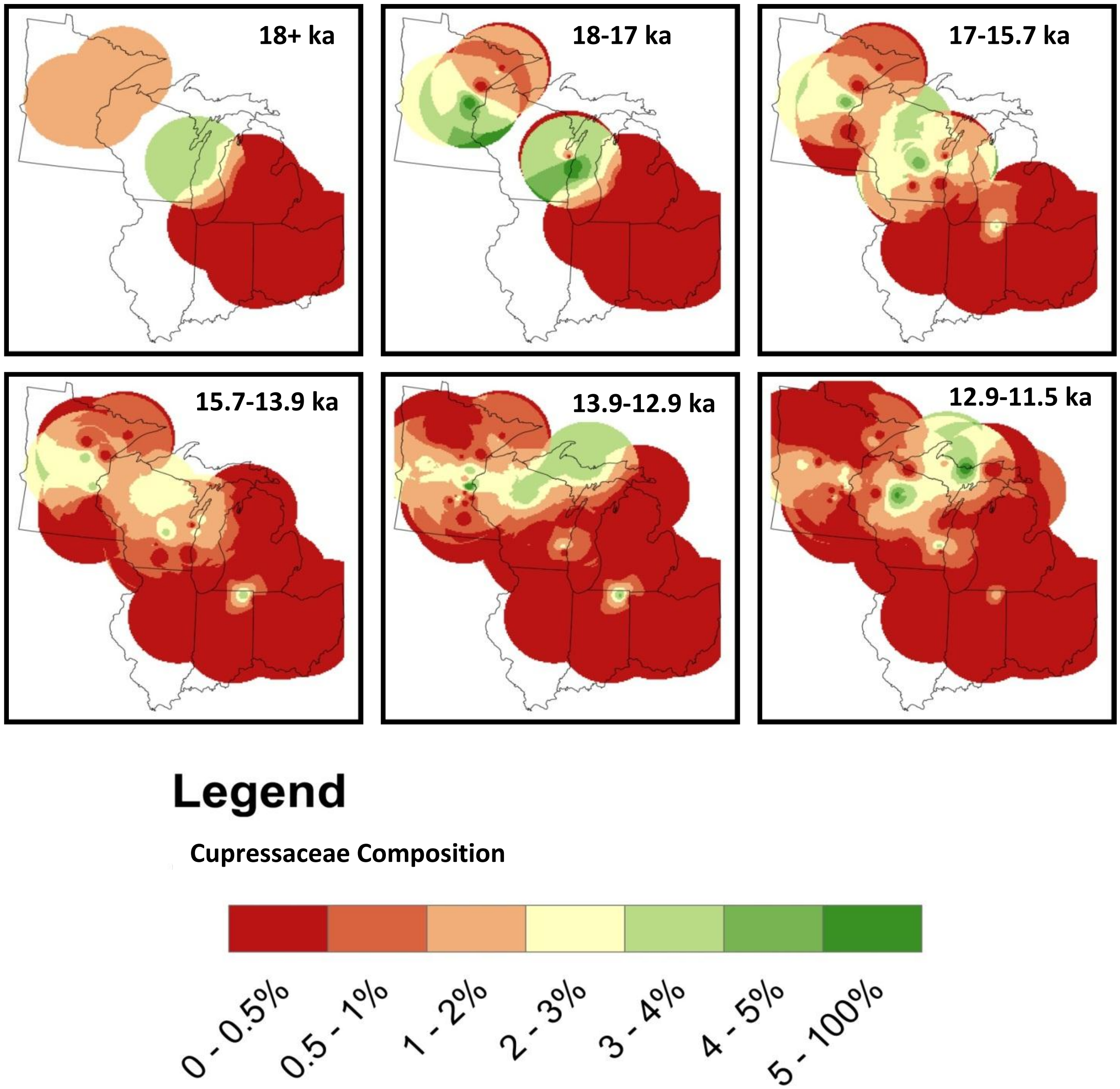

Figure A6: Cyperaceae (sedge family) abundance. Based on the thousand year averages of the sum of Cyperaceae pollen percentages, this series of images show how the Cyperaceae abundance changed from 18 ka to 11.5 ka. At 18+ ka, the eastern half of the study area had a north-south trend, with higher percentages (10-15%) in the south and lower percentages (0-5%) in the north. The northwest quadrant had higher percentages (>45%). By 17-15.7 ka, the north-south gradient was gone, with most of the study area, except for the northwest, being under 10%. At 13.9-12.9 ka, the high percentage areas in the northwest were gone, and by 12.9-11.5 ka, the entire study area was under 10%.

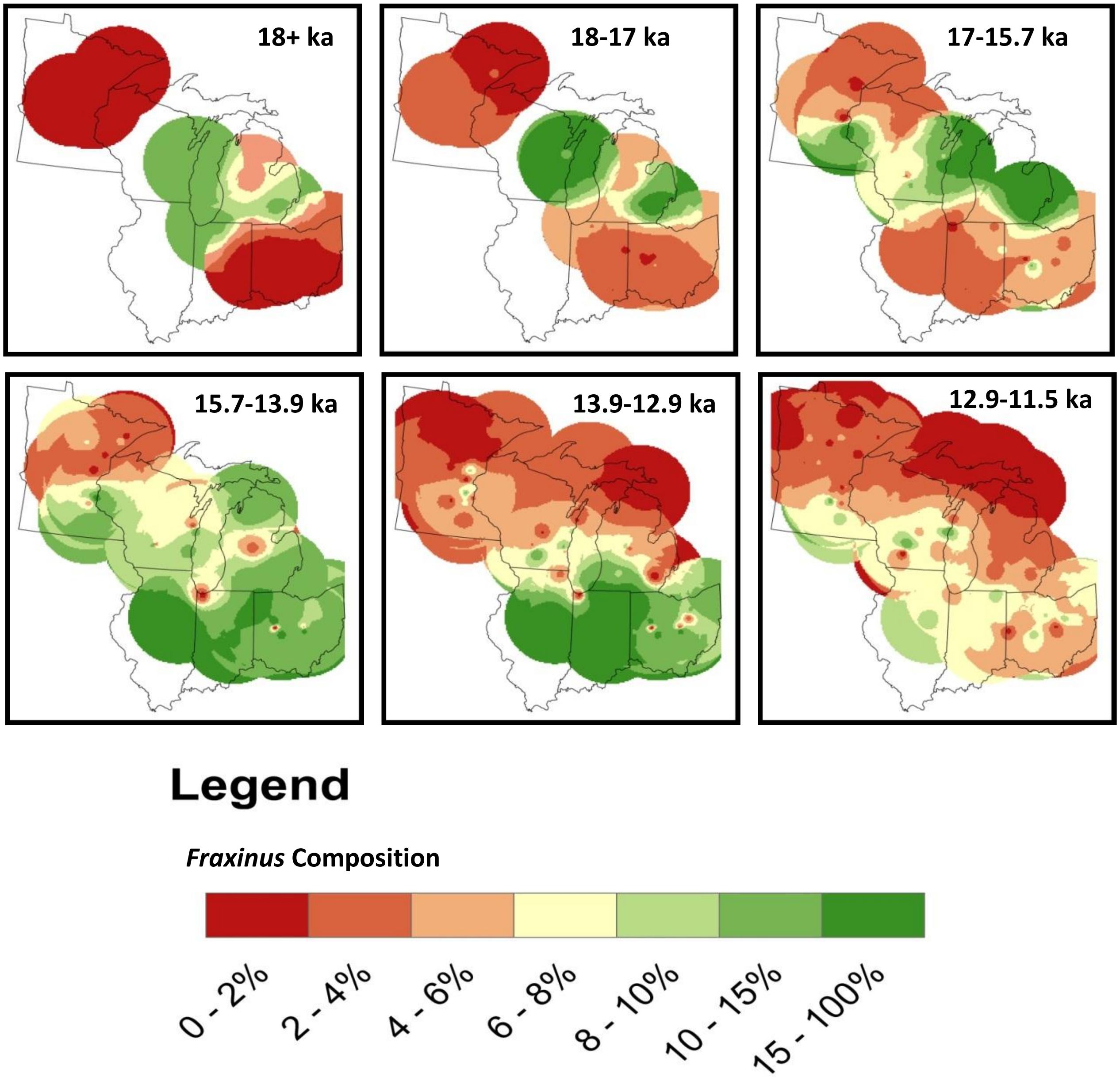

Figure A7: *Fraxinus* (ash) abundance. Based on the thousand year averages of the sum of *Fraxinus* pollen percentages, this series of images show how the *Fraxinus* abundance changed from 18 ka to 11.5 ka. At 18+ ka, a north-south gradient is observed for *Fraxinus* abundance on the eastern half of the study area, with low percentages (0-2%) in the south and higher percentages (up to 15%) in the north. This gradient is observed until 17-15.7 ka, where *Fraxinus* becomes fragmented. At 15.7-13.9 ka, the north-south gradient has revered, with low percentages in the north and high percentages (>15%) in the south. However, by 12.9-11.5 ka, the southern half of the study area mostly has an abundance of 6-8%, and the north has an abundance of 0-2%.

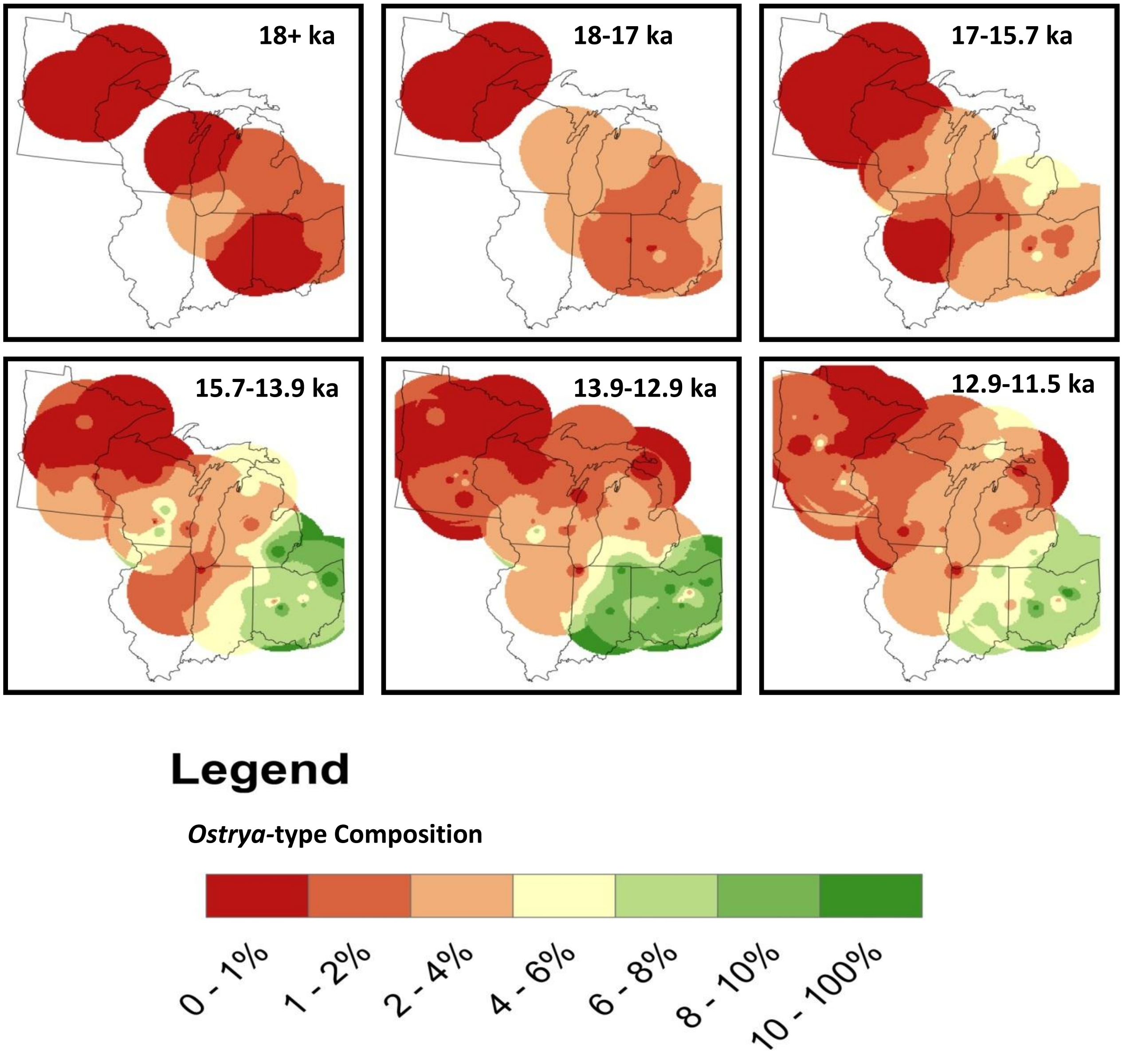

Figure A8: *Ostrya*-type (hophornbeam/hornbeam) abundance. Based on the thousand year averages of the sum of *Ostrya*-type pollen percentages, this series of images show how the *Ostrya*-type abundance changed from 18 ka to 11.5 ka. At 18+ ka, most of the study area had an *Ostyra*-type abundance of less than 4%. By 15.7-13.9 ka, a southeast-northwest gradient was observed. Though fragmented, higher percentages (>8%) were observed in the southeast and the lower percentages (<2%) were observed in the northwest. This gradient was present until 11.5 ka; however, the southeast quadrant's abundance slowly slight decreased (6-8%).

