LATE HOLOCENE CLIMATE AND VEGETATION CHANGE IN CENTRAL
MICHIGAN

by

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ABSTRACT

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Understanding the effects of drought and temperature change on eastern North America will be key in the context of future climate change. Perhaps the best method to understand how drought and temperature will impact this area is to study its paleoecological record. The records presented here, from Houghton Bog (44°23′4.50″N; 84°44′18.90″W) and Higgins Bog (44°28′58.90″N; 84°47′41.40″W) provide an opportunity to study the effects of drought and temperature on the interior of the Lower Peninsula of Michigan (hereafter central Michigan) during the Late Holocene (c. 4200 cal BP to present day). Pollen, charcoal, and testate amoebae records were analyzed to infer past drought and climate change events, and their effects on the vegetation assemblage. These records will add to the growing body of paleoecological data for the Lower Peninsula of Michigan.

Both Higgins Bog and Houghton Bog are characterized by a mixture of
boreal and deciduous forests, which is mainly dictated by the location of the forest tension zone. Early in their records, both bogs indicate that the area surrounding the bog was a temperate forest composed mostly of Acer, Betula, and Pinus, and both bogs were experiencing fairly dry conditions. At c. 2000 cal BP, both bogs record a significant change in their pollen records, which is reflected in CONISS clustering and DCA analysis. Both sites show a marked decline in temperate taxa at this time, and taxa indicative of early successional stages are abundant. The cause of this disturbance at c. 2000 cal BP is unknown, though it is unlikely to have been humans, as they were not abundant in the area (Howey 2012). After c. 2000 cal BP, temperate taxa recover, and succession continues until c. 1800 cal BP, when a drought event causes temperate taxa to once again decline. From here, a long-term succession towards a boreal taxa dominated forest continues in both sites until European settlement.

Droughts and pluvials overlay this long-term succession, and cause temporary disturbances. After the c. 1800 cal BP event, temperate species decline, and boreal taxa begin to increase, suggesting that while the drought may have temporarily caused many temperate and boreal taxa to decline, the boreal taxa are able to recover and continue to increase in abundance until c. 1000 cal BP. At c. 1000 cal BP another drought event is observed in both bog records. At this point some boreal taxa decline, while others (such as Tsuga) appear only temporarily affected. This may be because of the climatic effects of the Medieval Climate

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Anomaly (MCA), which warmed the area from c. 1000-700 cal BP, which, based on modern day studies, may have strengthened the lake effect and increased precipitation in central Michigan (Burnett et al. 2003). Boreal taxa increase after c. 1000 cal BP, until *Ambrosia* spikes at c. 100 cal BP, marking European arrival.

Prior studies had documented that the climate of the Late Holocene has been characterized by increasing moisture throughout the eastern United States. Within this context; however, several major droughts have been identified in Michigan, centering on 1850, 1800, 1650, 1000, 800, and 700 cal BP. (Booth et al. 2006). In Houghton and Higgins Bog, the 1800 and 1000 cal BP droughts were detected, suggesting a more regional signature for these events than the others. I found that both of these sites have remained very dry throughout their history, as indicated by the testate amoebae records from both sites.

Overall, both of my study sites show little human disturbance until European arrival, although assessment of the period of greatest mound building shows that most of the mounds in central Michigan were built between the c. 1800 and c. 1000 cal BP droughts found in these bogs. Both Houghton and Higgins Bog give insight into the succession of upland forests and bogs in central Michigan, and add to the growing body of evidence of long term succession driven by climate in central Michigan, which may have implications for future climate change.
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DEDICATION

To my parents, for not questioning my childhood friendship with a *Maclura pomifera*, and their continued support ever since.
INTRODUCTION

The Holocene assembly of temperate forests has been driven by millennial-scale climatic trends, such as post-glacial warming (Williams et al. 2000, Gill et al. 2012), and by centennial-millennial scale changes such as the mid-Holocene thermal optimum (Prentice et al. 2000), Medieval Climate Anomaly, and the Little Ice Age (Hotchkiss et al. 2007, Viau et al. 2012, Booth 2012b). Decadal to centennial-scale events are generally not named, but had the capacity to influence species distributions, especially close to the edge of their ranges (Schlesinger and Ramankutty 1994, Hurrell 1996, Ottersen et al. 2001).

Temperature trends have influenced the distribution of temperate and boreal forests throughout the eastern United States. Overall, the eastern United States experienced cooling temperatures for the last c. 3000-2500 cal BP, accompanied by increases in *Picea* (spruce) and *Abies* (fir) (Davis et al. 1980, Gajewski 1988, Williams et al. 2011, Esper et al. 2012, Viau et al. 2012, Marlon et al. 2016). Michigan follows this overall climatic trend towards a cooler climate, with the Late Holocene (c. 4200 calibrated radiocarbon years Before Present; hereafter cal BP) beginning with warmer temperatures (Bernabo 1981). Bernabo documented cool conditions between c. 1450 cal BP and 1150 cal BP, but this reversed with
warming to near modern levels c. 950 - 1150 cal BP, which most likely marks the beginning of the Medieval Climate Event. After this event, conditions cooled once more (Bernabo 1981).

Droughts in the Late Holocene have also had significant impacts on the structure of temperate forests. Drought-induced decreases in soil and atmospheric moisture availability stressed certain temperate tree species, making them vulnerable to other threats, such as invasive species and insects (Rouault et al. 2006). For example, the Tsuga (hemlock) decline over the mid-Holocene is thought to have been caused by a combination of sustained drought and pathogen outbreak (Foster et al. 2006, Booth et al. 2012a). At about the same time, Ulmus (elm) populations in the temperate forests of Europe also experienced a dieback, induced by drought and pathogen outbreak (Waller 2013). Increased tree mortality and reduced moisture often contributed to increased intensity and frequency of fire events in temperate forests, which had major impacts on the overall forest composition. Pinus (pine) and Quercus (oak) appear to have their highest abundances in the past during times of increased fire frequency (Abrams 1992), while Fagus (beech) and Tsuga are negatively affected by increased fire frequency (Clifford and Booth 2015). All of these aspects of drought have increased tree mortality throughout the temperate forests of North America (Van Mantgem and Stephenson 2007). The relationship between drought sensitivity and human activity
in these forests is not known. It may be inferred; however, that if human presence increased the probability of fire in the system, then the combination of people and drought would have elevated the intensity of disturbance above that of an equivalent natural event.

In Michigan, only two drought-induced mortality events have been documented in modern times- one that occurred in the late 1970s-1980s and another in 1984- but droughts are expected to increase in their severity and frequency with future climate change (Millers et al. 1989, Allen et al. 2010). During the late 1970s-1980s a large-scale drought disproportionately impacted *Quercus* spp. and *Carya* (hickory) spp. (Millers et al. 1989). The 1984 drought, in contrast, was a local drought that mainly affected *Acer* spp. (Millers et al. 1989).

Studies in other systems have shown that the droughts of the last two centuries (the period of record for Michigan) do not capture the full scale of droughts experienced in the past few millennia (Woodhouse and Overpeck 1998, Weiss et al. 2009). Past megadroughts, defined as decadal-scale droughts that exceed one standard deviation of natural variability from the long-term mean, have been identified using paleoecological proxies (Booth et al. 2005, Booth et al. 2006, Cook et al. 2007, Hubeny et al. 2011). The effects of these (and other) droughts on vegetation assemblages are observable through the pollen record. Pollen records
throughout North America indicate that some drought tolerant species are able to withstand droughts, while others decline during drought events. This re-ordering of temperate forests can be viewed through the pollen record, and can be used to identify species that may be vulnerable in the future.

Pluvials (anomalously wet periods) also influenced temperate forest structure in North America during the Late Holocene. While the overall trend for the northeastern United States during the Late Holocene has been toward increasing effective moisture, sudden increases in moisture availability can also be seen as disturbances (Marlon et al. 2016). For example, pluvials can increase erosion and/or “drown” plants (Parris et al. 2010). The effects of pluvials on the vegetation of Michigan is often more subtle, but could include: increased lake effect rains or snowfall, winter storms and icing of trees causing forest damage, or the flooding of low-lying sites, and changing soils from oxidative to reduced states (Mitsch 1986). With future climate change expected to strengthen the lake effect of the nearby Great Lakes (Burnett et al. 2003), understanding past increases in moisture, declining temperatures, and their effects on the vegetation becomes a valuable tool for future landuse planning and conservation. Understanding the past climatic conditions and their effects on ecosystems is particularly important for central Michigan, which experiences greater climate extremes than the coastal areas, as it does not benefit as much from the lake effect of the Great Lakes. The two sites
used for this study are situated in central Michigan, and so can provide insight into how this region might respond to future climate change.

The following questions will be discussed in this thesis through the analysis of peat cores from two Bogs in the Lower Peninsula of Michigan:

1) How did drought events affect the vegetation assemblages in central Michigan?

2) How was the vegetation in central Michigan affected by climate anomalies that occurred in the last 3000 years (Medieval Climate Anomaly and Little Ice Age)?

3) Did Native Americans exploit the interior of the Lower Peninsula of Michigan during wet events?

PEAT BOG FORMATION AND DEVELOPMENT

Peat formation occurs through three main processes: infilling (terrestrialization), primary peat formation, and then paludification (Figure 1, Rydin and Jeglum (2006)). Infilling occurs when plant material slowly fills a lake basin, eventually filling the lake. Primary peat formation is when peat forms directly over a wet, mineral rich soil. Paludification refers to the process by which
peat forms over a drier soil; this is the most common process in the northern boreal forests. Once peat bogs form, positive feedback loops promote the continued growth of the peat bog (Ireland and Booth 2012). Peat bog formation appears to be triggered by drought and moisture variability (Ireland and Booth 2011, Ireland et al. 2012, 2013, Booth et al. 2016).

![Figure 1. Processes of peat bog formation. From: Rydin and Jeglum 2006, pg 123.](image)

Once a peat bog is formed, its hydrology and hydroperiod become very important to its continued development. Peat bogs receive their moisture input either through groundwater and/or rivers (minerotrophic peat bogs) or from
atmospheric moisture (ombrotrophic peat bogs). Peat bogs in Michigan (a glaciated, sub-boreal region) can vary dramatically in their hydrology, with precipitation, groundwater, and stream inputs all contributing to the hydrological signal. Ombrotrophic bogs, which only receive moisture from precipitation, can provide the cleanest signal of past precipitation change, and so are the focus of most peat bog studies in Michigan (Booth 2002, Charman 2007, Booth 2008).

In a glaciated, sub-boreal region such as Michigan, the hydroperiod of peat bogs can also vary dramatically both annually and within a season (Booth 2008). This is especially true of ombrotrophic peat bogs, as their only input to their water table is precipitation, which is episodic (Rydin and Jeglum 2006). Peat bogs in Michigan often show this variability, with changes in the vertical distance to the water table depth having been measured as anywhere from 0 cm to 41 cm within a four week period (Booth 2002). Consequently ombrotrophic bogs in Michigan may or may not have standing water and their water table may reflect a mixture of regional and local signals (Booth 2008).

CLIMATE OF MICHIGAN

Quasi-periodic climate events that influence the climate of the Lower Peninsula of Michigan include the North Atlantic Oscillation (NAO), and the
Atlantic Multidecadal Oscillation (AMO). Annual climatic events that influence the climate of the Lower Peninsula of Michigan are lake effect of the Great Lakes and the polar jet stream.

PERIODIC CLIMATIC EVENTS

The NAO influences temperature and precipitation of eastern North America, especially during the boreal winter (Stenseth et al. 2003). The position of the NAO is determined by the strength of the Icelandic low pressure center relative to that of the Azores high pressure center. When the NAO index is positive, i.e. there is a larger than average pressure differential between the two stations, the westerlies are strong, the Atlantic jet stream intensifies, and the storm track shifts northward (Hurrell 1996). The NAO does not have a defined periodicity, but variability in the NAO causes variability in the direction and magnitude of the westerlies (Ottersen et al. 2001). This variability is particularly visible in northern Europe, but is also thought to have influenced temperature and precipitation in North America. For instance, during a positive NAO phase, temperatures typically warm across North America, although precipitation trends can vary (Ottersen et al. 2001, Trouet et al. 2009). In the Great Lakes region, the NAO has the greatest impact on Great Lakes ice cover. The Great Lakes tend to have lower ice cover
during positive NAO phases, and higher ice cover during negative NAO phases (Bai et al. 2012). This in turn affects the thermal insulation and lake effect snow of the Great Lakes, which influences regional climate.

The Atlantic Multidecadal Oscillation (AMO) is another large scale climate pattern that has affected North American climate. Over the past 8,000 years, the AMO has shown a persistent c. 55-70 year oscillation, which in turn has affected the climate of northeastern North America (Knudsen et al. 2011). This oscillation is shown in the changes of sea surface temperatures (SSTs) in the North Atlantic Ocean. The AMO index, which is used to identify warm and cold phases of the AMO, is calculated from a combination of the global mean SST anomalies and the North Atlantic SST anomalies (Knudsen et al. 2011).

The effects of the AMO are greatest during the boreal summer in northeastern North America (Hu and Feng 2012). In particular, warm phases of the AMO are associated with warm temperatures and increased drought frequency over North America (Sutton and Hodson 2005). A recent AMO warm phase was that of c. 1930-1960 (Gray et al. 2004, Sutton and Hodson 2005, Knudsen et al. 2011). During this time precipitation was reduced by 20% (0.1 to 0.3 mm/day) over the southern United States, and is coincident with the “Dust Bowl” (Sutton and Hodson 2005, Nigam et al. 2011). Variation in solar activity and the ocean’s thermohaline
circulation are thought to influence the warm and cool phases of the AMO (Schlesinger and Ramankutty 1994, Cubasch et al. 1997, Velasco and Mendoza 2008). The AMO and the NAO are known to have been active components of Holocene climate for at least 4200 years (Cook et al. 1998, Knudsen et al. 2011) and may have shaped the vegetation assemblages of the Lower Peninsula of Michigan throughout that time.

ANNUAL CLIMATIC EVENTS

The main air mass over northeastern North America is a continental polar air mass that is influenced by the position of the Northern Hemisphere (NH) polar jet stream (Blackmon et al. 1977). The air in a continental polar air mass tends to be cold and dry. In the boreal summer, the polar jet stream moves northward, moving the continental polar air mass northward, which warms northeastern North America. In the boreal winter, the polar jet stream moves south, bringing cold, dry air to northeastern North America. The magnitude of the shifts in the NH polar jet stream changes over time, and with modern climate change, the NH polar jet stream is shifting more poleward (Archer and Caldeira 2008). It is the mean position of the southern boundary of this arctic air in winter that defines the division between temperate and boreal forest system. Today this boundary occurs
at c. 43° latitude in Michigan (Figure 2).

Figure 2. Vegetation map of the Lower Peninsula of Michigan. From Webb 1974, Figure 2. Forest tension zone is shown at c. 43°, with the change from an Elm, Ash, Birch, Cottonwood and Beech, Maple forest to a more Pine dominated forest.

Evaporation from the Great Lakes induces an increase in downwind, lake-effect, precipitation. Lake effect brings a large amount of precipitation to the western and northern coastal regions of the Lower Peninsula Michigan. Because in winter, this moisture arrives as snow it insulates the soil from arctic air masses. The
effect of this insulation is that it keeps the coastal soils warmer than those of the interior during winter (Schaetzl et al. 2005). Consequently, the lake effect creates an important soil and air temperature gradient from the warmer coastal areas to the colder, less insulated inland areas. This gradient is thought to have played an important role in the habitability of the central region of the Lower Peninsula. For pre-Columbian populations, the lake effect made the coastal areas more habitable than the inner regions; for example, maize agriculture was feasible in the coastal regions of Michigan, but not in the inner areas (O'Shea 2003).

Warm winters in the lake-effect zone translate to longer growing seasons. The annual snowfall for the Lower Peninsula of Michigan increases with warmer winter air temperatures, the increased snowfall results in a deeper snowpack that provides stronger insulation. Buried by lake effect snow, soils stay cooler longer in the spring, but the warmer fall temperatures near the lake slow the cooling of soil in the fall (Burnett et al. 2003, Schaetzl et al. 2005). The soil and air temperature gradient from the coastal areas to central Michigan could have negatively impacted the interior region during a regional drought. The wetter environment receiving lake effect rains may have been more buffered against drought than the drier interior. Thus, drought may have had a large impact on the vegetation assemblages in the interior of Michigan.
Throughout the Late Holocene, the Lower Peninsula of Michigan was characterized by a mixture of boreal and deciduous forests. Common boreal taxa included: *Abies* (fir), *Betula* (birch), *Picea* (spruce), *Populus* (poplar), and *Tsuga* (hemlock). *Pinus* (pine) and *Betula* could occur in any setting. Temperate forests tended to be rich in *Acer* (maple), *Fagus* (beech), *Fraxinus* (ash), *Nyssa* (tupelo), *Quercus* (oak), *Tilia* (basswood), and *Ulmus* (elm) (Whitney 1987, Hupy and Yansa 2009, Goring et al. 2015b). Early and mid-succession taxa were *Nyssa*, *Populus*, *Pinus*, and *Quercus* (Bazzaz, 1968, Munoz and Gajewski, 2010, Williamson, 1975). Mature forests were dominated by *Acer, Betula, Fagus*, and *Tsuga* (Williamson, 1975). These species occurred in various combinations and abundances throughout the state, forming assemblages that changed through time (Hupy and Yansa 2009). The forest tension zone, where deciduous forests gave way to boreal forest, showed geographic variability across Michigan during the Late Holocene (Hupy 2012). The relative location of the forest tension zone was driven by temperature, moving as much as 150 km north during warm events and 170 km south during cool times, for a variation of c. 320 km over the last 10,000 years (Hupy 2012).

In the last 4200 years both temperature and precipitation patterns were
variable. Temperature within the Michigan peninsula remained fairly stable between c. 4200 and 3000 cal BP. At c. 3000 cal BP, Michigan became cooler and wetter (Dorale et al. 1992, Singer et al. 1996, Finkelstein et al. 2005). *Tsuga*, while present in the upper peninsula of Michigan since c. 5000 cal BP, became much more abundant in the upper peninsula at c. 3000 cal BP, possibly due to the wetter climatic conditions (Davis et al. 1986, Brugam et al. 1997). Even with the lake effect insulating the coastal areas, the small shift in climate c. 3000 cal BP caused a detectable vegetation shift. Peat bog records indicated that *Betula alleghaniensis* (yellow birch) started to expand into the Lower Peninsula of Michigan (Booth et al. 2002, Booth et al. 2004). As *Betula alleghaniensis* saplings are particularly drought-intolerant this expansion also suggested that conditions were becoming wetter, (Godman and Krefting 1960). Soon after the expansion of *Betula alleghaniensis*, mesic taxa such as *Abies, Acer, Fagus, Picea,* and *Tsuga,* began to increase in abundance within the Lower Peninsula of Michigan. Other changes in the vegetation of Michigan are discussed in more detail below.

**VEGETATION SURVEYS**

The first European surveys of Michigan (A.D. 1785-1907), documented the vegetation before widespread European settlement (Whitney 1987, Hotchkiss et al.
2007, Paciorek et al. 2016). Models created using Public Land Survey (PLS) data (commonly referred to as witness tree data) predicted that the pre-settlement Michigan forest was dominated by *Quercus*, with *Fagus* as an important component in the southern half of the peninsula. In the colder, northern half of the peninsula *Tsuga, Acer*, and *Pinus* (Goring et al. 2015b) indicated the presence of the transition to boreal forest. Specifically, survey notes indicated that *Tsuga, Pinus strobus*, and *Populus* dominated wet-mesic sites in pre-settlement Michigan (Leahy and Pregitzer 2003). Today *Acer saccharum, Betula papyrifera* (paper birch), and *Quercus* spp. dominate these sites (Leahy and Pregitzer 2003). Clearance of the pre-Columbian forests began c. 1870, with almost no stands of natural forest remaining by c. 1920 (Whitney 1987).

**CLIMATE ANOMALIES AND VEGETATION SHIFTS**

Despite the prevailing cool, wet conditions, two interesting climate anomalies occurred within the last 3000 years. These climate anomalies were particularly important, as they are the most recent examples of natural climate change in North America (Marlon et al. 2016): the Medieval Climate Anomaly (MCA, c. 1000-700 cal BP) and the Little Ice Age (LIA, c. 600-250 cal BP). Both of these events were underlain by changes in the position of the NAO, which was
most likely caused by changes in solar radiation (Trouet et al. 2009, Marlon et al. 2016).

The MCA induced several drought events, specifically at 1000, 800, and 700 cal BP, which were identified through analysis of testate amoebae in ombrotrophic peats (Figure 3, Booth et al. (2006)). These droughts are associated with major changes in the vegetation of Michigan, such as increases in Pinus and decreases in Fagus (Booth et al. 2006, Booth 2012b). Quercus, Ulmus, and Fraxinus also increased from c. 1000-800 cal BP, and show an overall positive correlation with temperature (Bernabo 1981). The droughts at 1000, 800, and 700 cal BP were widespread, affecting areas across North America (Willard et al. 2003, Cook et al. 2004).
The LIA caused a slight cooling of North America right after the MCA. The eastern United States experienced an overall decline in *Fagus* and *Tsuga*, and an increase in open areas during the cooler temperatures of the Little Ice Age, although this decline may have been influenced by other factors (Fuller et al. 2006). The LIA induced cooling of eastern North America may be one of the driving factors behind a major switch in the vegetation that occurred in several records at
500-600 cal BP (Booth 2012b, Paquette and Gajewski 2013, Clifford and Booth 2015). *Betula, Pinus, Picea,* and *Tsuga* all increased in abundance after c. 500 cal BP, and were negatively correlated with temperature throughout the Lower Peninsula of Michigan (Bernabo 1981). Vegetation shifts during the LIA were similar to those that occurred at c. 3000 cal BP (Clifford and Booth 2015).

Minden Bog, a peat bog located in the Lower Peninsula of Michigan near Lake Huron, contained a detailed testate amoebae record of the Late Holocene. The analysis of Minden Bog fossil amoebae revealed several major hydrological shifts, which in turn affected the vegetation (Booth and Jackson 2003). At c. 3200-2300 cal BP and at c. 1900-1300 cal BP, Minden Bog experienced an increase in moisture. After c. 1300 cal BP there was a decline in moisture that continued until the present day (Booth and Jackson 2003).

The vegetation assemblages throughout the Lower Peninsula of Michigan also shifted with the changes in moisture. *Picea* increased during drier periods, and decreased during the long highstand between c. 1900 and 1300 cal BP (Booth and Jackson 2003). *Fagus* also was sensitive to the changes in moisture observed at c. 3200 and c. 1900 cal BP; however, *Fagus* tended to increase during wet periods, and decrease during dry periods. During the MCA (a dry period for Michigan), *Pinus* abundances increased over the entire Lower Peninsula of Michigan. *Quercus*
behaved in a similar way to *Pinus*; however, it was less spatially consistent than *Pinus* (Booth 2012b). *Fagus* also declined throughout the MCA. A decline in *Fagus* and increase in *Pinus* and *Quercus* at c. 1200-1000 cal BP was recorded in other bogs in the Lower Peninsula of Michigan (Figure 4). No definite reason for this transition was given in the paper; it is simply “associated with the Medieval Climate Anomaly” (Hupy 2012, pg 483). The causes of this specific forest transition have been largely unexplored.
Figure 4: Fossil pollen evidence of forest succession in two lakes from the Lower Peninsula of Michigan. Data from Hupy, 2012, accessed through the Neotoma database (Goring et al. 2015a). Pollen diagrams showing the forest succession from two inland lakes in Michigan (Left: Cowden lake, Right: Demont Lake). The yellow line highlights the change from an *Acer/Fagus* forest to a more *Pinus/Quercus* forest at both sites. At Demont Lake, Poaceae also increases at the same time, indicating an opening in the forest.