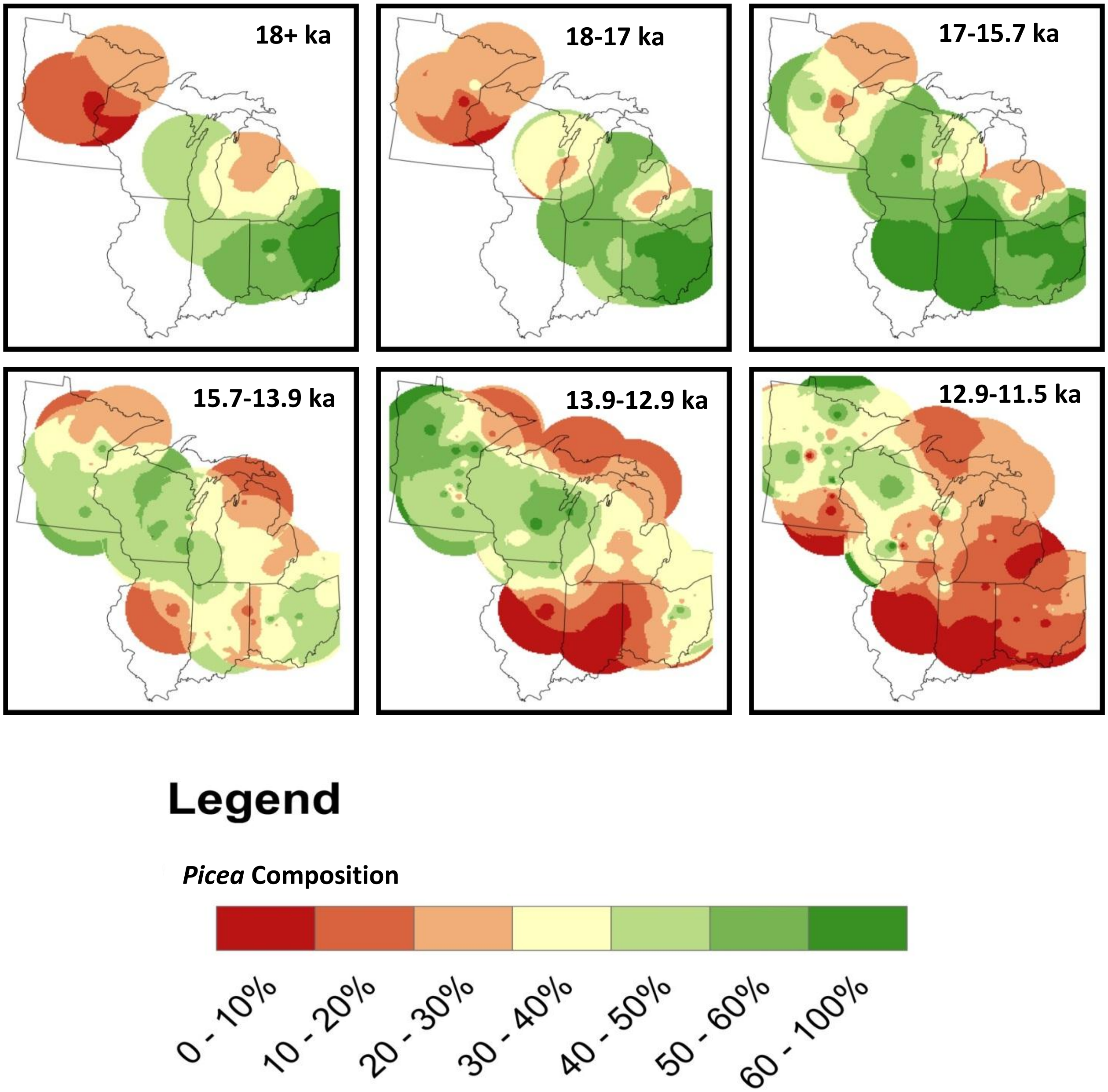

Figure A9: *Picea* (spruce) abundance. Based on the thousand year averages of the sum of *Picea* pollen percentages, this series of images show how the *Picea* abundance changed from 18 ka to 11.5 ka. At 18+ ka, a slight gradient is observed, with higher percentages (>50%) in the southeast and lower percentages (<30%) in the northwest. This gradient is present until 15.7-13.9 ka, when *Picea* abundance becomes fragmented; however, most of the study area is still between 30% and 50%. At 13.9-12.9 ka, *Picea* abundance begins to decrease in the south and increase in the north. The northern shift is still present at 12.9-11.5 ka; however, fragmentation has increased.

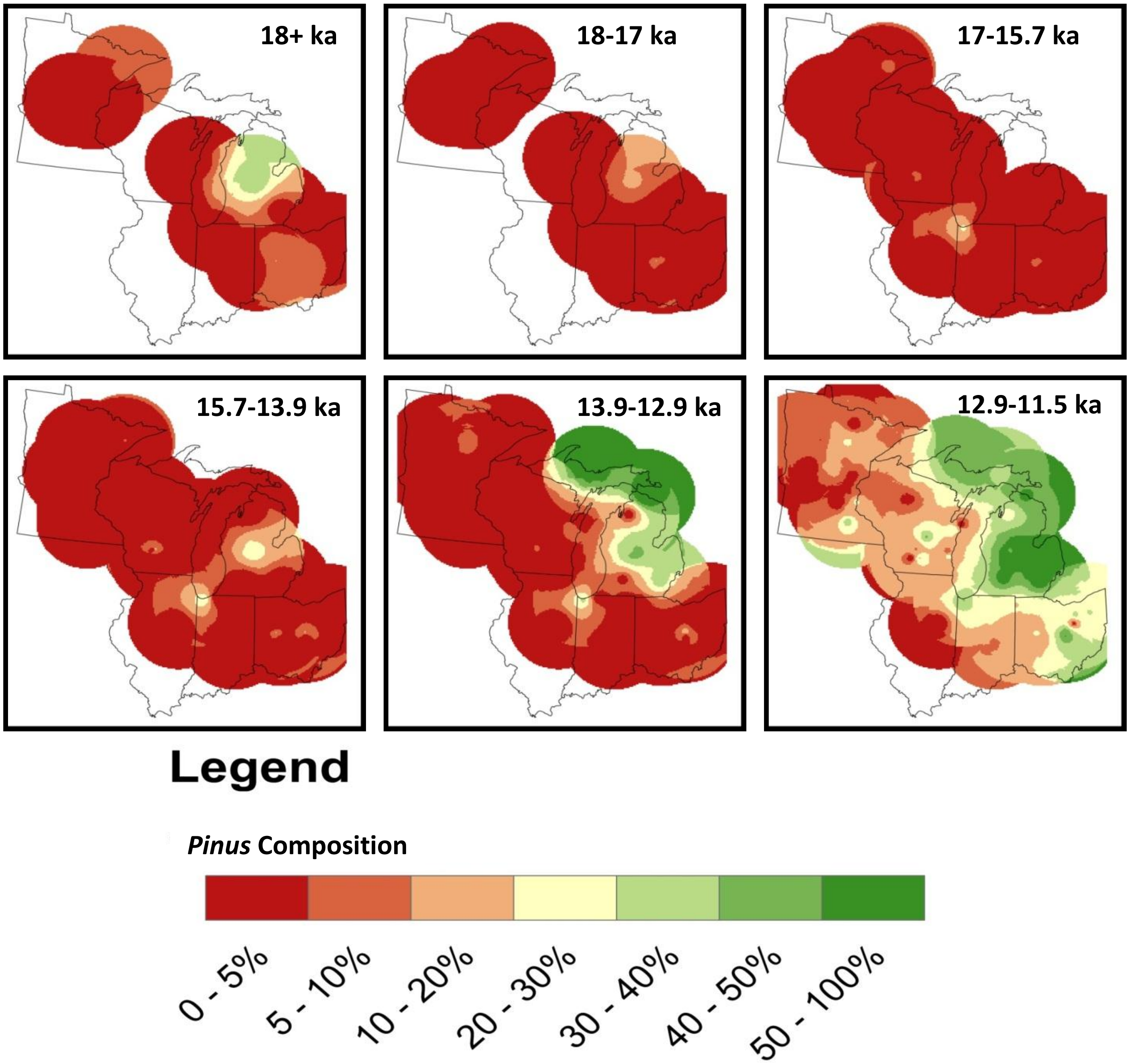

Figure A10: *Pinus* (pine) abundance. Based on the thousand year averages of the sum of *Pinus* pollen percentages, this series of images show how the *Pinus* abundance changed from 18 ka to 11.5 ka. Up until 13.9-12.9 ka, the majority of the study area has a *Pinus* abundance of less than 5% with some areas up to 10%. At 13.9-12.9 ka, the northeast quadrant has higher percentages (>50%) while the rest of the study area remains below 5%. By 12.9-11.5 ka, a northeast-southwest gradient is observed, with higher percentages (>50%) in the northeast and lower percentages (5-20%) in the southwest. At this time most of the study area has a *Pinus* abundance greater than 5%.

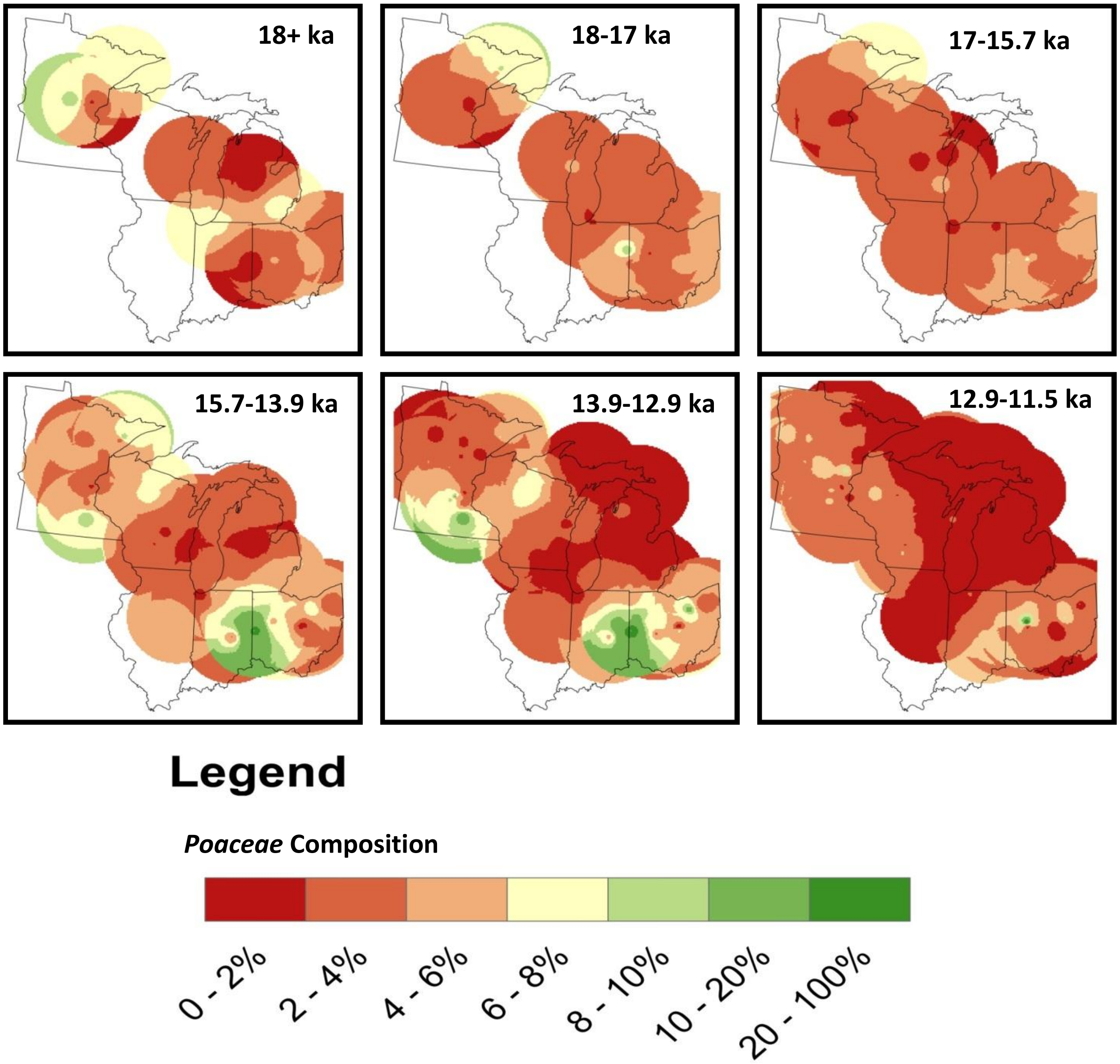

Figure A11: Poaceae (grass) abundance. Based on the thousand year averages of the sum of Poaceae pollen percentages, this series of images show how the Poaceae abundance changed from 18 ka to 11.5 ka. Up until 15.7 ka, most of the study area had a Poacea abundance of less than 4% except for the northwest quadrant. At 15.7-13.9 ka, the Poaceae abundance was fragmented with higher percentages in the northwest and southeast, but the center (modern day Wisconsin and Michigan) still had lower percentages. This trend was observed through 11.5 ka. At 12.9-11.5 ka, most of the study area was again less than 4%.