THE ROLE OF FIRE IN MICHIGAN ECOSYSTEMS

Charcoal serves as a proxy for fire, which is an important part of boreal/temperate ecosystems in Michigan. Fire return intervals (FRIs) are particularly important in maintaining forest structure. *Betula, Carya* (hickory),
most *Pinus* species (e.g. *Pinus banksiana* and *Pinus resinosa*), and *Quercus* have fire resistant traits, and so often outcompete other species (such as *Acer*, *Fagus*, and *Tsuga*) when fire is frequent in the landscape (Abrams 1992, Foster et al. 2004). *Pinus* dominated ecosystems are generally maintained by low-to-mixed-severity surface fires (Bergeron et al. 2004, Drobyshev et al. 2008), while fewer fires favor deciduous species (Whitney 1987).

The sensitivity of *Fagus* to climate changes, especially moisture and fire regime, has been documented at a number of Michigan sites (Davis et al. 1986, Minckley et al. 2012, Booth 2012b). *Fagus* pollen increased during the wetter periods, and declined from c. 1000 cal BP to present. This last decline was coincident with the onset of the MCA. Charcoal was also shown to increase around the same time (Booth and Jackson 2003). The overall decline of *Fagus* and increase in charcoal indicated a decrease in moisture in this area since 1000 cal BP, which resulted in an increase in wildfires and the expansion of *Pinus*.

FRIs in pine-dominated and deciduous forests can vary drastically, especially in a heterogeneous landscape, such as central Michigan. In fire-prone areas, such as areas with understory brush and dry soils, FRIs can be anywhere from 10-100 years. In moist uplands; however, FRIs have been identified as over 1000 years (Foster et al. 2004). These different forests often existed close to each
other, and even areas with long FRIs were still shaped by fire (Foster et al. 2004). One study found that when comparing a *Pinus resinosa* (red pine) dominated forest with a nearby mixed forest, FRIs were identified as c. 6 years per fire for both forest types (Nyamai et al. 2014). A more regional study of the northwestern area of Michigan showed that forests dominated by *Pinus resinosa* had a FRI of c. 12 to 32 years, while more mixed forests had a FRI of c. 14-24 years (Drobysh et al. 2008). These fire return intervals were often shortened markedly with the beginning of European settlement, as fires were often used to clear land and maintain it in an early successional state (Drobysh et al. 2008).

**PLUVIALS**

Throughout NE North America, there has been a general increase in moisture during the last c. 3000 years (Marlon et al. 2016). In Michigan, pluvials have been identified at c. 3200-2300 cal BP and c. 1900-1300 cal BP (Booth and Jackson 2003). *Picea* decreased during the later wet period, and increased during drier periods. *Fagus* also declined during dry periods, while *Pinus* and *Quercus* increased slightly (Booth and Jackson 2003). These periods of increased moisture indicate times when drought sensitive species, such as *Fagus* and *Picea* were able
to maintain substantial populations in the temperate forests of Michigan.

DROUGHTS

The most widespread drought in the northeastern United States occurred c. 1400-1200 cal BP (Marlon et al. 2016). Michigan specifically has experienced several drought events during the Late Holocene. Six major droughts, all between 2100 and 600 cal BP, have been identified through a variety of proxies in Michigan (Booth et al. 2006). Major droughts centered on 1850, 1800, 1650, 1000, 800, and 700 cal BP have been recorded in the testate amoebae record (Booth et al. 2006, Booth 2012b). Of these droughts, the three latest were the most severe, and all occurred during the MCA. Temperature estimates based on tree ring, ice core, coral, sediment, and speleothem data indicated that the Midwest region warmed by about c. 0.3 to 0.5° C during the MCA (Mann et al. 2009). Precipitation and moisture estimates were determined through testate amoebae.

TESTATE AMOEBAE

Testate amoebae are an accepted means to determine moisture conditions in paleoecosystems, as they are highly sensitive to changes in moisture, particularly in
ombrotrophic bogs (Charman 2001, Booth 2002, 2010). Testate amoebae are single celled protists that grow a hard outer shell, called a test, to protect themselves (Ogden and Hedley 1980, Charman 2001). They live on the roots of *Sphagnum* mosses, with different species living on different parts of the roots. Testate amoebae are particularly useful for paleoecological studies because of their distinctive tests and typically good preservation, which makes it possible to identify them to species. Beyond their distinct morphologies, testate amoebae are also sensitive to changes in the water table depth, with indicator species reflecting a narrow range of moisture conditions.

Several Michigan bogs have provided records of testate amoebae, leading to inferred quantification of past moisture variability. Records of testate amoebae indicate a large scale regional drought at c. 4200 cal BP, and then wetter conditions beginning c. 3000 cal BP (Booth et al. 2005). The amoebae also indicated abruptly lowered water-tables and inferred droughts centered on 1850, 1800, 1650, 1000, 800, and 700 cal BP (Booth et al. 2006). Low moisture levels have also been identified at c. 300 and c. 100 cal BP in Michigan (Booth et al. 2004). Over the last c. 1300 cal BP; however, there has been an overall trend towards wetter conditions (Minckley et al. 2012).

Within the Great Lakes region, pollen and testate amoebae records are used
to determine drought events and the comparison of data provides an assessment of the effects of drought on the vegetation. Pollen records at sites in Michigan indicated that during droughts, *Fagus* tends to decrease in abundance, *Pinus* tends to increase, and *Quercus* decreases in central Michigan, but increased in the southern areas. While some of these changes are attributed to climate and drought events, the *Fagus* decline throughout the region is not completely explained by drought (Booth 2012b). One other possible explanation of the changes in the composition of Michigan forests is human activity.

**HUMAN OCCUPATION OF MICHIGAN**

Humans have occupied the Great Lakes region since the end of the Pleistocene Epoch (Howey 2012). For much of this history, Native Americans in Michigan were nomads because there was no way to cultivate a reliable food source (Howey 2007). A nomadic lifestyle allowed them to maintain a constant food source all year round, despite the harsh weather conditions and short growing season.

The nomadic lifestyle eventually ended with advent of agriculture, and the development of defined cultural boundaries (Howey 2007). One way Native Americans defined cultural boundaries was to build mounds and earthworks.
Recent archaeological excavations have documented burial mounds, many barely more than 1 m high in the interior of peninsular Michigan (Figure 5, (Howey and O'Shea 2006, Howey 2012, Howey et al. 2016)). These earthworks have been interpreted to indicate that Native Americans had permanent boundaries and widespread settlements in central Michigan by A.D. c. 1000/1100 (c. 850/950 cal BP), and that these permanent boundaries persisted until c. A.D. 1600 (c. 350 BP). Humans may have exploited the warmer conditions of the MCA, taking advantage of the warmer climate to build permanent settlements in central Michigan.

In any permanent settlement, humans need access to a constant supply of food. Fishing and hunting were available all year round, as well as a variety of natural food resources, such as walnuts, acorns, chestnuts, and berries that also supplemented the fish and wild game (Abrams and Nowacki 2008, Hart and Lovis 2013). In addition to natural resources, agriculture could have provided the necessary food supply to support a large Native American community. *Zea mays* (maize) was introduced to the region around A.D. 500 (c. 1450 cal BP), and became widespread by c. A.D. 1000 (Crawford et al. 1997, O'Shea 2003, Boyd and Surette 2010). Maize has been found in various mound sites and cache deposits. Specifically, maize has been found and dated in mounds near large inland lakes, such as Houghton Lake and Higgins Lake, and dated to around A.D. 1030-1240 (c. 920-710 cal BP) (Howey 2012). The addition of maize to the Native American diet
also influenced their cultural rituals and tribal identities (Howey 2012).

Figure 5: Map of archeological sites and lakes/bogs in Michigan with pollen data available. Lakes and bogs with pollen data are shown in blue letters. Archeological sites are in brown and dark blue. Many of these archeological sites are located within central Michigan.

Crop taxa are a useful indicator of human influence in an ecosystem and
changes in cultural identities. Common Native American crop taxa found in the Great Lakes region include: *Cucurbita* (squash), *Zea mays* (maize), and *Zizanica aquatica* (wild rice) (Hayes et al. 1989, Crawford et al. 1997, Monaghan et al. 2006). Of these three taxa, *Zea mays* is the most cited as culturally significant, and is easily identifiable in the pollen record.

Sediment cores raised from Higgins and Houghton Lakes exhibited slumping and reworking, with consequent problems in deriving a robust chronology (^{14}C dates are provided in Appendix 1). Rather than pursue what appear to be compromised archives, I investigated the stratigraphic record provided by two peat bog systems that had developed near the lakes. Peat bogs preserve a highly localized signal, and so unless maize was growing on the bog or right next to it, it is unlikely to have been preserved in these particular pollen records.

Another ecological indicator of human influence is charcoal evidence. Fire plays a role in the vegetation shifts observed in the paleoecosystems of Michigan. The extent to which Native Americans influenced fire regimes is debated (Clark and Royall 1995, Booth and Jackson 2003). Charcoal analysis at a known archeological site in Ontario determined that the highest rate of charcoal accumulation, with the exception of European settlement, occurred from A.D. 1360-1650 (590-300 cal BP) (Clark and Royall 1995). This finding led to the
inference that Native Americans were using fire to influence the landscape. Yet
droughts can also cause natural fires. For example, a brief, high magnitude dry
event around 4000 cal BP caused widespread wildfires in Michigan (Booth et al.
2005). Fires, especially where the bog surface burns, can be registered in peat archives, but in general lakes are preferred over bogs to establish detailed fire chronologies (Booth 2012b).

Finally, studies of forest succession can show Native American impacts on
an area. Prior studies showed that within the Great Lakes region, Native Americans created small-scale clearings, which caused the succession of an *Acer/ Fagus* forest to a *Pinus/Quercus* forest, as well as an increase in *Ambrosia* (ragweed), *Artemisia* (sagebrush), *Rumex* (docks and sorrels), and other taxa associated with human disturbance (Munoz and Gajewski 2010). Any agricultural activity could potentially have had a substantial impact on the landscape, causing successional changes in the vegetation (Munoz et al. 2010). Due to the short growing season and lack of adequate precipitation; however, it is more likely that these small openings in the forest were created by droughts rather than maize agriculture.
HYPOTHESES

Hypothesis 1: Mature (Boreal) forest taxa will decrease in abundance at times of known drought in the Lower Peninsula of Michigan (1850, 1800, 1650, 1000, 800, and 700 cal BP), and will be replaced with early and mid-successional taxa (temperate and open area taxa).

Hypothesis 2: Charcoal peaks will align to lowest water tables (most drought) indicated by testate amoebic indices.

Hypothesis 3: Mounds and earthworks in central Michigan were built during wet periods.
SITE DESCRIPTION

Six cores were originally collected from a peat bog near Houghton Lake (hereafter Houghton Bog) and a peat bog near Higgins Lake (hereafter Higgins Bog). Sites were selected using Google Earth, geologic surveys, and distance from the Native American mounds. These sites experience 70-100 frost-free growing days (Van Den Brink et al. 1971). The mean annual temperature is 5.5 °C, with the low being -8.5 °C and the high 19.6 °C (MRCC 2014). Both peat bogs formed through infilling, and were most likely once part of the larger lakes. Both peat bogs also receive their moisture from precipitation; that is, they are ombrotrophic bogs.