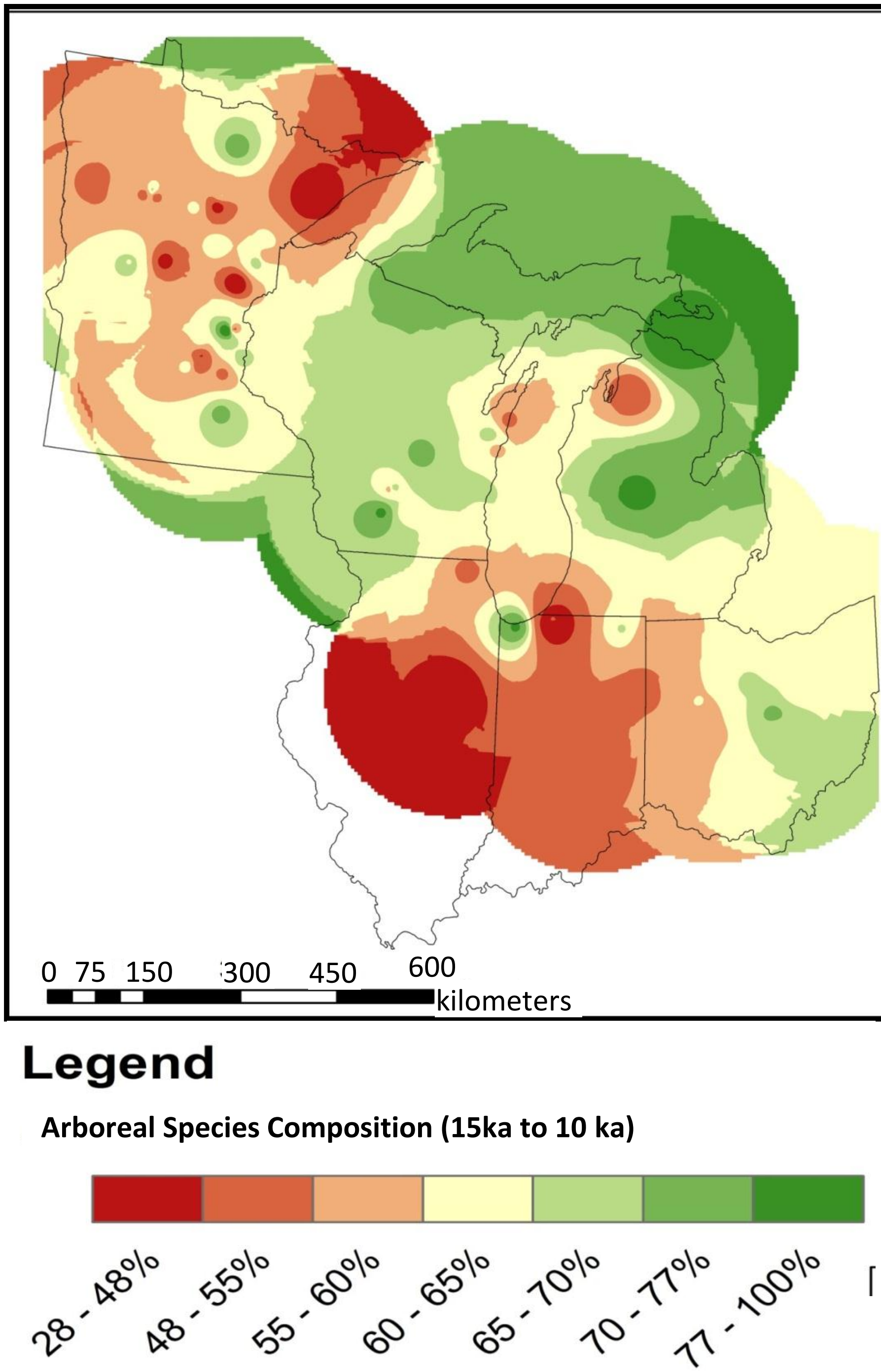

Figure A12: Arboreal species abundance, based on the five thousand year averages of the sum of *Betula,* Cupressaceae*, Fraxinus, Ostrya*-type*, Picea,* and *Pinus* pollen percentages. The areas with the highest percentages were in the central part of the study area (modern day Wisconsin and Michigan). The lowest percentages were observed in the southern portion of the study area (modern day Illinois and Indiana).

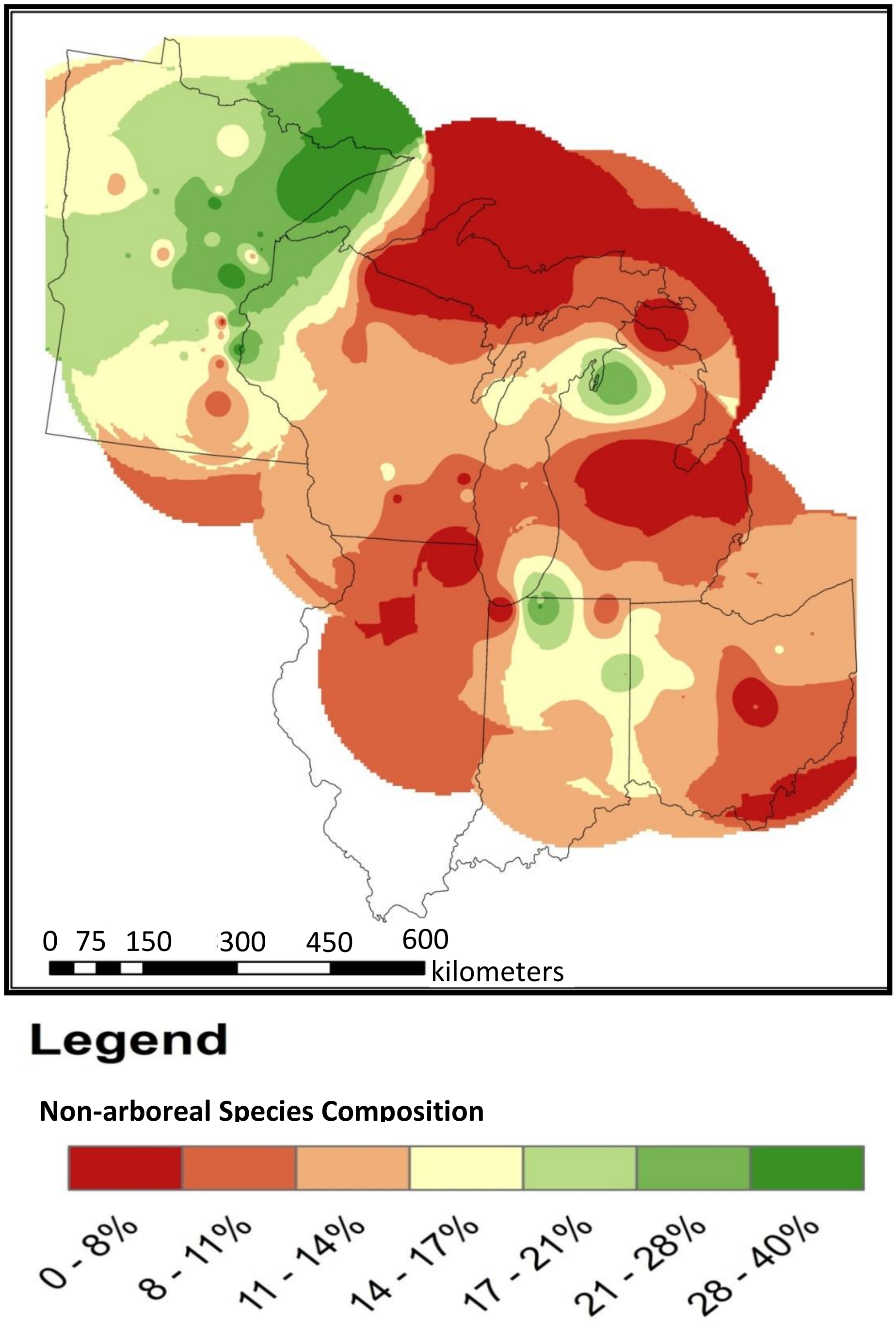

Figure A13: Non-arboreal species abundance, based on the five thousand year averages of the sum of Artemisia, Cyperaceae, and Poaceae pollen percentages. The northwest quadrant had the highest nonarboral abundance (>17%) while the central portion of the study area had the lowest abundance (0-14%). The southeast quadrant mostly had an abundance of 11-17%.

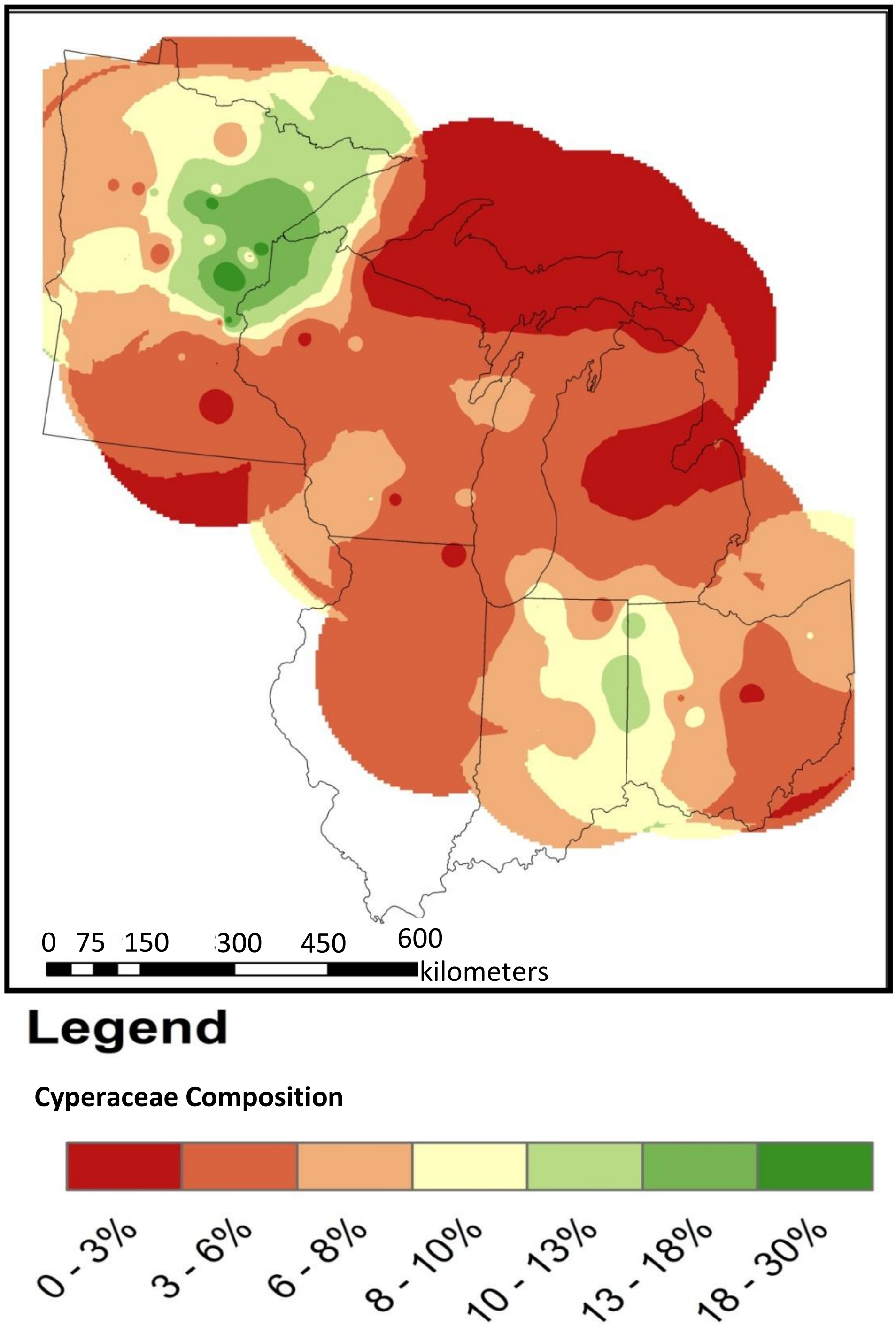

Figure A14: Cyperaceae abundance, based on the five thousand year averages of Cyperaceae pollen percentages. Most of the study area had a Cyperaceae abundance of less than 6%. Higher percentages were observed in the northwest and southeast quadrants. The northwest quadrant had an abundance of 6-30% and the southeast quadrant had an abundance of 6-13%.