Houghton Bog is located approximately 5 km northwest of the nearest Native American mounds at Houghton Lake (Figure 6). Shrubs from the Ericaceae family growing on a moist surface comprised of Sphagnum mosses dominate the bog. Polytrichum (haircap moss) species are also present in the surface moss cover, and pine (Pinus strobus) and spruce (Picea glauca) dot the landscape. Other shrubs include Rhododendrom tomentosum (marsh labrador). This bog is surrounded by a forest, which includes Acer, Betula, Fagus, Quercus, Picea, and Pinus. The bog also has small peninsulas of higher ground partitioning it. The bog and surrounding forest are not obviously disturbed by human activity.
Higgins Bog is located approximately 12 km east of the Native American mounds associated with Higgins Lake (Figure 7). This site is much larger than Houghton Bog. The vegetation in this bog is very similar to the vegetation found at the previous location. Pinus and Picea species, as well as various grass and sedge species (such as Eriophorum) are scattered throughout Higgins Bog. This site also contains patches of marsh, which hold more standing water than the bog area and contain more grass species. A forest similar to the one at Houghton Bog surrounds
Higgins Bog. In contrast to Houghton Bog, this site appears to be dominated by *Acer* and *Picea* species. Both the forest and the bog are relatively undisturbed by human activity.

Figure 7. Map of Higgins Lake. Location of the drilling sites (marked as Core 1, Core 2, and Core 3) in relation to the nearest mounds (marked as 20R08) by Higgins Lake.
MATERIALS AND METHODS

CORE COLLECTION

Cores were collected using a Russian Borer, developed by Aquatic Research Instruments. The borer collected cores up to 0.5 m long, and was pushed down into the peat by adding extensions to the borer. Coring occurred until the borer hit sand (which made further progress impossible).

Once the core was brought back up to the surface, the core was removed from the borer, and placed in precut PVC pipes. Each core was then photographed and measured. Field extrusion occurred when the core appeared too fragile to be transported safely. The cores and PVC pipes were then labeled and wrapped with plastic wrap. Extrusions were sectioned at 1 cm intervals and the subsamples placed in Whirlpack bags.

Three cores were collected from each bog (Table 1, Figures 6 and 7) at a distance of c. 15 m from each other. The longest core from each site was selected as the pollen core, and the second longest core from each site was selected as the charcoal and amoebae core (Table 2). A single core would not provide sufficient sedimentary volume to support all analyses. The second longest and longest cores
(Cores 2 and 3 for both sites) were then stratigraphically cross-correlated using changes in the sediment from sand to peat.

Table 1. Location of cores collected from Houghton and Higgins Bog

<table>
<thead>
<tr>
<th>Houghton Bog</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Higgins Bog</th>
<th>Latitude</th>
<th>Longitude</th>
</tr>
</thead>
<tbody>
<tr>
<td>Core 1</td>
<td>44°23'2.60&quot;N</td>
<td>84°44'17.40&quot;W</td>
<td>Core 1</td>
<td>44°29'16.60&quot;N</td>
<td>84°47'28.00&quot;W</td>
</tr>
<tr>
<td>Core 2</td>
<td>44°23'4.80&quot;N</td>
<td>84°44'18.30&quot;W</td>
<td>Core 2</td>
<td>44°28'58.60&quot;N</td>
<td>84°47'40.40&quot;W</td>
</tr>
<tr>
<td>Core 3</td>
<td>44°23'4.50&quot;N</td>
<td>84°44'18.90&quot;W</td>
<td>Core 3</td>
<td>44°28'58.90&quot;N</td>
<td>84°47'41.40&quot;W</td>
</tr>
</tbody>
</table>

Table 2. Cores collected from Houghton and Higgins Bog

<table>
<thead>
<tr>
<th>Houghton Bog</th>
<th>Proxy</th>
<th>¹⁴C Dates</th>
<th>Higgins Bog</th>
<th>Proxy</th>
<th>¹⁴C Dates</th>
</tr>
</thead>
<tbody>
<tr>
<td>Core 1</td>
<td>Archive</td>
<td>None</td>
<td>Core 1</td>
<td>Archive</td>
<td>None</td>
</tr>
<tr>
<td>Core 2</td>
<td>Pollen</td>
<td>2</td>
<td>Core 2</td>
<td>Pollen</td>
<td>2</td>
</tr>
<tr>
<td>Core 3</td>
<td>Charcoal and Amoebae</td>
<td>2</td>
<td>Core 3</td>
<td>Charcoal and Amoebae</td>
<td>1</td>
</tr>
</tbody>
</table>

AGE MODEL

The age model for Houghton Bog core 2 was based on two ¹⁴C dates and the well-documented spike in *Ambrosia* pollen, a weed signaling forest clearance by European colonists (Brugam 1978). In this area the *Ambrosia* spike is well-
constrained at c. A.D. 1850 (Booth et al. 2004). The age model for Houghton Bog core 3 was also based on two $^{14}$C dates, but the *Ambrosia* spike was not identified. The age model for Higgins Bog core 2 was based on the same criteria as Houghton Bog core 2. However, one of the dates on Higgins Bog core 3 was rejected due to an improbably young age, probably due to a root from farther up the core contaminating the sample sent to the lab for $^{14}$C dating. All $^{14}$C dates were analyzed by the NOSAMS lab, and results were calibrated by Calib 7.10 (Reimer et al. 2013). All age models were created using the Bacon model through the R program (Blaauw and Christen 2011).

**POLLEN PREPARATION AND ANALYSIS**

Samples to be processed for pollen were taken every centimeter. Each sample was $0.5 \text{ cm}^3$. Processing followed Faegri and Iversen (1989), with *Lycopodium* spore tablets added as an exotic marker (Table 3, (Imbrie and Kipp 1971)). Pollen in these samples was then identified and counted. Processed samples were counted at x400, using a Nikon microscope. At each level, 300 individual pollen were counted. Pollen was identified using McAndrews et al. (1973), and the database (Bush and Weng 2007) and modern pollen reference
Table 3. Pollen processing steps

<table>
<thead>
<tr>
<th>Step</th>
<th>Procedure</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Measure 0.5 cm$^3$ of sample, transfer to centrifuge tubes, then add one Lycopodium tablet.</td>
</tr>
<tr>
<td>2</td>
<td>Add 3 ml of 10% HCl, stir, and heat for c. 10-20 minutes. Centrifuge* and decant.</td>
</tr>
<tr>
<td>3</td>
<td>Wash with 7 ml of distilled H$_2$O, centrifuge* and decant.</td>
</tr>
<tr>
<td>4</td>
<td>Add 5 ml of 10% KOH, stir, and heat sample for c. 10 minutes. Repeat step 3.</td>
</tr>
<tr>
<td>5</td>
<td>Add 5 ml of 0.1M Na$_4$P$_2$O$_7$, stir, and heat sample for c. 30 minutes.</td>
</tr>
<tr>
<td>6</td>
<td>Place sample in an ultrasonic bath for 30 seconds, centrifuge*, and decant. Repeat step 3.</td>
</tr>
<tr>
<td>7</td>
<td>Add 5 ml of 100% CH$_3$COOH, centrifuge*, and decant.</td>
</tr>
<tr>
<td>8</td>
<td>Add 1 ml of acetolysis solution 9:1 (CH$_3$CO)$_2$O: H$_2$SO$_4$, heat for 3 minutes. Centrifuge*, and decant.</td>
</tr>
<tr>
<td>9</td>
<td>Wash with 100% CH$_3$COOH, centrifuge*, and decant.</td>
</tr>
<tr>
<td>10</td>
<td>Repeat step 3 three times.</td>
</tr>
<tr>
<td>11</td>
<td>Transfer the samples to vials using H$_2$O.</td>
</tr>
<tr>
<td>12</td>
<td>Centrifuge* excess H$_2$O if needed.</td>
</tr>
</tbody>
</table>

*Centrifuge for 3 minutes at 1500 RPM
CHARCOAL PREPARATION AND ANALYSIS

Charcoal samples were collected from a parallel core taken at the same location as the pollen cores. Subsamples of 0.25 cm$^3$ were taken from the core at every centimeter and filtered at 180 µm. The retained material was transferred to a petri dish using distilled water and viewed under a stereoscope. Charcoal particles were identified and photographed at a magnification of x20. The area of the particles was found using Image J.

TESTATE AMOEBAE PREPARATION AND ANALYSIS

Testate amoebae samples were also collected from the same core used for charcoal analysis. Samples were taken at two-centimeter intervals, and were 1 cm$^3$. Processing was modified from Hendon and Charman (1997) (Table 4). *Lycopodium* spores were added as an exotic marker. Testate amoebae were identified and counted at x400, using a Nikon microscope. At each level, 150 testate amoebae were counted. Testate amoebae were identified using Charman et al. (2000) and Ogden and Hedley (1980).
Table 4: Testate amoebae processing steps

<table>
<thead>
<tr>
<th>Step</th>
<th>Procedure</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Measure 1 cm$^3$ of sample, transfer to centrifuge tubes, then add one <em>Lycopodium</em> tablet.</td>
</tr>
<tr>
<td>2</td>
<td>Add 0.1M Na$_4$P$_2$O$_7$, stir, and let sample sit for c. 24 hours.</td>
</tr>
<tr>
<td>3</td>
<td>Wash with 7 ml of distilled H$_2$O, centrifuge*, and decant.</td>
</tr>
<tr>
<td>4</td>
<td>Stir sample, then filter through a 300 um filter, using distilled H$_2$O when necessary.</td>
</tr>
<tr>
<td>5</td>
<td>Transfer material that went through the filter to centrifuge tubes using distilled H$_2$O.</td>
</tr>
<tr>
<td>6</td>
<td>Stir, centrifuge*, and transfer samples to vials using distilled H$_2$O.</td>
</tr>
<tr>
<td>7</td>
<td>Centrifuge* excess H$_2$O if needed.</td>
</tr>
<tr>
<td></td>
<td>*Centrifuge for 4 minutes at 900 RPM</td>
</tr>
</tbody>
</table>

STATISTICAL ANALYSIS

CONstrained Hierarchical Clustering

While there are many methods of constrained hierarchical clustering, this study used CONISS, a method which creates constrained clusters using incremental sum of squares, and is useful when analyzing stratigraphic data (Grimm 1987). In this study, the dissimilarity distance matrix was calculated using Bray-Curtis distance. All other default parameters were accepted. Rare species (<1% abundance throughout the entire record) were excluded. This cluster analysis was conducted
using the rioja package in the R program (Juggins et al. 2016).

DETRENDED CORRESPONDENCE ANALYSIS (DCA)

While DCA and NMDS both have strengths and weaknesses and often generate similar results, DCA (Hill 1979, Hill and Gauch 1980) has been criticized for excessive data manipulation under arbitrary assumptions, which can distort the data (Chardy et al. 1976, Beals 1984, Minchin 1987). DCA can, however, provide an accurate species biplot when dealing with a single, long, environmental gradient (McCune and Mefford 1999). As these conditions are often met with paleoecological data, DCA is considered to be an appropriate tool for paleoecological studies (Birks and Gordon 1985). The default parameters for DCA calculations were used in the vegan package in the R program, and two DCAs were run, one with rare species were excluded and one with all of the species (Oksanen et al. 2010). Coefficients of determination ($r^2$) were calculated using Euclidean distance (McCune and Mefford 1999).

NONMETRIC MULTIDIMENSIONAL SCALING (NMDS)

NMDS is appropriate for analyzing matrices with many complex
environmental gradients and was calculated using the vegan package in the R program. Default parameters were accepted for NMDS analysis, except when noted:

- Distance measure: “Bray-Curtis”
- The number of runs with real data was 100.
- The autotransformation was set to “False.”
- “bestnmds” command was used, which runs the number of iterations (in this case, 100) in random initial locations, and returns the best result of the set.