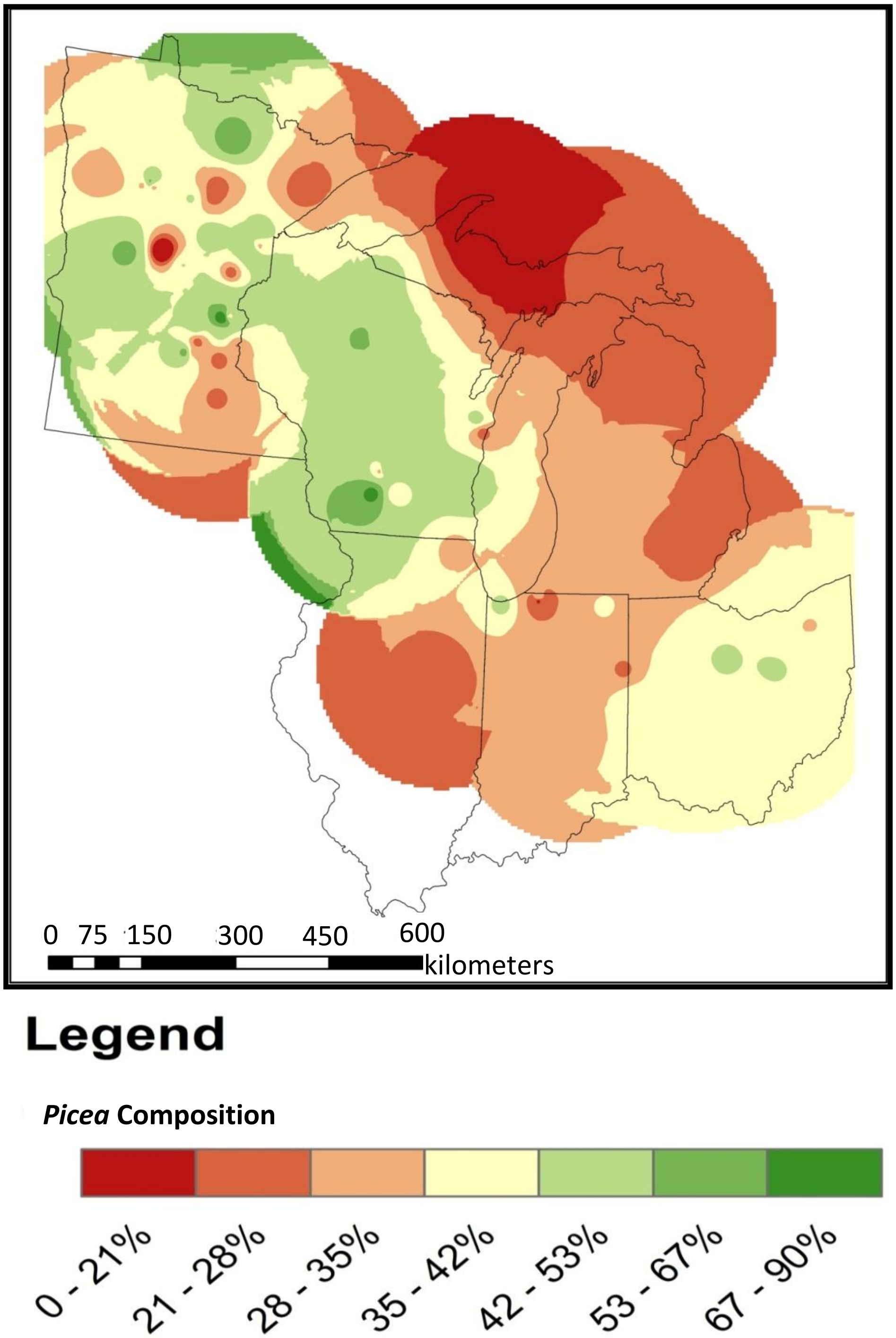

Figure A15: *Picea* abundance, based on the five thousand year averages of *Picea* pollen percentages. *Picea* abundance looked very fragmented. The highest percentages (>53%) were located in portions of the northwest quadrant. Lower percentages (<28%) were observed in the northeastern portion of the study area. The southeastern quadrant had intermediate *Picea* abundances (28-42%).

APPENDIX B

Appendix B consists of line graphs created for the purpose of comparing pollen percentage data between mammoths and mastodons. For these line graphs, all proboscidean sites were used, whether they had associated radiocarbon dates or not. To do this, each proboscidean site was duplicated six times, one for each time period.

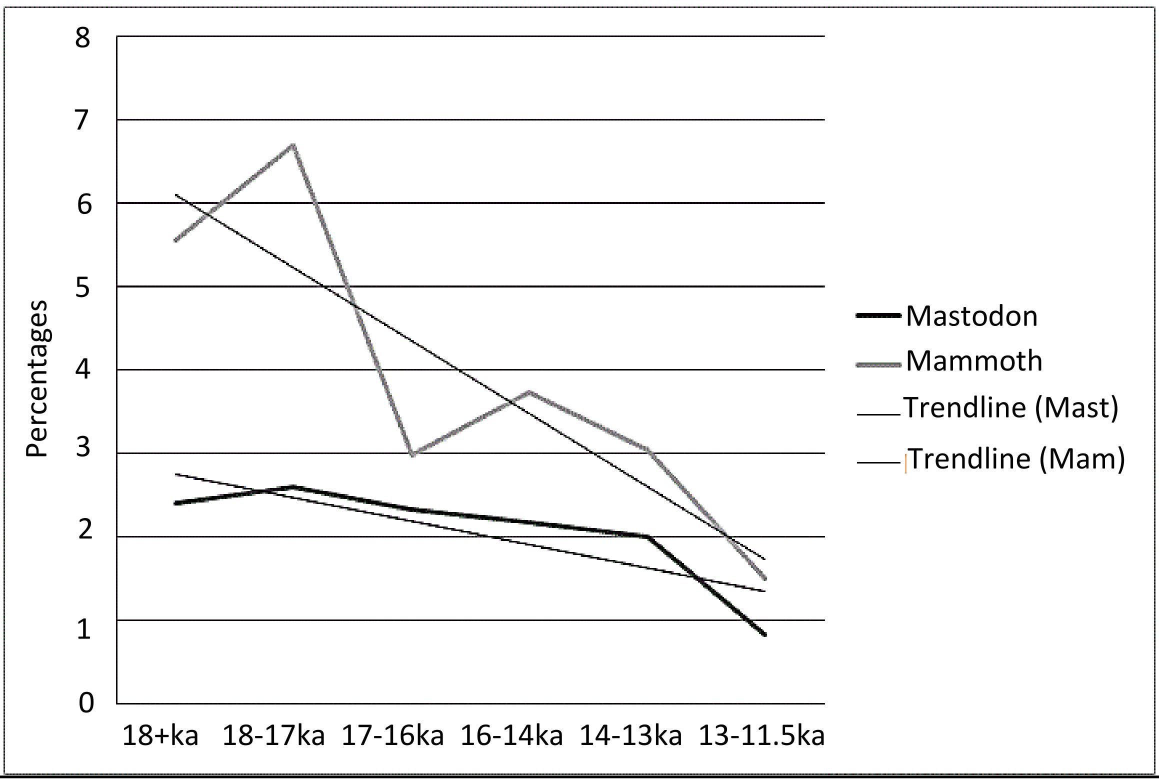

Figure B1: Comparison of *Artemisia* pollen percentages for all mammoth and mastodon localities.

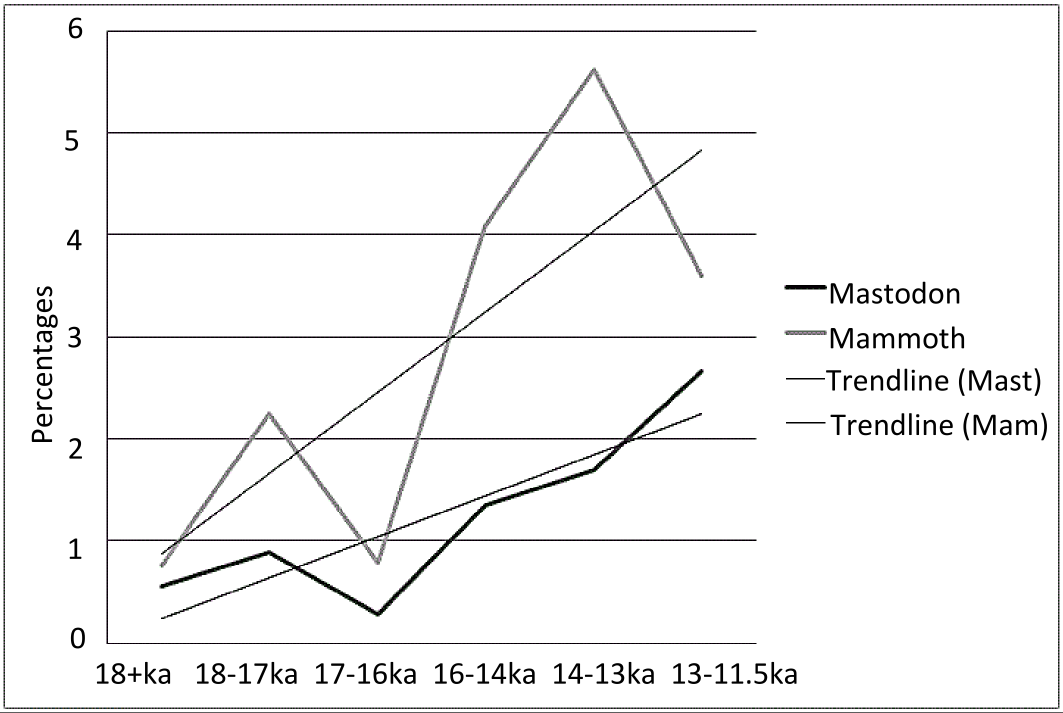

Figure B2: Comparison of *Betula* pollen percentages for all mammoth and mastodon localities.

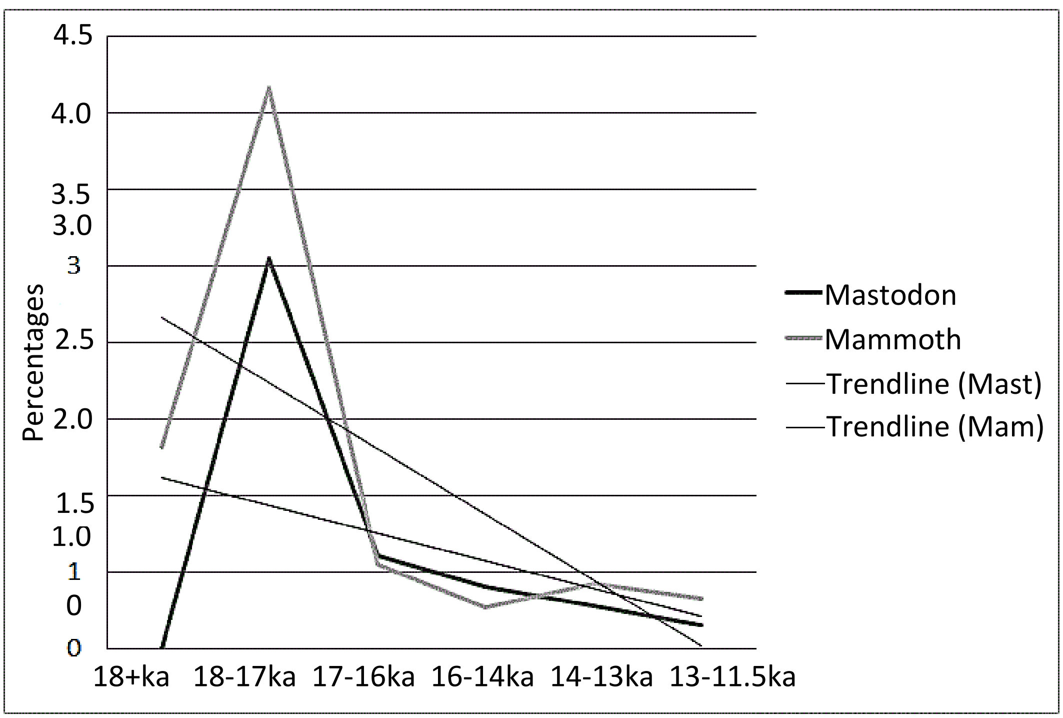

Figure B3: Comparison of Cupressaceae pollen percentages for all mammoth and mastodon localities.

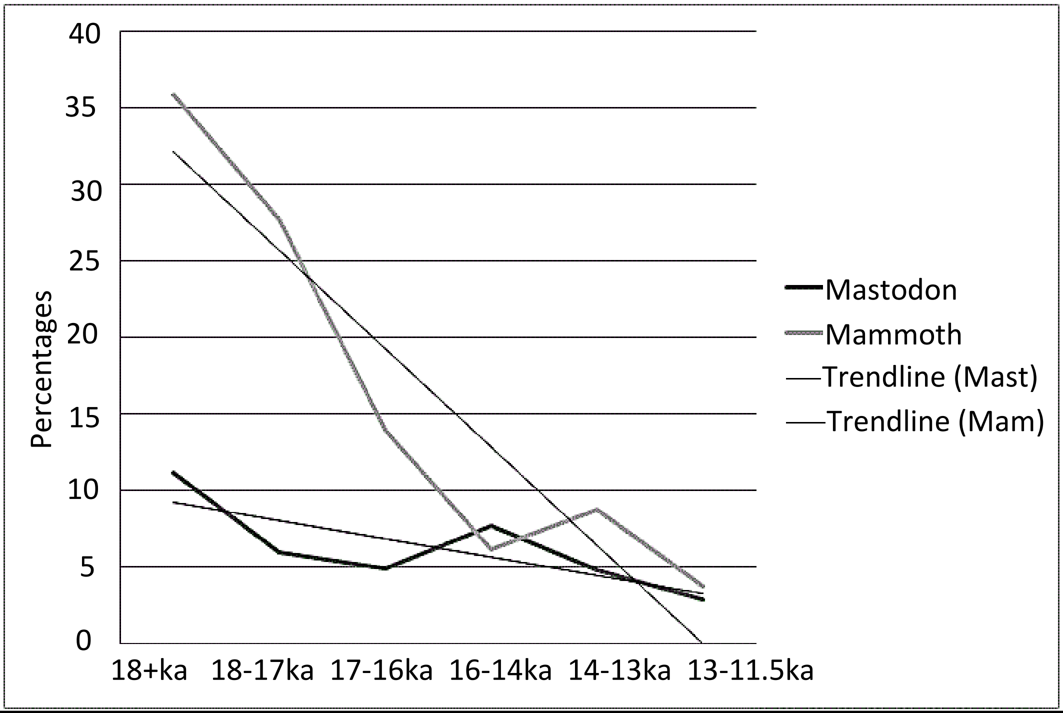

Figure B4: Comparison of Cyperaceae pollen percentages for all mammoth and mastodon localities.

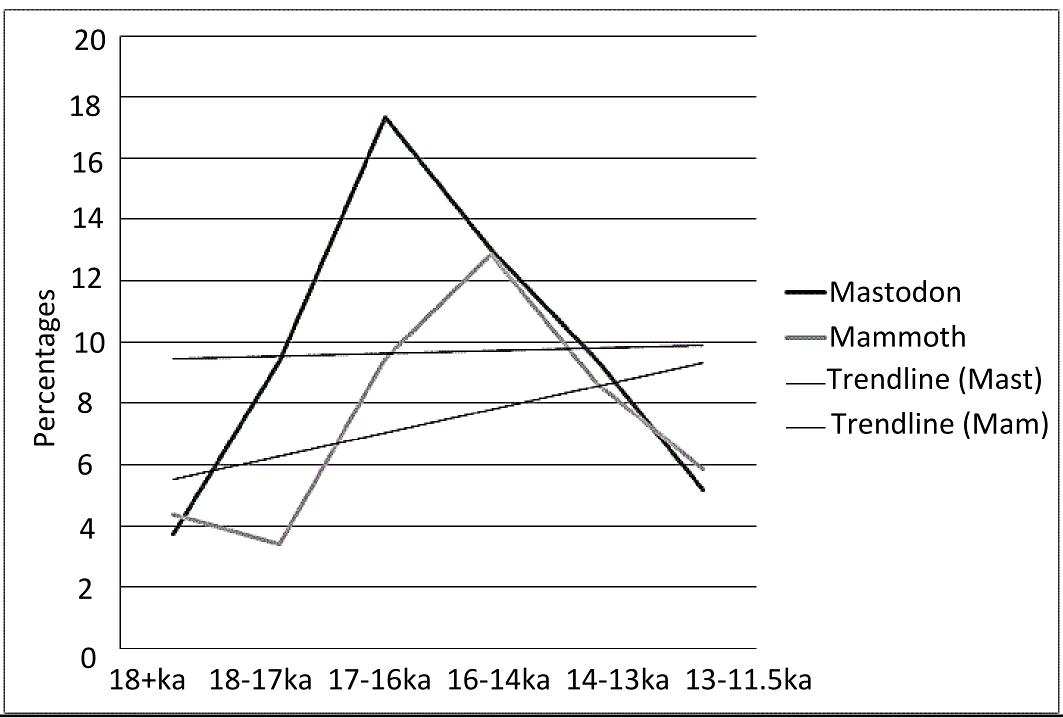

Figure B5: Comparison of *Fraxinus* pollen percentages for all mammoth and mastodon localities.

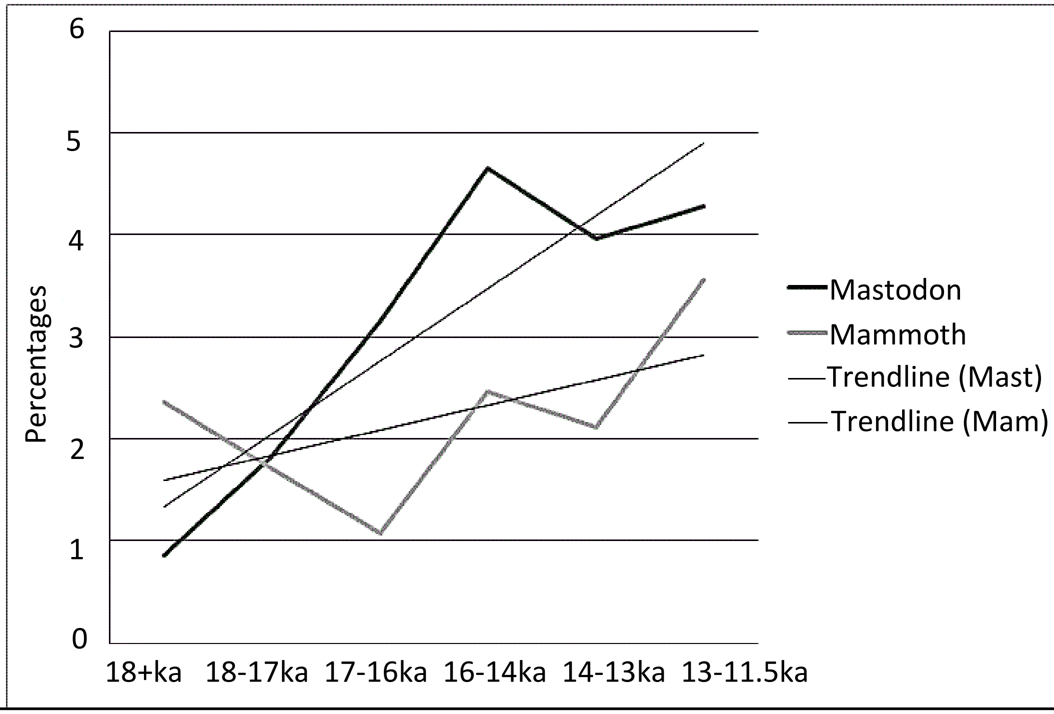

Figure B6: Comparison of *Ostrya*-type pollen percentages for all mammoth and mastodon localities.

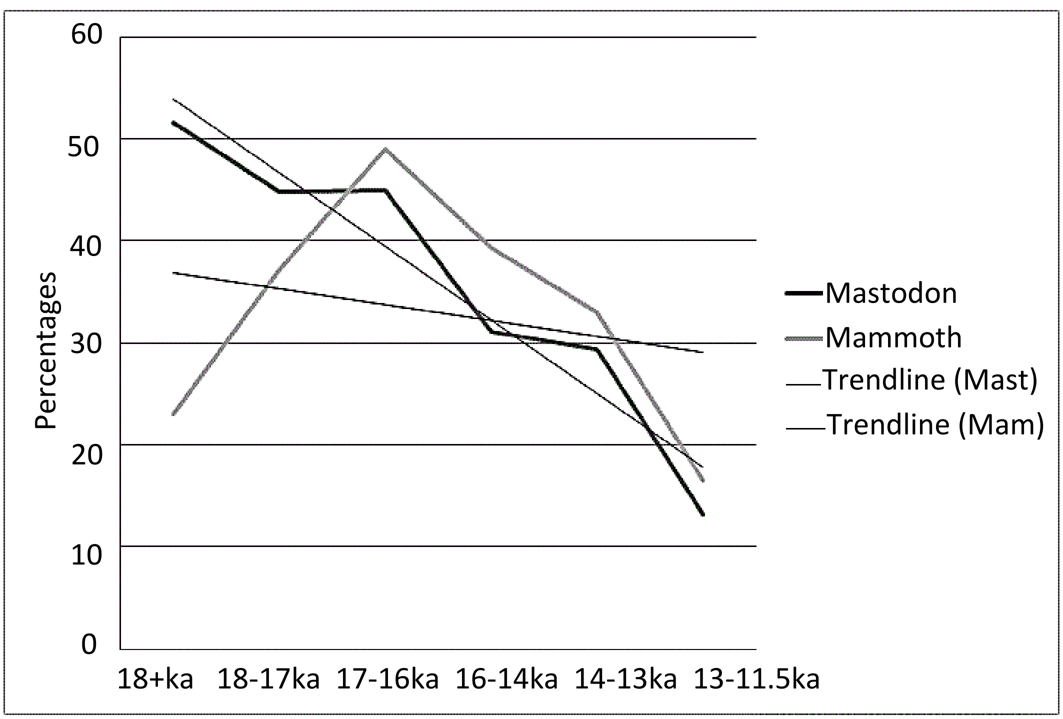

Figure B7: Comparison of *Picea* pollen percentages for all mammoth and mastodon localities.