TRANSFER FUNCTIONS

A transfer function developed by Robert Booth (Booth 2002) was used to ascertain the water table level relative to ground surface at each site across the chronosequence represented by the core. This transfer function has been calibrated using modern testate amoebae assemblages from eleven peat bog sites (both ombrotrophic and minerotrophic) from Michigan. The water table level was measured at each of the eleven sites when the peat was collected, which was a 4-week period from late June to late July (Booth 2002). Using this calibrated dataset,
a transfer function was developed that can predict the water table depth from fossil
data to within +/- 7.5 cm of the actual water table depth (Booth 2002).
RESULTS

LAKE CORES

Houghton Lake and Douglas Lake were originally cored in summer 2013 for this project. Douglas Lake is c. 135 km north of Houghton Lake (Figure A1). When \(^{14}\text{C}\) dating was attempted; however, the returned dates for Houghton Lake were clearly too old, and the dates for Douglas Lake showed a reversal (Table A1). The chronological problems suggested that reworking of glacial-aged sediments was a problem at both sites. The utility of these sites for paleoecological studies was clearly impaired, and further analyses were not pursued.

HOUGHTON BOG

STRATIGRAPHY

The first core from Houghton Bog was determined to be the archive core, and is not described in detail here, as it was not used in this study. The second core retrieved from Houghton Bog comprised 105 cm of sediment (Figure 8). The sediment from 105-100 cm was sand. 100-90 cm was mostly sand, overlain by a thin layer of mud. Peat began at 66 cm, and gradually becomes less humified nearer the surface. The top 6 cm of the core were extruded in the field because the section
was unconsolidated and may have become mixed during travel. The uppermost 7 cm of this core was water. This water was not counted as part of the total depth; 0 cm was set as the beginning of sediment in every core.

The third core retrieved from Houghton Bog contained 100 cm of sediment (Figure 8). The bottom 12 cm were extruded in the field, to avoid damage during transportation. The sediment from 100 - 65 cm was sand. Peat began at 66 cm, and gradually became less humified up the core. The top 6 cm of this core were also extruded in the field. This core was raised from beneath 25 cm of water.
Figure 8. Core stratigraphy for Houghton Bog. Depth is indicated on the left. Stars indicate $^{14}$C dates (details in Table 5). Black stars indicate $^{14}$C dates for Core 2, grey stars indicate $^{14}$C dates for Core 3.

AGE MODEL

For Houghton Bog, core 2, the *Ambrosia* spike was identified at a depth of 9 cm, and used in addition to the two $^{14}$C dates for this core (Table 5). All of the
$^{14}$C dates were accepted for core 3. Using the Bacon chronology, the average peat accumulation rate for core 2 was 1 cm/50 years, and 1 cm/200 years for core 3 (Figures 9 and 10).

Table 5. $^{14}$C dates for Houghton Bog. Calibrated Years BP are shown with the weighed mean in bold, and the minimum and maximum in parentheses.

<table>
<thead>
<tr>
<th>Core 2</th>
<th>Core 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lab ID</td>
<td>Depth (cm)</td>
</tr>
<tr>
<td>9</td>
<td>100</td>
</tr>
<tr>
<td>132707</td>
<td>28</td>
</tr>
<tr>
<td>130348</td>
<td>78</td>
</tr>
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*Ambrosia spike
Figure 9. Depth-age model for sediment samples from Houghton Bog, Core 2. Blue dots represent imputed $^{14}$C dates, and their associated errors (Table 5). Accumulation rate is shown in the top middle graph.
Figure 10. Depth-age model for sediment samples from Houghton Bog, Core 3. Blue dots represent imputed $^{14}$C dates, and their associated errors (Table 5). Accumulation rate is shown in the top middle graph.
CONISS

CONISS was used to determine the zonation of the Houghton Bog pollen assemblage. CONISS identified four major pollen zones: Zone HB-1 (2500-2000 cal BP), Zone HB-2 (1900-1500 cal BP), Zone HB-3 (1400-750 cal BP), and Zone HB-4 (700-0 cal BP) (Figure 11). The CONISS zonation and characteristics of these zones are described in more detail below.

Figure 11. CONISS results for the pollen assemblage at Houghton Bog, from 2500-0 cal BP. Four clusters were identified, marked here in black, red, green, and blue. Zone HB-1 (blue): 2500-2000 cal BP, Zone HB-2 (green) 1900-1500 cal BP, Zone HB-3 (red) 1400-750 cal BP, and Zone HB-4 (black) 700-0 cal BP.
POLLEN AND CHARCOAL

A total of 59 samples were analyzed for their pollen assemblage, and 57 taxa were identified. For the past c. 2500 years, the composition of the pollen assemblage at Houghton Bog was relatively stable. However, there were some changes in the vegetation assemblage warranting investigation (Figure 12). Forty samples from core 3 were analyzed for charcoal (Figure 12).

TESTATE AMOEBAE

Eight samples were analyzed for testate amoebae, in which, 52 distinct species were identified. These eight samples were then used in the amoebae-water table transfer function. The transfer function was run by Robert Booth of Lehigh University, using 39 species. Testate amoebae showed little fluctuation over the total record (Figure 13).
Figure 12. Pollen abundance of taxa with >1% abundance at Houghton Bog from c. 2500 cal BP to present. Charcoal is reported as area (mm/cm³), and pollen abundance is based on pollen percentages.
Figure 13. Testate amoebae at Houghton Bog from c. 4000 cal BP to present. Charcoal is reported as area (mm/cm³), testate amoebae are shown as percentages, and the last column shows the results of the transfer function, which calculates the depth to the water table (DTW) in centimeters.
POLLEN ZONATION

Zone HB-1. (c. 2500-2000 cal BP, 60-43 cm)

The sediment of this zone is fully humified peat, with very little fibrous material. Munsell soil color charts identify this zone as black (Munsell 1994). Zone 1 is characterized by high abundances of *Acer, Betula, Fraxinus, Ilex, Nyssa, Pinus,* and *Quercus.* *Cyperus* briefly spikes c. 2000 cal BP (Figure 12). *Artemisia,* *Populus, Salix, Tsuga,* and *Ulmus* are present in moderate amounts. *Juglans* is present in low amounts. *Abies* and *Picea* are virtually absent, as are *Amaranthaceae, Cyperus, Fagus,* and *Poaceae.* *Pinus* dominates the assemblage throughout this zone. Zone 1 ends with a spike in the abundance of *Vitis* (frost grape).

Dominant testate amoebae during this zone are *Bullinaria indica* and *Cyclopyxis arcelloides,* although *C. arcelloides* declines at the end of this zone (Figure 13). Both of these species are dry indicators, *Hyalosphenia subflava* (dry indicator) peaks during this zone, and *Trignopyxis arcula* (wet indicator) is also fairly abundant. *Diffugia pristis* (wet indicator) increases slightly during this zone, as does *Diffugia pulex* (dry indicator). Depth to the water table (DTW) during this zone is c. 35-38 cm.
Zone HB-2. (c. 1900-1500 cal BP, 42-26 cm)

This zone is also composed of somewhat fibrous peat, whose color is reddish black (Munsell 1994). *Abies* and *Picea* peaked during this zone, at c. 1800 cal BP. *Tsuga* and *Acer* slightly increase during this zone, relative to the previous zone. *Ulmus* reaches its highest abundance during this zone (c. 1900 and c. 1500 cal BP). Ericaceae also reaches its highest levels during this zone. Poaceae, *Rumex*, and *Salix* all spike at c. 1750 cal BP, and *Ambrosia* and *Quercus* are present at moderate levels throughout this zone. *Ilex* declines form c. 2000 to 1400 cal BP. *Betula* also declines from c. 2000 to 1600 cal BP. Initially, *Pinus* also has low abundances, but recovers for a short period (c. 1900-1700 cal BP) before declining again. *Fagus* appears briefly, but only at very low abundances. Two of the three charcoal spikes in this entire record occurs during this zone, at c. 1950 and c. 1600 cal BP.

DTW during this zone is c. 39-40 cm, making it perhaps a little drier than the earlier period. *Pseudodifflugia fulva* spikes during this zone. *Cyclopyxis arecelloides* also recovers, and peaks once again. *Hyalosphenia subflava* declines slightly at the beginning of this zone, but remains abundant throughout. *Bullinularia indica* remains at fairly low levels throughout this zone.
Zone HB-3. (c. 1400-750 cal BP, 25-17 cm)

This zone is characterized by somewhat fibrous peat, whose color is reddish black (Munsell 1994). The largest charcoal spike of this record occurs at the beginning of this zone. *Pinus* begins to decline c. 1400 cal BP and remains at low levels until c. 1000 cal BP. *Acer* and *Betula* also decline at c. 1400 cal BP, and never increase to their previous levels. *Ilex* initially declines, then reaches its peak abundance at c. 1000 cal BP. *Tsuga* dramatically increases during this zone, reaching peaks at c. 800 and c. 700 cal BP. *Cyperus* peaks at c. 1400 cal BP, and *Salix* peaks at c. 1300 cal BP. *Acer, Abies, Alnus, Betula, Nyssa, Picea, Quercus* and *Ulmus* are present at moderate levels throughout this zone. *Fagus, Juglans*, Amaranthaceae, *Ambrosia, Populus*, Poaceae, and *Rumex* are virtually absent during this zone.

*Diffugia pristis* peaks during this zone, as does *Bullinularia indica.* *Cyclopyxis arceloides* begins the zone at high levels, but declines throughout. *Hyalosphenia subflava* remains at about the same abundance during this zone as it was in the previous zone. *Arcella discoides* (wet indicator) increases during this zone. While *Trignopyxis arcula* initially decreases at the beginning of this zone, it begins to increase by the end of this zone. DTW is the lowest it has been during
any of the zones, as it is c. 27 cm.

*Zone HB-4. (c. 700-0 cal BP, 16-0 cm)*

This zone is characterized by less humified peat than any of the other zones, with very fibrous peat. The material is also somewhat lighter than any of the other previous zones, and is dark reddish brown (Munsell 1994). *Ilex* declines once again during this zone, from c. 600-400 cal BP, peaks at c. 300 cal BP, and then declines at c. 200 cal BP. *Tsuga* is present at its greatest abundance during this zone, but declines suddenly at c. 100 cal BP. *Betula* and *Pinus* are present in large abundances, but they are not as high as their abundances in Zone 1, although *Betula* increases at c. 100 cal BP. *Ericaceae* increases at the beginning of this zone, and remains at moderate levels throughout the zone. *Abies, Acer, Fraxinus, Nyssa, Picea,* and *Quercus* are present in moderate amounts. *Cyperus, Poaceae, Populus,* and *Ulmus* are virtually absent from this zone until c. 100 cal BP. *Rumex* and *Salix* are present at low levels throughout this zone. *Ambrosia* remains at low levels throughout this zone, until c. 100 cal BP, where it spikes to its largest abundance in the entire record.
European Settlement

European settlement is clearly marked across eastern North America by a sharp rise in *Ambrosia* (Clifford and Booth 2015). While this may differ depending on the particular region, in Michigan it occurs at A.D. 1850 (Booth and Jackson 2003). At Houghton Bog, the *Ambrosia* spike is concurrent with an immediate decrease in *Betula, Picea, Pinus, Quercus, Tilia*, and *Tsuga*. When these taxa decrease, Amaranthaceae, *Artemisia, Plantago, Poaceae, Populus*, and *Rumex* all increase. Soon after European settlement, *Betula, Picea, Pinus, Quercus, Tilia*, and *Tsuga* increase once again. This pattern has been observed in other records (Booth and Jackson 2003, Booth et al. 2004).

MULTIVARIATE ANALYSES

Pollen

Pollen zones determined through CONISS for Houghton Bog were portrayed in multivariate space using DCA and NMDS. A DCA was run with all of the genera (59 total, with *Pinus* separated into two subgenera). Eigenvalues for this DCA (Axis 1= 14.50, Axis 2=10.84, Axis 3=6.08) explained 31.42% of the variance. Another DCA was run, excluding genera whose abundances never rose
above 1%, which resulted in a DCA and NMDS using 25 species for Houghton Bog. Eigenvalues for this reduced DCA (Axis 1=14.14, Axis 2=8.57, Axis 3=6.12) explained 28.83% of the total variance (Figure 14). Since the eigenvalues for each DCA are very similar, and the DCA scores plotted through time have an identical pattern, it was determined that rare taxa were not distorting the analysis. The DCA results of the run using all genera will be discussed in detail below.

While DCA and NMDS produce similar results for Houghton Bog, DCA provides a stronger separation of the CONISS-defined pollen zones than the NMDS analysis. DCA Axis 1 appears to be driven by the abundance of *Vitis* (frost grape) and *Cephalanthus* (buttonbush) at the positive extreme, and Asteraceae (asters) and Caltha (marsh marigold) at the negative extreme (Figure 15). DCA Axis 1 does not show a strong trend with regard to time. DCA Axis 1 shows an abrupt change at c. 2000 cal BP, which is when *Vitis* spikes (Figure 16). Ecologically, the positive extreme of Axis 2 is characterized by *Carex* (sedge) and *Cyperus* (sedge), whereas the negative extreme is characterized by *Ilex* (holly), *Typha* (cattail), and *Rumex* (dock).

The highest score on Axis 2 was for a sample dated to c. 138 cal BP, i.e. immediately before the *Ambrosia* spike. The most negative scores were all from pollen zone HB-3 between 750 and 1020 BP, coincident with the Medieval Climate
Anomaly. The site scores show a steady decline in DCA values on Axis 2 from c. 1500-1000 cal BP, and a marked change at c. 2000 cal BP (Figure 17). The c. 1000 cal BP site score change is unclear in the CONISS zonation, but the change at c. 2000 cal BP is shown in the CONISS zonation, as it marks the end of HB-1. Finally, there is a dramatic change in the DCA Axis 2 scores c. 100 cal BP, probably driven by *Ambrosia*. 
Figure 14. DCA site scores based on the pollen percentages at Houghton Bog. Symbols indicate the different zones based on the pollen record. Zones are based on CONISS results. Eigenvalues (Axis 1=14.50, Axis 2=10.84, Axis 3=6.08) explained 31.42% of the variance.
Figure 15. DCA species scores based on the pollen assemblages at Houghton Bog. Species are plotting according to DCA1 and DCA2 axes scores. Eigenvalues (Axis 1= 14.50, Axis 2=10.84, Axis 3=6.08) explained 31.42% of the variance.
Figure 16. DCA Axis 1 scores for fossil pollen data from Houghton Bog over time. The horizontal axis indicates age, while the vertical axis indicates the DCA site scores.

Figure 17. DCA Axis 2 scores for fossil pollen data from Houghton Bog over time. The horizontal axis indicates age, while the vertical axis indicates the DCA site scores.
NMDS analysis did not show the CONISS zonation as clearly as the DCA analysis (Figure 18). There appears to be some clustering of Zone HB-1 and HB-3 along NMDS Axis 1, but Zones HB-2 and HB-4 appear scattered along this axis. Zone HB-2 especially is located along the entire axis. NMDS Axis 2 shows Zone HB-3 clearly, but no real pattern or clustering appears for any of the other CONISS zones along this axis.
Figure 18. NMDS scores based on the pollen assemblage at Houghton Bog for the past c. 2500 cal BP. Symbols indicate the different zones based on the pollen record. Zones are based on CONISS results. Number of axes used=3. Stress=11.984.

Testate Amoebae

DCA and NMDS were run using the nine testate amoebae samples. Because the sample size is so low, neither analysis showed a clear clustering (Figures 19 and
DCA and NMDS were run using the entire species assemblage.

Figure 19. DCA site scores based on testate amoebae percentages at Houghton Bog. Eigenvalues (Axis 1=20.66, Axis 2=14.50, Axis 3=7.63) explained 42.79% of the variance.
Figure 20. NMDS scores based on testate amoebae percentages at Houghton Bog. Symbols indicate the different zones based on the pollen record. Zones are based on CONISS results. Number of axis = 3, Stress = 0.005.
HIGGINS BOG

STRATIGRAPHY

Like Houghton Bog, the first core from Higgins Bog was set aside as the archive core, and so is not described in detail here. The second core from Higgins Bog was the longest of any of the cores and was collected from beneath 21 cm of water. From 150-138 cm, the sediment from this core was clay. This was the only core with clay. Sand formed the next 137-118 cm of this core. Everything from 118-0 cm of this core was peat (Figure 21). The top 9 cm of this core were extruded in the field.

Core 3 from Higgins Bog was collected from beneath 10 cm of water and was 90 cm long (Figure 21). Due to a malfunction with the Russian Borer, the first section of this core was only 40 cm long, instead of the usual 50 cm. 90-82 cm of this core was sand. 82-0 cm of this core was peat. The top 5 cm of the first section were extruded in the field.
Figure 21. Core stratigraphy for Higgins Bog. Depth is indicated on the left. Stars indicate $^{14}$C dates (details in Table 6). Black stars indicate $^{14}$C dates for Core 2, grey stars indicate $^{14}$C dates for Core 3.
AGE MODEL

The *Ambrosia* spike in Higgins Bog, core 2, was identified at a depth of 5 cm, and was used in addition to the two $^{14}$C dates for this core (Table 6). However, for core 3, one of the $^{14}$C dates was rejected, and so the Bacon chronology for this core was based on one $^{14}$C date. Using the Bacon chronology, the average peat accumulation rate for core 2 was 1 cm/20 years, and 1 cm/50 years for core 3 (Figures 22 and 23).

Table 6. $^{14}$C dates for Higgins Bog. Calibrated Years BP are shown with the weighed mean in bold, and the minimum and maximum in parentheses.

<table>
<thead>
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<th></th>
<th>Core 3</th>
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<td>$^{14}$C Years BP</td>
<td>Cal Years BP (2 $\sigma$)</td>
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*Ambrosia* spike spike **Rejecte $^{14}$C date
Figure 22. Depth-age model for sediment samples from Higgins Bog, Core 2. Blue dots represent imputed $^{14}$C dates, and their associated errors (Table 6). Accumulation rate is shown in the top middle graph.
Figure 23. Depth-age model for sediment samples from Higgins Bog, Core 3. Blue dots represent imputed $^{14}$C dates, and their associated errors (Table 6). Accumulation rate is shown in the top middle graph.
CONISS

CONISS was also used to determine the zonation of the pollen assemblage at Higgins Bog (Figure 24). The pollen record at Higgins Bog extends back to c. 3300 cal BP.
POLLEN AND CHARCOAL

A total of 92 samples were analyzed for their pollen assemblage, in which 59 species were identified. The pollen record at Higgins Bog spans the last c. 3300 years (Figure 25). Sixty-six samples from core 3 were analyzed for charcoal (Figure 25).

TESTATE AMOEBAE

Fourteen samples were analyzed for testate amoebae from Higgins Bog, core 3, in which 27 distinct species were identified. These 14 samples were used in the transfer function to determine depth to water table (Figure 26). The transfer function was run by Robert Booth, using 39 species, some of which did not occur at this site, but were included as zero values. Overall, this Bog is very dry. The large rise in water table depth at c. 850 cal BP is most likely due to the high number of Pseudodifflugia fulva, which is a poorly defined species taxonomically and ecologically (Charman et al. 2000). Due to the nature of this site, testate amoebae were not preserved >32cm downcore, and so further analysis was impossible.
Figure 25. Pollen abundance of taxa with >1% abundance at Higgins Bog from c. 3300 cal BP to present. Charcoal is shown as area (mm/cm$^3$), and pollen abundance is based on pollen percentages.
Figure 26. Testate amoebae at Higgins Bog from c. 1100 cal BP to present. Charcoal is shown as area (mm/cm³), testate amoebae are shown as percentages, and the last column shows the results of the transfer function, which calculates the depth to the water table (DTW) in centimeters.
POLLEN ZONATION

Zone HI-1. (3300-2600 cal BP, 94-60 cm)

This zone is characterized by very little to no fibrous material, and has a reddish black color (Munsell 1994). *Pinus* dominates this zone, which has its peak abundance (c. 60%) in this zone (Figure 25). *Cyperus* also peaks during this zone at c. 3100 cal BP. *Acer, Betula, Ericaceae, Nyssa, Picea, Populus,* and *Quercus* are all present in moderate amounts during this zone. Although Ericaceae, *Picea, Populus,* and *Tsuga* are all moderately abundant in this zone, this zone has their lowest abundances of the entire record. *Abies* is present in its lowest levels throughout the entire record. *Ambrosia, Alnus* and *Ulmus* are present at very low levels throughout this zone. *Fagus, Ilex, Juglans, Poaceae, Rumex,* and *Salix* are virtually absent during this period. No amoebae were preserved in this section of the core.

Zone HI-2. (2500-2100 cal BP, 59-38 cm)

This zone has slightly more fibrous material than the previous zone, but is a very dusky red color (Munsell 1994). *Pinus* decreases slightly c. 2500 cal BP. *Abies, Acer, Alnus, Ambrosia, Fagus, Fraxinus, Juglans, Nyssa, Picea, Poaceae, Quercus, Rumex, Salix, Tsuga,* and *Ulmus* all occur at around the same levels as
they did in the previous zone. *Betula* abruptly spikes at c. 2100 cal BP, as does Ericaceae and *Populus*. No testate amoebae were preserved in this section of the core. Charcoal is also present at c. 2100 cal BP.

**Zone HI-3. (2000-1000 cal BP, 37-17 cm)**

The material of this zone has the same characteristics as the previous zone. *Pinus* abruptly declines at c. 2000 cal BP, and never regains its previous abundance. At the same time, *Abies* and *Picea* increase, and remain at moderate levels throughout this zone. *Tsuga* increases steadily throughout this zone. At c. 1800 cal BP, *Pinus* declines from its previous high percentages to lower levels, and doesn’t begin to regain those levels until c. 1000 cal BP. *Ilex* spikes at c. 1800 cal BP, but this is the only major appearance of *Ilex* in this record. *Fagus* appears from c. 1800 to 1000 cal BP before almost disappearing entirely. Ericaceae spikes at c. 1300 cal BP, then declines to its previous levels for the rest of this period. *Acer, Alnus, Ambrosia, Fraxinus, Juglans, Nyssa, Poaceae, Quercus, Rumex, Salix* and *Ulmus* all occur at around the same levels as they did in the previous zone. Four charcoal spikes are present during this time period.

The testate amoebae record starts c. 1100 cal BP. From this time until c. 1000 cal BP, the record is dominated by *Cyclopyxis arecelloides* and *Hyalosphenia*.
subflava, which are both dry indicators. *Arcella discoides* is present in low levels, as is *Diffugia pulex* and *Pseudodiffugia fulva*. *Diffugia pristis* is also present in very low levels. The DTW during this period is c. 37-38 cm.

**Zone HI-4. (900-0 cal BP, 16-0 cm)**

This zone is composed of very fibrous material, as the peat is not well humified. The material has a reddish black color (Munsell 1994). This zone has the greatest amount of charcoal spikes, with most of these spikes occurring from c. 500-200 cal BP. These charcoal spikes; however, do not occur until the DTW indicates dry conditions (Figures 25 and 26). *Pinus* increases slightly at the beginning of this zone. *Abies, Acer, Alnus, Ambrosia, Betula, Fraxinus, Juglans, Nyssa, Picea, Populus, Quercus, Rumex, Tsuga,* and *Ulmus* all occur at around the same levels as they did in the previous zone. *Fagus* is absent from this zone, and Poaceae is absent until c. 100 cal BP. *Salix* briefly appears at c. 800 cal BP before disappearing until c. 100 cal BP. *Ambrosia* remains at low levels throughout the zone until c. 100 cal BP, where it reaches its highest levels in the entire record.