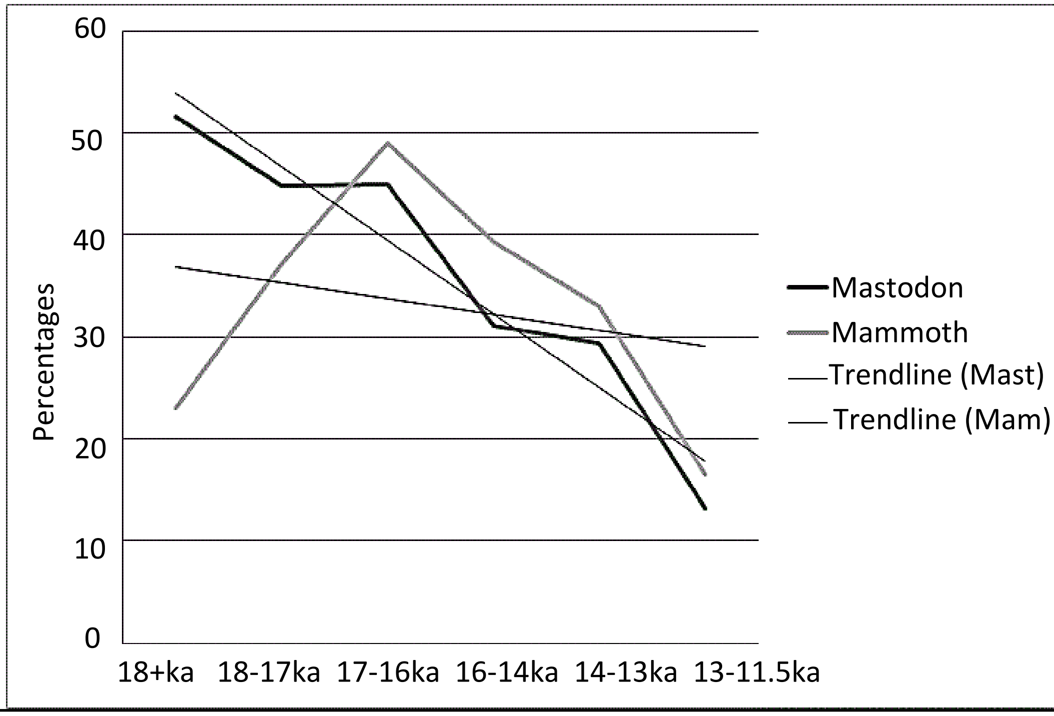

Figure B8: Comparison of *Pinus* pollen percentages for all mammoth and mastodon localities.

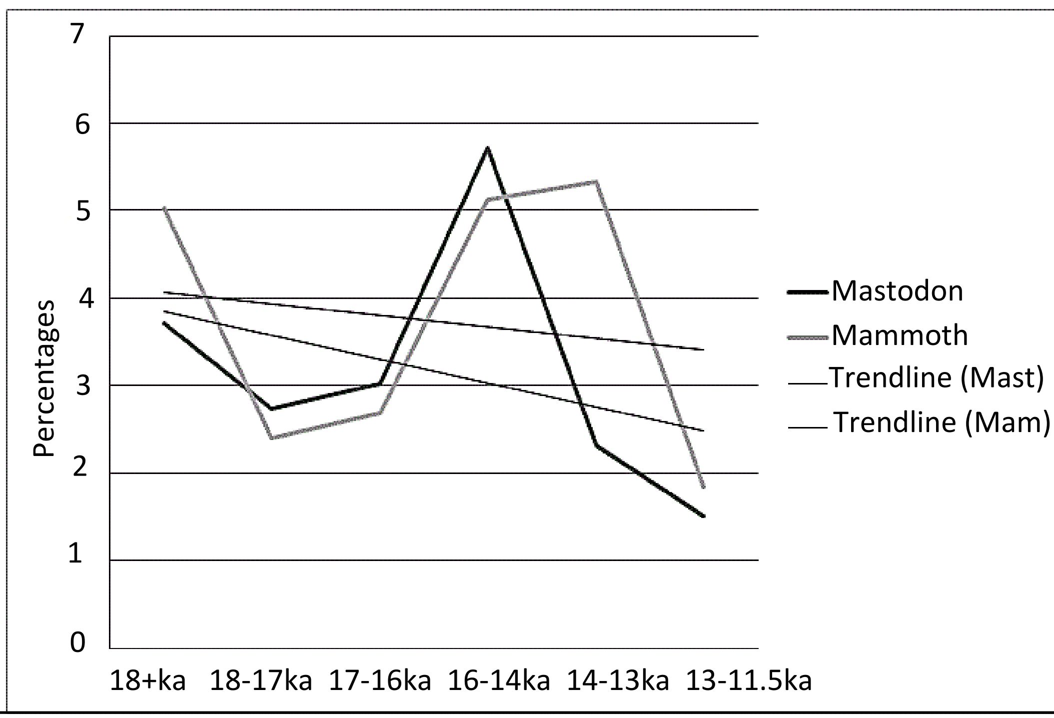

Figure B9: Comparison of Poaceae pollen percentages for all mammoth and mastodon localities.

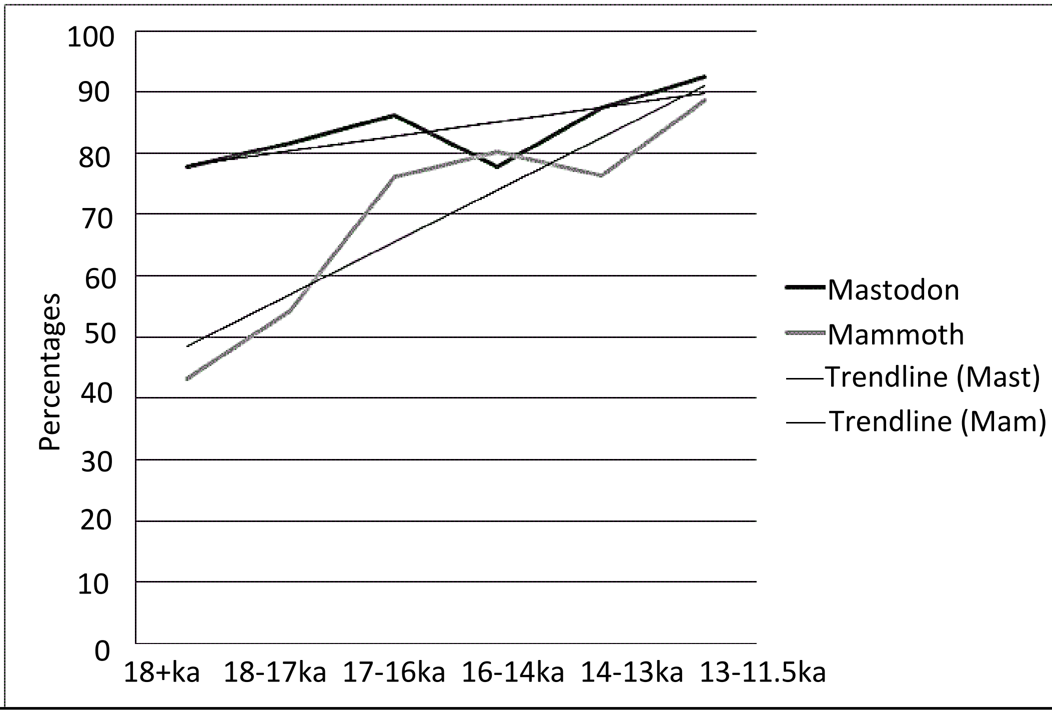

Figure B10: Comparison of AP pollen percentages for all mammoth and mastodon localities.

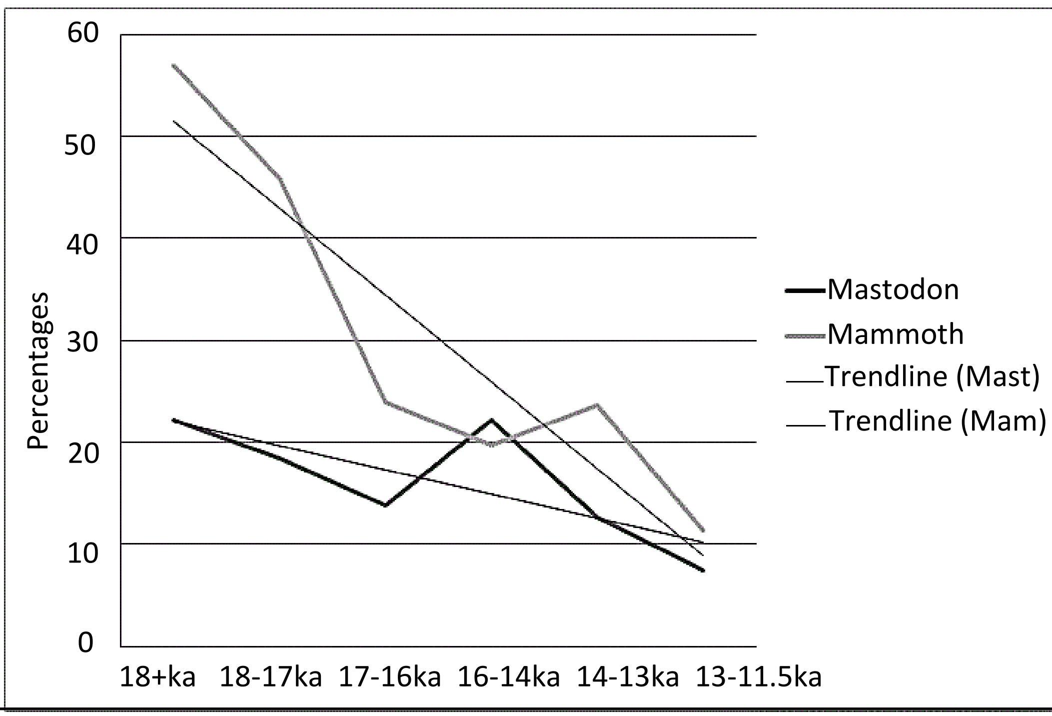

Figure B11: Comparison of NAP pollen percentages for all mammoth and mastodon localities.

APPENDIX C

Appendix C consists of line graphs created for the purpose of comparing pollen percentage data between mammoths and mastodons. For these line graphs, only proboscidean sites associated with a radiocarbon date were used. Pollen percentages were calculated for each site depending on their dated time period, meaning that each site was only used once. Due to the nature of having few dated proboscidean sites, some time periods were not represented, such as 18+ ka for mastodons.

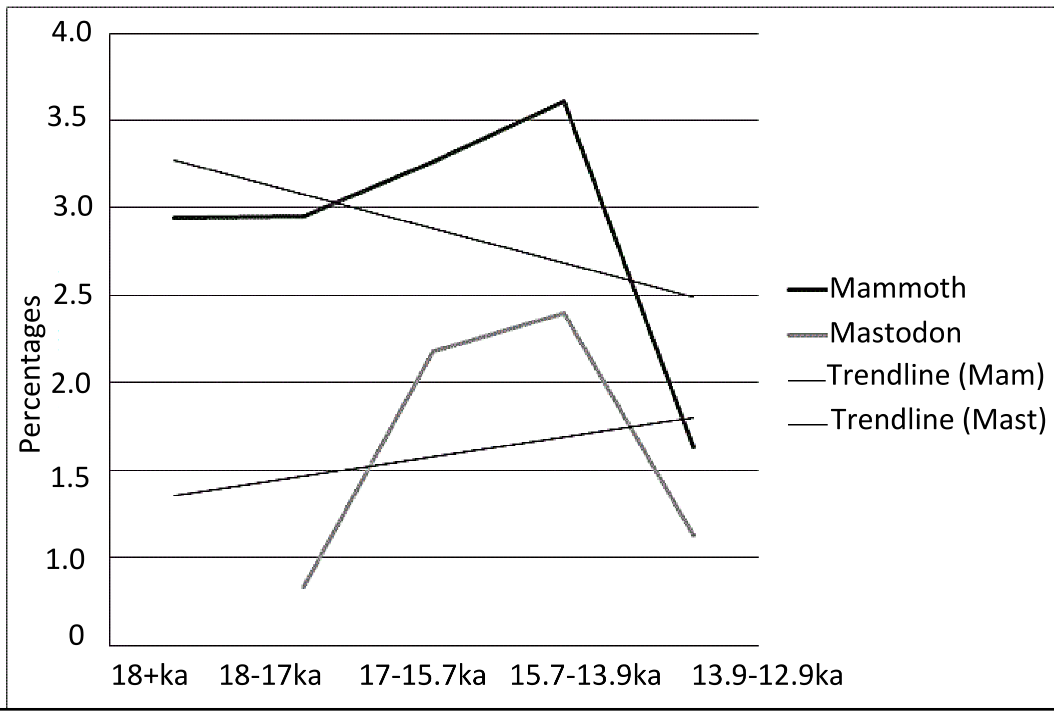

Figure C1: Comparison of *Artemisia* pollen percentages for dated mammoth and mastodon localities.