The beginning of this record is marked by a dramatic decrease in *Cyclopyxis arecelloides* and *Hyalosphenia subflava*, and an increase in *Pseudodiffugia fulva* and *Diffugia pulex*. *Diffugia urceolata* also makes a brief appearance. The DTW
at the beginning of this zone is also the lowest of the entire record (c. 14 cm) indicating wet conditions. By c. 700 cal BP, conditions have returned to back to being very dry, with DTW between c. 34 and 42 cm. *Cyclopyxis arecelloides* and *Hyalosphenia subflava* both return to being the dominate species, and *Difflugia pulex* and *Pseudodifflugia fulva* decline for the rest of the record.

*European Settlement*

European settlement is clearly marked across eastern North America by a sharp rise in *Ambrosia* (ragweed) (Clifford and Booth 2015). While this may differ depending on the particular region, in Michigan it occurs at A.D. 1850 (Booth and Jackson 2003). While the *Ambrosia* spike is clearly visible at Higgins Bog, the *Ambrosia* spike does not occur at the same time as any major forest turnover. Perhaps the location of Higgins Bog made it an undesirable location for the European settlers to extensively log and settle.
MULTIVARIATE ANALYSES

Pollen

Pollen zones determined through CONISS for Higgins Bog were tested using multivariate analyses (DCA, and NMDS) based on the pollen percentages of 92 samples from Higgins Bog. A DCA was run with all of the genera (60 total, with *Pinus* separated into two subgenera). Eigenvalues for this DCA (Axis 1=10.00, Axis 2=4.92, Axis 3=2.43) explained 17.35% of the variance. Another DCA was run, with genera whose abundances never rose above 1% abundance removed from the dataset, which resulted in a DCA and NMDS using 24 species for Higgins Bog. Eigenvalues for this reduced dataset (Axis 1=9.35, Axis 2=4.52, Axis 3=2.27) explained 16.14% of the total variance. Since the eigenvalues for each DCA were very similar, and the DCA scores plotted through time have an identical pattern, it was determined that rare taxa were not over influencing the data. The DCA results of all of the genera will be discussed in detail below. Like Houghton Bog, DCA and NMDS produced similar results for Higgins Bog, but DCA showed the differences between the different pollen zones determined by CONISS more clearly than the NMDS.

DCA site scores on Axes 1 and 2 provide quite a good separation of the zones (Figure 27). The species with the highest scores on Axis 1 were *Ilex* and
Larix (larch), whereas Galium (bedstraw), Celtis (hackberry) and Stellaria (chickweed) had the lowest scores (Figure 28). On Axis 2, Urtica (nettles), Celtis, and Poaceae (grasses) had high scores, whereas Platanus (sycamore), and Morus (mulberry) characterized the lowest scores. The DCA site scores for Axis 1 show a dramatic change at c. 1800 cal BP, which is near the end of zone HI-2 identified through CONISS (Figure 29). DCA species scores for Higgins Bog can provide more insight into what drives this axis. Betula spikes at c. 1800 cal BP, and the abundance of Betula closely follows the pattern of the DCA Axis 1 so that even though it is not the most diagnostic species of this axis, the abundance of Betula appears to be driving this axis.

DCA Axis 2 does not show variability coinciding with the CONISS zonation as clearly as DCA Axis 1, but the site scores on this axis do show an abrupt change at c. 2000 cal BP (Figure 30). After c. 2000 cal BP, the DCA scores become predominantly negative, with relatively little variance apart from a more extreme negative excursion at c. 1400 cal BP. The species biplot shows that Ericaceae is an important factor in driving the DCA scores for axis 2, and Ericaceae spikes at both c. 2000 cal BP and c. 1400 cal BP.
Figure 27. DCA site scores based on the pollen percentages at Higgins Bog. Symbols indicate the different zones based on the pollen record. Zones are based on CONISS results. Eigenvalues (Axis 1=10.00, Axis 2=4.92, Axis 3=2.43) explained 17.35% of the variance.
Figure 28. DCA species scores based on the pollen assemblages at Higgins Bog. Species are plotting according to DCA1 and DCA2 axes scores. Eigenvalues (Axis 1=10.00, Axis 2=4.92, Axis 3=2.43) explained 17.35% of the variance.
Figure 29. DCA Axis 1 scores for fossil pollen data from Higgins Bog over time. The horizontal axis indicates age, while the vertical axis indicates the DCA site scores.

Figure 30. DCA Axis 2 scores for fossil pollen data from Higgins Bog over time. The horizontal axis indicates age, while the vertical axis indicates the DCA site scores.
NMDS was also used to analyze the pollen record from Higgins Bog (Figure 31). The NMDS results are very similar to those of the DCA, though the clusters are not so clearly defined. The NMDS analysis is not discussed further.

Figure 31. NMDS scores based on the pollen assemblage at Higgins Bog for the past c. 3300 cal BP. Number of axes=3. Stress=10.344.
Testate Amoebae

DCA and NMDS were run using the entire species assemblage from the 14 testate amoebae samples from Higgins Bog. Because the sample size was so small, neither analysis showed a clear clustering (Figures 32 and 33).

Figure 32. DCA sites scores based on testate amoebae percentages at Higgins Bog. Eigenvalues (Axis 1 = 18.36, Axis 2 = 5.27, Axis 3 = 4.34) explained 27.97% of the variance.
Figure 33. NMDS scores based on testate amoebae percentages at Higgins Bog. Number of axes used=3, Stress=2.8656.
DISCUSSION

Houghton and Higgins Bogs both yielded relatively short, c. 1 m, peat cores that had basal ages within the last 3300 years. The onset of peat formation at this time suggests that the last 3000 years of the Holocene were wetter than the mid-Holocene in central Michigan, an observation supported by other regional records (Brugam et al. 1997, Booth and Jackson 2003, Marlon et al. 2016). Overall, the regional floras were quite stable through this period, though some trends were evident. Those trends were partially captured in the ordinations of the pollen data.

Houghton Bog DCA Axis 1 may reflect temperature, though this is not certain. *Vitis* and *Cephalanthus* are more thermophilous species (Voss 1996) than their counterparts at the negative extreme of this axis, e.g. *Caltha* (marsh marigold). In general boreal forest taxa, such as *Tsuga* (hemlock), *Abies* (fir) and *Picea* (spruce) have negative scores on this axis, whereas more thermophilous trees such as *Fraxinus* (ash), *Ulmus* (elm), *Nyssa* (tupelo), and *Tilia* (basswood) have positive scores. *Cephalanthus* generally occurs south of the climatic tension zone that separates temperate from boreal forest and disappears from the record after c. 1800 cal BP, whereas after this time there is a slow but steady rise of *Tsuga*, which suggests that the forest is responding to a slow cooling of central Michigan.
Axis 2 appears to be driven by moisture conditions (Figure 28) as *Cyperus* and *Carex*, both of which are aquatic sedge genera, are located near the positive extreme, whereas taxa of drier settings, e.g. *Ilex*, *Typha* and *Rumex*, are at the negative extreme. The abundance of *Ilex* strongly suggests that these shrubs are growing on the bog surface, which suggests that the bog was dry enough for *Ilex* to grow directly on the bog. *Ilex mucronata* (mountain holly) is a common component of Michigan bogs, usually at the periphery (Voss 1996). For *Ilex* to show its peak of occurrence between 1750 and 750 cal BP would be consistent with drier conditions.

Higgins Bog shows a parallel but different history, at least for some species oscillations, to that of Houghton Bog. With regards to different initial conditions, Higgins is a larger feature, with deeper standing water over much of its surface than Houghton. The most thermophilous taxa recorded at Houghton were not found at Higgins and so the separation of temperate from boreal forest taxa was not as clear in the ordination, but the trend of Axis 1 is very similar to that of Houghton Bog with a major cooling trend evident after c. 2000 cal BP. Axis 2 of the gradient, with *Urtica* so prominently featured, would appear to be driven by a particular disturbance that occurred between c. 2200 and 2000 cal BP, and without the same gradient from thermophilous to cooler taxa evident. Nevertheless some of the overall patterns were very similar, a steady increase in boreal forest taxa over the last 2000 years, and a dry oscillation centered on 1400-1000 cal BP.
DROUGHTS AND PLUVIALS

The main significance of these two records is to identify drought events and pluvials, and their effects on the vegetation. Testate amoebae have been shown to provide a sensitive proxy for drought events. Using a transfer function that related abundance of amoebic tests to water table depth, Booth et al. (2006) identified major drought events in Michigan at 1850, 1800, 1650, 1000, 800, and 700 cal BP. In contrast, when the testate amoebae record from Houghton Bog and Higgins Bog were run through the transfer function, the DTW was remarkably stable. It was even slightly lower at c. 1000 cal BP at Houghton Bog, and at c. 800 and c. 700 cal BP at Higgins Bog, suggesting that these areas might have even experienced a slight pluvial. The c. 850 cal BP wet event at Higgins Bog comes near the end of the MCA, and could mark a return to slightly wetter conditions. These testate amoebae records suggest that perhaps these two bogs represent stable, dry areas in Michigan.

HOUGHTON BOG VEGETATION AND MOISTURE

CONISS and DCA scores both showed the first major change in the vegetation assemblage at c. 2000 cal BP. Before c. 2000 cal BP, the area was a temperate forest, composed mainly of *Acer*, *Betula*, and *Pinus*. Although boreal
elements were present, they were a minor component of the flora. At c. 2000 cal BP, *Cephalanthus, Fraxinus, Nyssa, Plantago, Poaceae, Salix, Ulmus,* and *Vitis* all increased abruptly, suggesting that the forest structure changed from a previously *Acer, Betula, Ilex, Nyssa, Pinus,* and *Tsuga* dominated forest to a more open area (Figure 34). The *Vitis* spike is particularly indicative of an abrupt unknown disturbance event, but the response was by thermophilous taxa. This disturbance event is unlikely to have been caused by humans, as they did not have a large population in central Michigan at the time (O'Shea 2003, Howey and O'Shea 2006, Howey 2012). However, the testate amoebae record at c. 2000 cal BP indicated that this was a relatively dry time compared with the c. 400 years before it, and Hupy (2012) identified 2000 yr. BP as one of three major movements of the forest tension zone. Also, the charcoal record indicated a small peak at c. 2000 cal BP, suggesting that conditions were dry enough for fire, at least in the forest surrounding the bog. This finding supported my initial hypothesis, that mature/boreal forest taxa (such as *Tsuga*) decreased in abundance at times of known drought, although this drought has not been identified at a regional level. The occurrence of charcoal during this possible drought also supported my second hypothesis that charcoal records from these sites will line up with drought events identified by testate amoebae from these sites. The transition from a forested area to more open area suggested that c. 2000
cal BP was the beginning of a new succession for the area, possibly due to drought and/or a movement of the forest tension zone.
Figure 34. Taxa growing in the forest surrounding Houghton Bog. Data are based on a reduced pollen sum of species that were regional forest types, rather than those that would grow on the bog surface. Only taxa shown here were summed, and their percentages were recalculated. Taxa are ordered according to the forest type in which they are most abundant. Black lines indicate the center of drought events.
Figure 35. Taxa growing directly on Houghton Bog. Data are based on a reduced pollen sum. Only taxa shown here were summed, and then their percentages were recalculated. Taxa are listed in order of increasing drought tolerance. Black lines indicate the center of drought events.
After the disturbance event at c. 2000 cal BP, the vegetation growing directly on the bog undergoes a series of rapid oscillations, in which Ericaceae species were an important component (Figure 35). Ericaceae is a diverse family with many species of *Vaccinium* (blueberry) and *Gaylussacia* (huckleberry), *Empetrum* (crowberry) and *Arctostaphylos* (bearberry), all of which can grow on bogs. In general, the bogs must be a floating mat or solid surface rather than open pools for these plants to thrive. The large abundance of Ericaceae species agrees with the testate amoebae record, suggesting that Houghton Bog was relatively dry throughout this time.