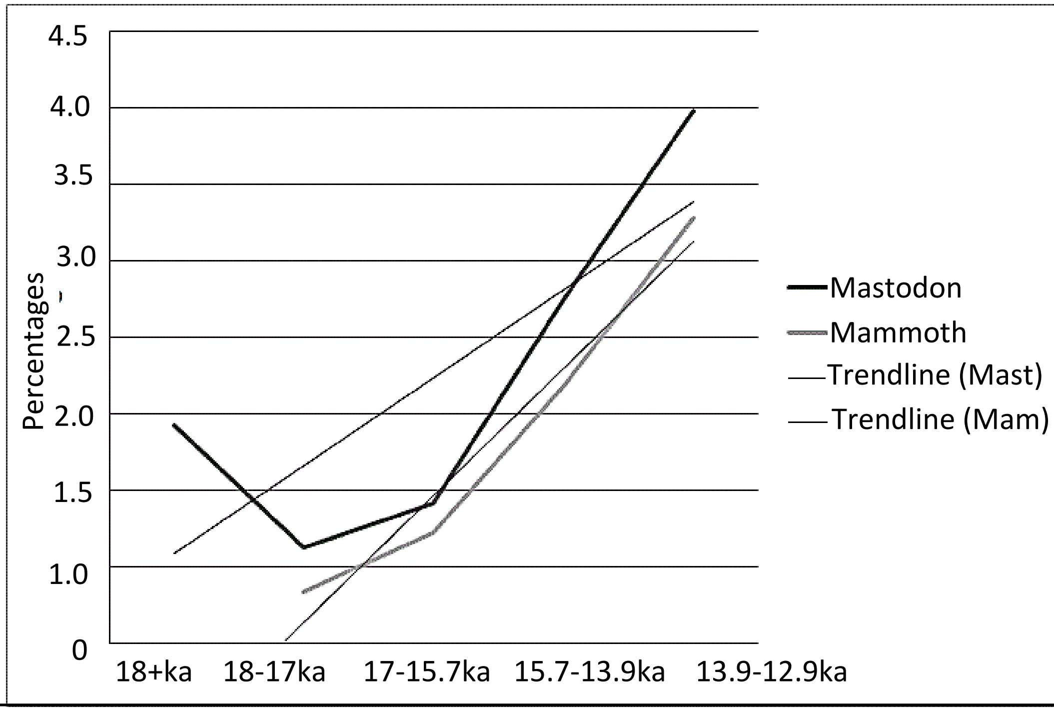

Figure C2: Comparison of *Betula* pollen percentages for dated mammoth and mastodon localities.

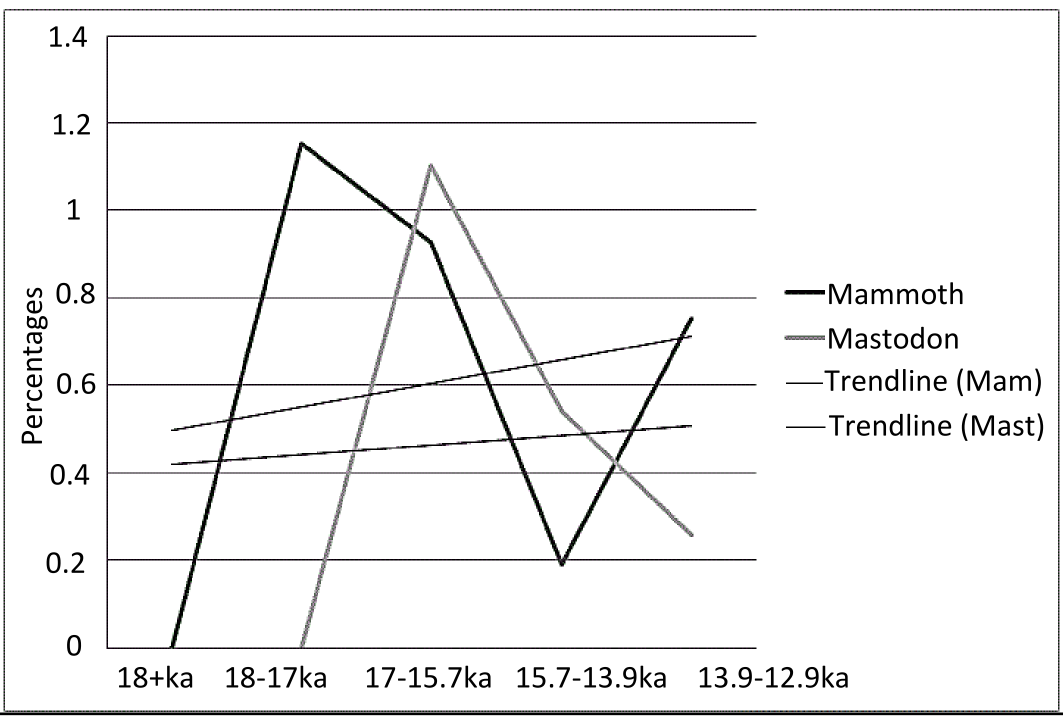

Figure C3: Comparison of Cupressaceae pollen percentages for dated mammoth and mastodon localities.

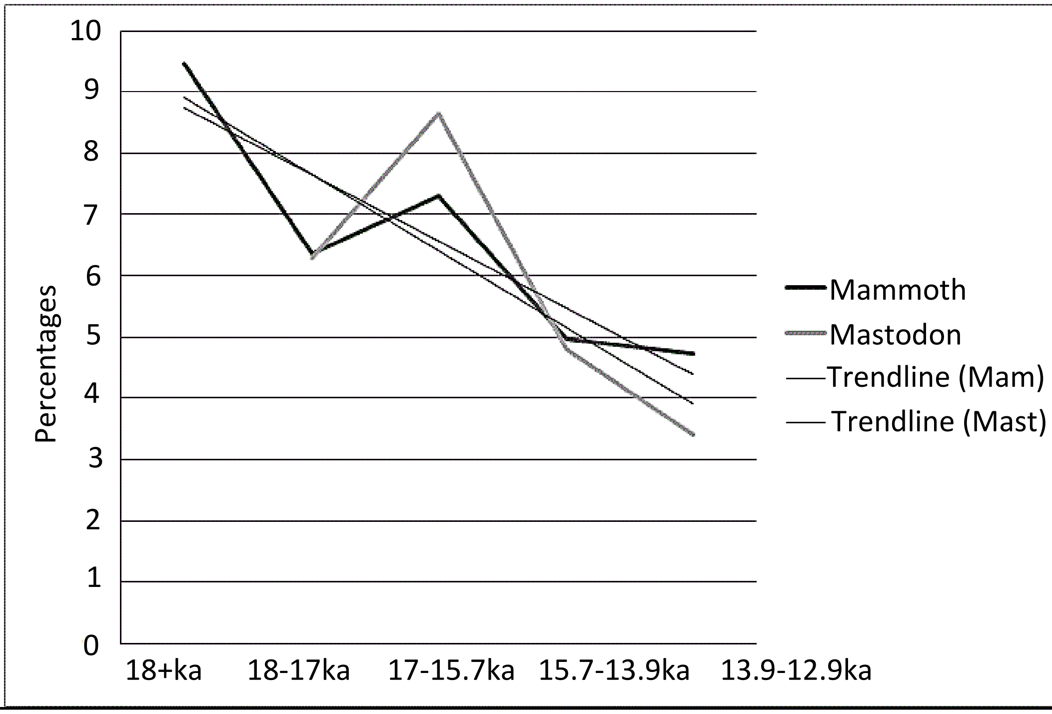

Figure C4: Comparison of Cyperaceae pollen percentages for dated mammoth and mastodon localities.

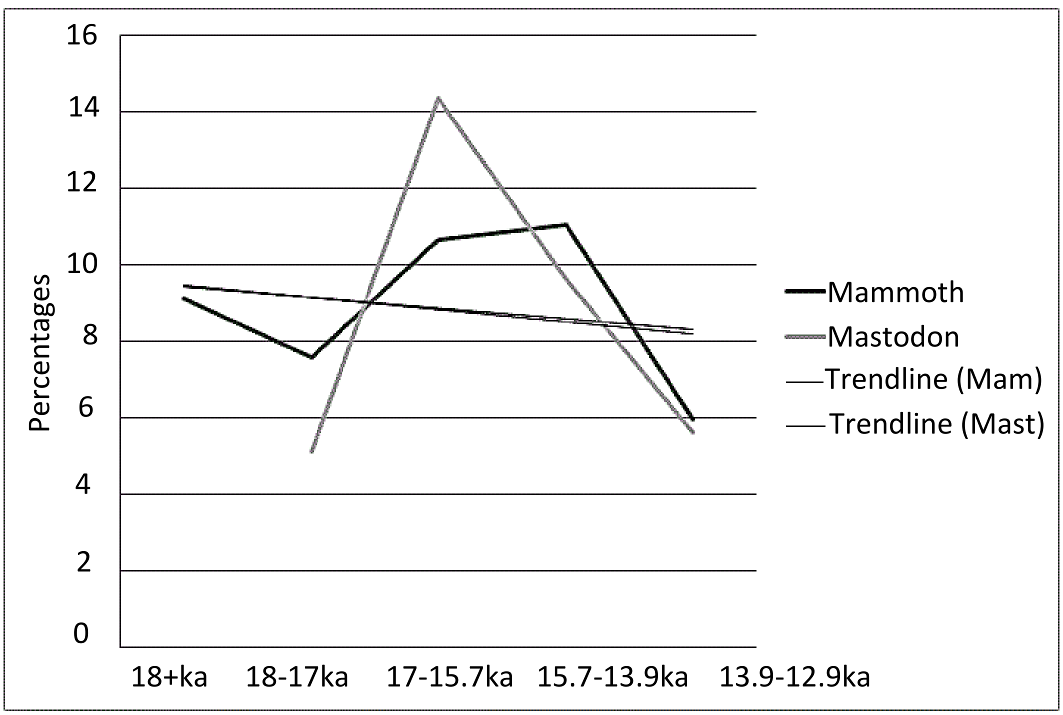

Figure C5: Comparison of *Fraxinus* pollen percentages for dated mammoth and mastodon localities.

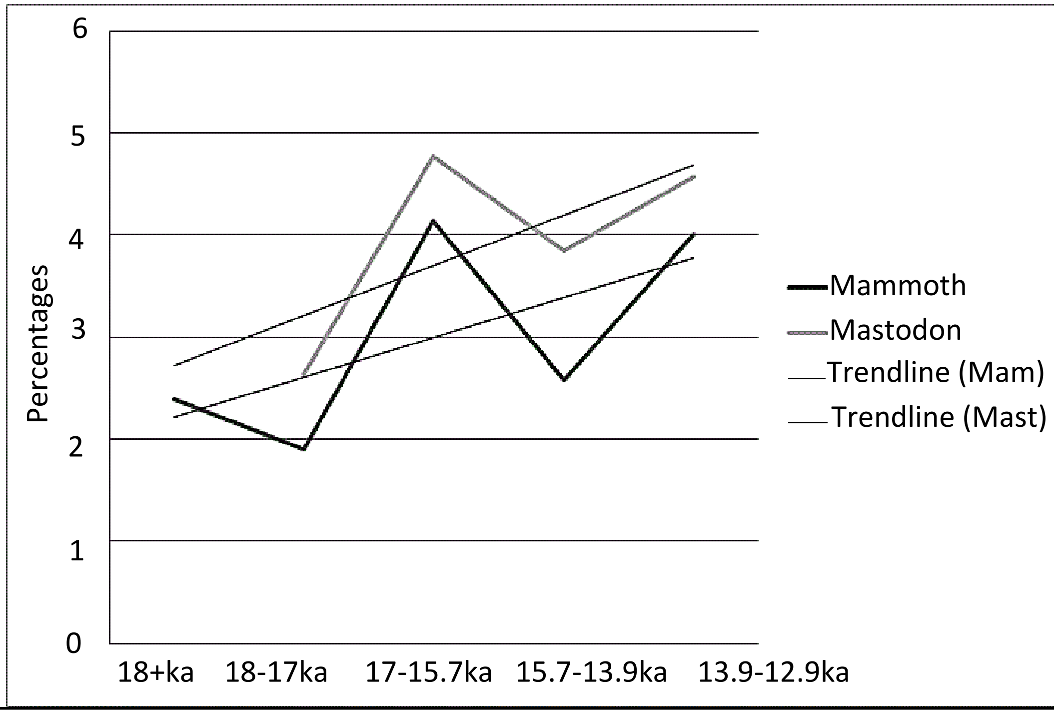

Figure C6: Comparison of *Ostrya*-type pollen percentages for dated mammoth and mastodon localities.

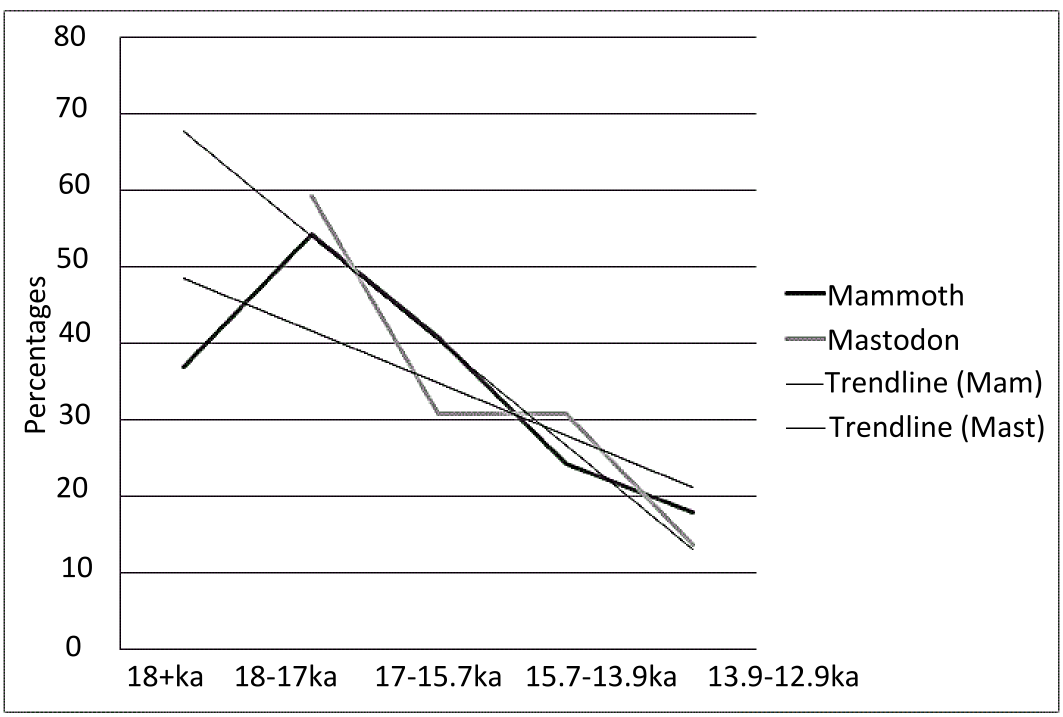

Figure C7: Comparison of *Picea* pollen percentages for dated mammoth and mastodon localities.

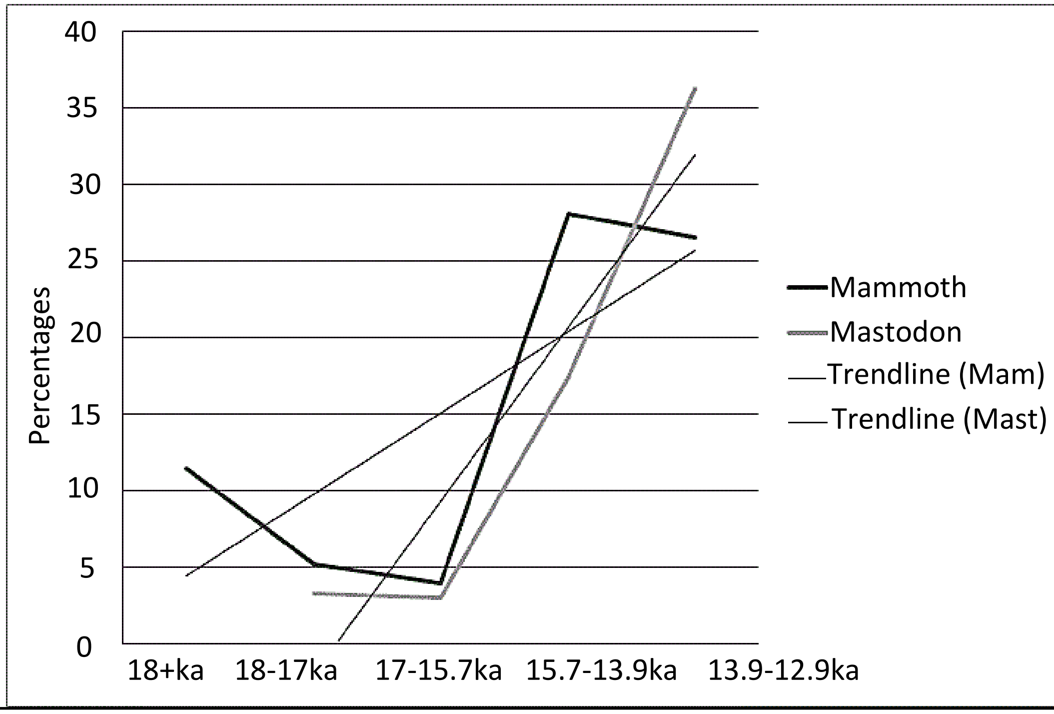

Figure C8: Comparison of *Pinus* pollen percentages for dated mammoth and mastodon localities.

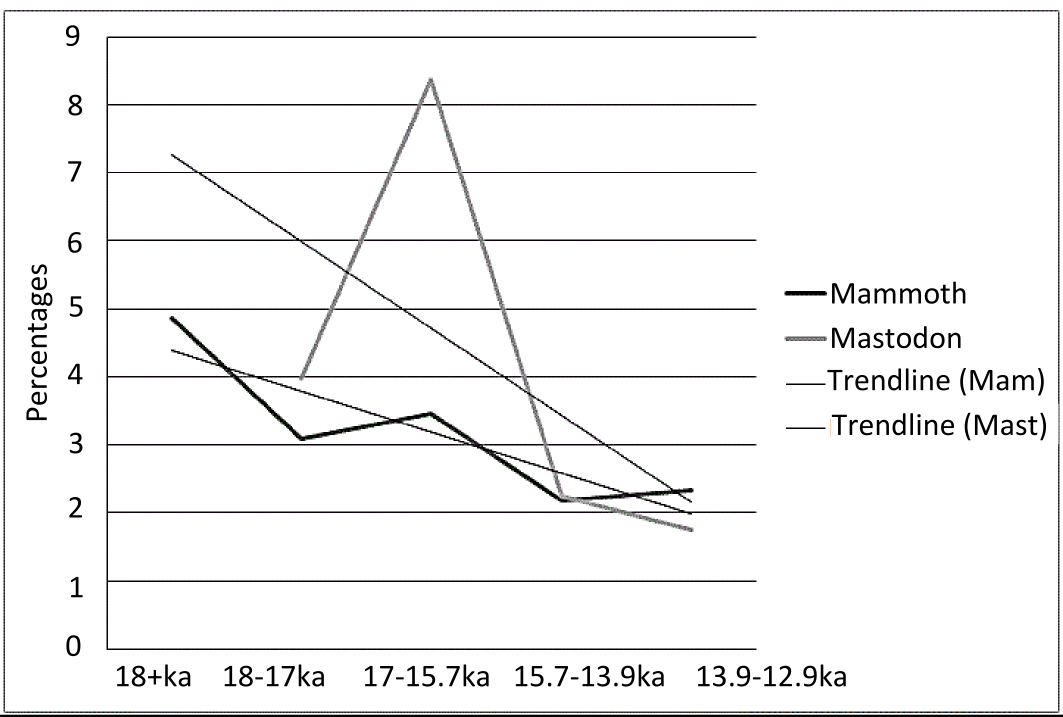

Figure C9: Comparison of Poaceae pollen percentages for dated mammoth and mastodon localities.

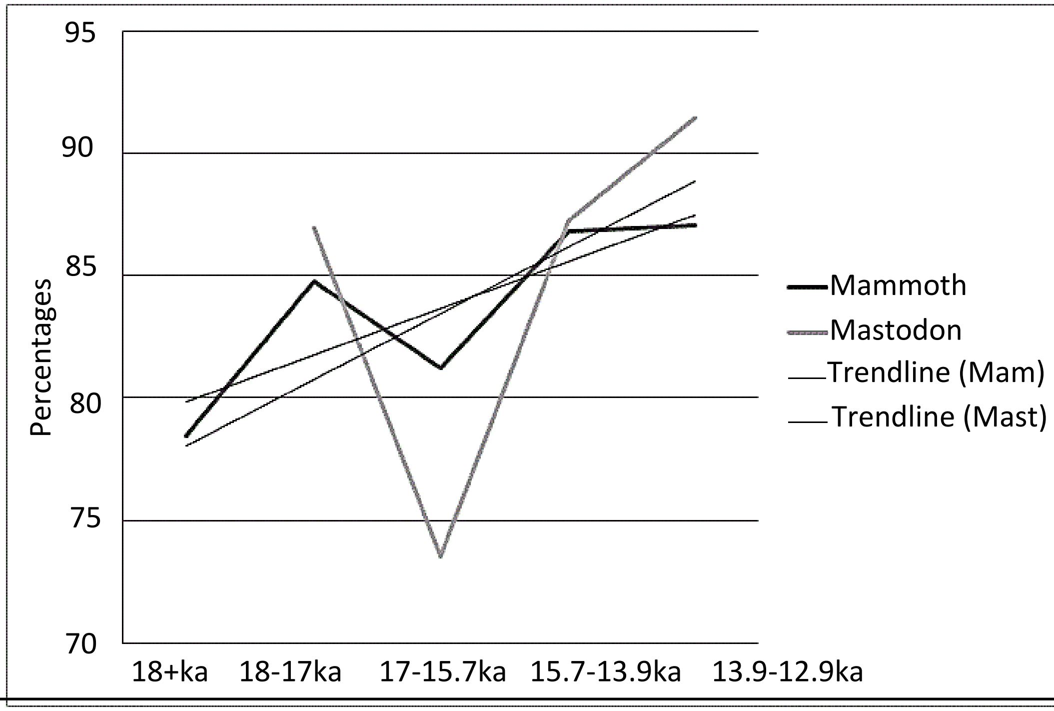

Figure C10: Comparison of AP pollen percentages for dated mammoth and mastodon localities.

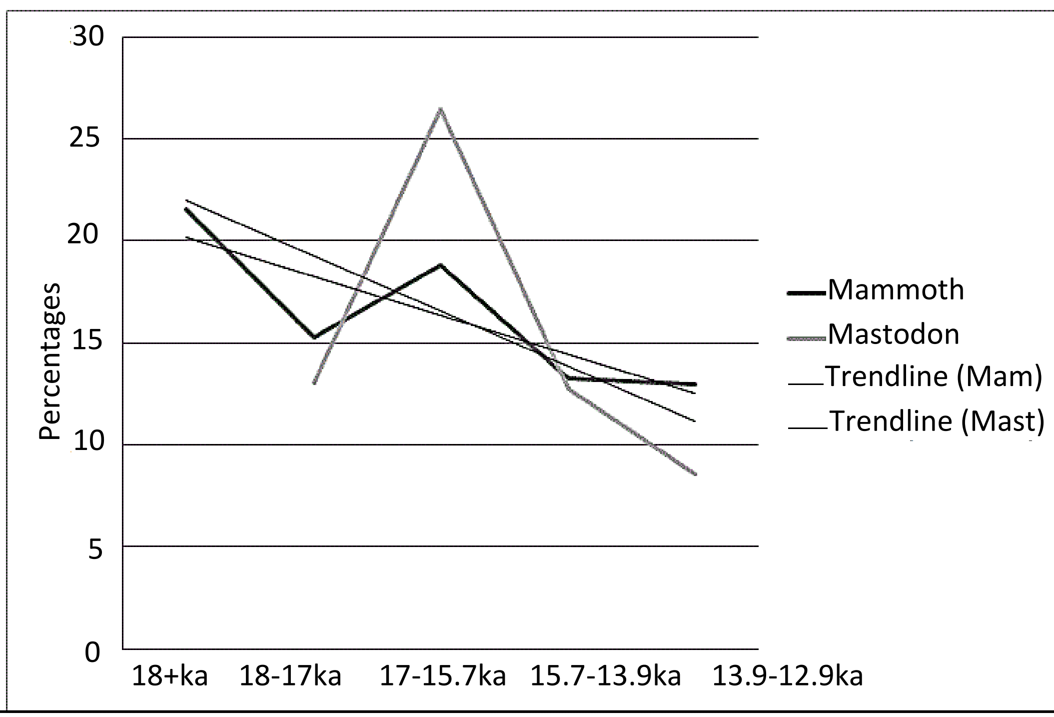

Figure C11: Comparison of NAP pollen percentages for dated mammoth and mastodon localities.

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