Directly after c. 2000 cal BP, temperate taxa (i.e., *Fraxinus* and *Pinus*) begin to increase, and even *Tsuga*, a boreal forest taxa, suddenly increases (Figure 35). However, there appears to be a drought centered on c. 1800 cal BP indicated in the testate amoebae record at Houghton Bog, and supported by previous testate amoebae records from Michigan (Booth et al. 2006). Immediately after c. 1800 cal BP *Acer, Alnus, Cyperus, Caltha, Ericaceae, Ilex, Nyssa, and Salix* all increase (Figure 35). These are all species that can grow directly on the bog, and their rise suggests that the bog was invaded by these taxa, while the intermediate species that dominated from c. 2000 cal BP to 1800 cal BP declined. Between 2000 and 150 cal BP there was an increase in the abundance of boreal taxa. *Picea* and *Abies* peaked between 1800 and 1000 cal BP, somewhat earlier than the later successional *Tsuga*. 
The period when *Picea* was most important in this record coincided with the peak of *Ilex* growing on the bog surface. At c. 1700 cal BP *Ilex* replaced Ericaceae as the dominant shrub growing on the surface of Houghton Bog, and this dominance lasted until c. 700 cal BP. The peak of the *Ilex* abundance at c. 1000 cal BP coincided with the drought documented in other records (Booth et al. 2006, Booth et al. 2012b).

Effects of the NAO, AMO, NH polar jet, and the lake effect are well known to influence regional precipitation patterns (Ottersen et al. 2001, Burnett et al. 2003, Stenseth et al. 2003, Archer and Caldeira 2008, Knudsen et al. 2011). The changes in precipitation and vegetation during the MCA and LIA have been well studied in Michigan (Booth and Jackson 2003, Mann et al. 2009). These studies show that the lake effect strengthens as climate warms, as it did during the MCA. This warming would bring more precipitation to central Michigan, consequently, and Houghton Bog. The increased lake effect during the MCA may explain why boreal forest taxa are able to survive, and in some cases (i.e., *Nyssa* and *Tsuga*), actually increase in abundance during the MCA, while when this bog experienced drought in the past (i.e., c. 1800 and c. 1000 cal BP), these boreal forest taxa declined.
Finally, at c. 100 cal BP, *Ambrosia* spikes, and most temperate and boreal taxa initially decline, and then begin to recover. This disturbance indicates European settlement, and the early beginnings of a new succession for this area.

**HIGGINS BOG VEGETATION AND MOISTURE**

Higgins Bog shows a change in the vegetation c. 2000 cal BP, similar to the switch at Houghton Bog (Figures 35 and 36). At Higgins Bog, there is a spike in the charcoal record followed by three more fire events within the next c. 600 years. Two of these charcoal spikes occur during two droughts identified by other testate amoebae records from Michigan (i.e., c. 1850 and c. 1800 cal BP). Even though there is no testate amoebae record from Higgins Bog for this time period, it is reasonable to believe that these charcoal spikes line up with a drought event, thus continuing to support my second hypothesis. These fires probably influenced the forest structure, as *Pinus* decreased at the beginning of these events, and *Betula* briefly increased. *Ilex* also makes a brief appearance at c. 1800, during a known regional drought event (Figure 36). It is possible that *Ilex*, which is drought tolerant, is able to invade further onto the bog at this time.

The testate amoebae record began at c. 1100 cal BP, and indicated that, like Houghton Bog, this bog was very dry for most of its history. An exception to this
pattern may have been a wet event c. 850 cal BP. The charcoal record indicated a small fire event occurring immediately before c. 800 cal BP, and then an absence of fire until c. 500 cal BP. The testate amoebae indicated a return to dry conditions by 500 cal BP. The latter half of the observed wet period coincided with the LIA (c. 650-250 cal BP), which is a known wet period for North America.

*Tsuga* increases steadily over the entire record, suggesting that it was relatively immune to precipitation change, and was responding to cooler temperatures. In general, the pollen data from Higgins Bog provide evidence of a trend toward a more boreal forest, as does the pollen data from Houghton Bog.
Figure 36. Taxa growing in the forest surrounding Higgins Bog. Data are based on a reduced pollen sum of species that were regional forest types, rather than those that would grow on the bog surface. Only taxa shown here were summed, and their percentages were recalculated. Taxa are ordered according to the forest type in which they are most abundant. Black lines indicate the center of drought events.
Figure 37. Taxa growing directly on Higgins Bog. Data are based on a reduced pollen sum. Only taxa shown here were summed, and then their percentages were recalculated. Taxa are listed in order of increasing drought tolerance. Black lines indicate the center of drought events.
The vegetation at both bog sites show a few major similarities. Both are dominated by *Pinus* from the beginning of their record until c. 2000 cal BP, where both show a change in the vegetation that can be most likely attributed to drought or a shift in the forest tension zone. *Tsuga* and other boreal taxa generally increase over the entire record of both bogs, although it is more evident at Higgins Bog. The *Ambrosia* spike indicating European settlement is also clearly visible at both bogs.

**REGIONAL VEGETATION AND MOISTURE**

Previous studies have also recorded a long term cooling of Michigan over the Late Holocene, with disruptions from c. 2000-1000 cal BP (Bernabo 1981, Bartlein et al. 1984, Gajewski 1988). Michigan pollen records from these studies and others are available through Neotoma (Goring et al. 2015a). Five of these lakes were chosen to compare with the long-term trend towards a boreal forest in the records from Houghton Bog and Higgins Bog (Figure 38). When comparing the ratio of temperate forest taxa to boreal forest taxa, Houghton Bog and Higgins Bog show a clear long-term trend towards boreal forest, which is interrupted slightly at c. 2000 cal BP and c. 1800 cal BP, and finally at c. 100 cal BP at Houghton Bog. The two sites north of Houghton Bog and Higgins Bog (Irwin Smith Bog and Cub Lake) also show this trend, although they both show a major switch from temperate
to boreal forest slightly earlier than Houghton Bog and Higgins Bog, at c. 2500 cal BP instead of c. 2000 cal BP. This may indicate a movement of the forest tension zone, as at c. 2000 cal BP, the forest tension zone began to move south. This time has been identified as one of the major shifts in the forest tension zone in the past 10000 years, and so sites north of Houghton Bog and Higgins Bog would be expected to transition to a more boreal forest earlier. (Hupy and Yansa 2009, Hupy 2012).

Data from Demont Lake, Cowden Lake, and Frains Lake, which are south of Houghton Bog and Higgins Bog, do not show the succession of temperate to boreal forest as clearly as the more northern sites. While all three still experience a slight shift in their vegetation assemblage at c. 2000 cal BP, Cowden Lake actually becomes more of a temperate forest, while Demont Lake has slightly more boreal forest taxa. Frains Lake shows a small trend towards a more boreal forest, but is generally dominated by temperate forest taxa throughout its history. All three also experience more changes c. 1000 cal BP, most likely due to the MCA.

This c. 1000 cal BP change is also present at Irwin Smith Bog. Irwin Smith Bog also has a testate amoebae record associated with it, which indicates a drought at c. 1800 and c. 1000 cal BP, and the surface of Irwin Smith Bog actually burned during the later drought. While the overall vegetation assemblage at Houghton Bog
and Higgins Bog appears to have barely changed at c. 1000 cal BP, the invasion of *Ilex* onto the bog surface at Houghton Bog, the decline of *Cyperus* at Houghton Bog, and the testate amoebae record from Higgins Bog signal a drought event. Houghton Bog and Higgins Bog add to the growing body of evidence of a large drought c. 1000 cal BP, which clearly had large effects on the vegetation of Michigan.

At c. 500 cal BP, all of the sites in Figure 38 indicate a return to boreal forest except Cowden Lake and Frains Lake. This shift to a boreal forest occurs near the beginning of the LIA, and so reflects the slightly cooler conditions at this time. Then, at c. 100 cal BP, the sites with data from this time indicate another change in the vegetation assemblage, with the exception of Higgins Bog and Demont Lake. This change is most likely due to European settlement and logging.
Figure 38. Ratio of temperate: boreal forest based on pollen percentages through time at various sites in central Michigan. Sites are ordered from North-South. Specific locations of the sites are in Figure 5, in the introduction. Boreal taxa included in the ratio were: Abies, Picea, Tilia, and Tsuga. Temperate taxa included were: Betula, Carya, Fagus, Fraxinus, Pinus, Quercus, and Ulmus. Higher ratios indicate a more boreal forest; lower ratios indicate a more temperate forest.
HUMAN ACTIVITY: MOUNDS AND EARTHWORKS

Although many of the mounds in Michigan have not been radiocarbon dated, 95 of the c. 300 known mounds located in the Lower Peninsula of Michigan are known to have been built during A.D. 500-1000 (c. 1450-950 cal BP). While this is a large time period, it is interesting to note that this is between the two droughts recorded at Houghton Bog and Higgins Bog at c. 1800 and c. 1000 cal BP. In fact the earliest date from the mounds that are closest to Houghton Bog is from a charcoal piece dated at 1570 +/- 60 BP (Howey 2012). Perhaps the humans living in central Michigan exploited the favorable conditions between these two droughts, and built most of their mounds and earthworks between major droughts. This supports my third hypothesis, which suggested that the mounds would most likely have been built during wet events, which were exploited by local human populations.
CONCLUSIONS

Late Holocene climate patterns and events have been influencing the vegetation of Michigan for the last c. 3000 years, and some of these effects are evident in Houghton Bog and Higgins Bog. Temperature appears to be the main driver of the flora at both sites, with the effects of droughts and pluvials overlaying a long-term cooling. Before c. 2000 cal BP, the vegetation assemblage at both Houghton Bog and Higgins Bog was that of a temperate forest. As temperatures begin to cool slightly, boreal taxa begin to increase at both sites, at the expense of the temperate forest.

Both sites indicate a disturbance event at c. 2000 cal BP that is unlikely to have been caused by humans, as they were not present in large numbers in this area at the time. Indeed, Houghton Bog and Higgins Bog show no indication of human activity, even though there are known mound sites built on Houghton Lake. It is most likely that a drought disturbed Houghton Bog and Higgins Bog at c. 2000 cal BP, marking the beginning of a long-term succession, or that both bogs are showing the known movement of the forest tension zone.

This succession is interrupted at c. 1800 cal BP by a drought. From c. 1800-1000 cal BP, taxa with the ability to grow directly on bogs increase in abundance, and most likely invade the bog. Interestingly, during this time boreal taxa also
increase steadily, although at a much lower rate than the taxa with the ability to grow directly on the bogs. This is most likely due to the long term cooling trend overlaying all of these droughts and pluvials, which still allows the boreal taxa to survive.

This series of droughts and pluvials culminates at c. 1000 cal BP, with another drought. This events marks the beginning of the MCA at this site, and this area temporarily warms until c. 700 cal BP. After this, temperature continues to be the main driver, and as cooling continues, boreal taxa begin to increase in abundance once more.

The pollen, charcoal, and testate amoebae records at Houghton Bog and Higgins Bog suggest that both systems are driven mainly by long-term temperature trends, with an overall succession towards boreal forest taxa. This trend extends to most of central Michigan, which has clearly been on a path of long-term succession for the last c. 3000 years, with little human activity to disrupt this climatically-driven pattern. As global temperatures continue to increase, these climatically-driven vegetation assemblages are likely to be reversed, sending the region into a new succession. This could disrupt the ecosystems of central Michigan, especially the region north of the current location of the forest tension zone, as most of this region has not experienced a major vegetation shift since c. 2000 or c. 1800 cal BP.
Future research should focus on the sites north of the forest tension zone, and how their successional patterns may be affected by future climate change.


APPENDIX

Figure A1. Douglas Lake, one of the sites of the original lake cores. Core from Douglas Lake is 136 cm, and the core from Houghton Lake is 155 cm.

Table A1. $^{14}$C dates for Houghton Lake and Douglas Lake

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<th>Years BP</th>
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<td>20710 +/- 100</td>
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<td>780 +/- 30</td>
<td>750 +/- 30</td>
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Figure A2. Complete pollen record from Houghton Bog, based on pollen percentages.
Figure A3. Complete pollen record from Higgins Bog, based on pollen percentages.