Vegetation and climate changes at Spicer Lake, Indiana, during the Holocene

by

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Abstract: Many paleoclimate studies have shown that the midcontinent of North America experienced a warmer and drier-than-present climate during the early and middle Holocene and relatively humid climate during the late Holocene, interspersed with several centennial-scale megadroughts. In response to this climate variability, the ranges of individual taxa shifted and some tree taxa (e.g. *Tsuga canadensis*, *Fagus grandifolia*) experienced episodic declines in their abundances, which appear to be linked to hydroclimatic variability. This study focuses on climate and vegetation changes during the Holocene at Spicer Lake in northern Indiana (41°44'52" N, 86°31'19" W, 237 elevation), a kettle lake located in New Carlisle, near the southeastern edge of Michigan. Reported data include radiocarbon dates, loss-on-ignition data, and fossil pollen analysis, which together are used to reconstruct the vegetation, climate and environment at Spicer Lake. *Picea*-dominated conifer forest was the main vegetation type at Spicer Lake before 11,800 years BP, followed by a period of high *Pinus* abundances. After 10,300 years BP, conifer forest decreased and deciduous forest expanded during this time, resulting in deciduous forests with high abundances of *Acer*, *Quercus*, *Ulmus* and *Fagus* pollen. *Fagus* increased and became highly abundant after about 6,800 years BP. Fagus pollen abundances during the middle and late Holocene are highly variable, with declines at roughly 5,000, 4,000, 3,800 – 1,900 and 1,000 years BP. These declines at Spicer Lake may be associated with *Fagus* pollen declines at other lakes in north central United States, perhaps caused by regional drought events, but cross-correlation is confounded by dating imprecision in earlier records. Bayesian time-series models also suggest that *Fagus* pollen abundance changes may be partly related to LOI variability at Spicer Lake. The LOI variability in the lake sediment may be a signal of changing lake-level and hence

moisture balance, but the exact reasons for the increases or decreases of minerals may change according to the different relative position of lake level and core position.

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Introduction

The Earth's climate has changed significantly during the past 21,000 years, in North America and globally. From the last glacial maximum, when the Laurentide Ice Sheet covered the northern half of North America with dryer-than-present and colder-than-present climates, through the current interglacial period, with an overall trend of warming interrupted by abrupt cooling reversals – the climate has continuously changed. As documented by multiple Greenland ice cores (Grootes et al., 1993) and analyzed by climate models (Clark et al., 2012; Shakun et al., 2012), North Atlantic climates (and perhaps Northern Hemispheric climates) changed from cold and dry conditions to the warmer Bølling-Allerød period (ca. 14,700 – 12,700 years BP) with increased rates of ice melt in the Northern Hemisphere; then abruptly reverted to the cold Younger Dryas (ca. 12,800 – 11,500 ^{14}C years BP), followed by rising temperatures at 11,700 years ago, with the start of the Holocene. These climate changes generally are consistent with changes in vegetation composition from fossil pollen records from eastern North America although the timing varies (Yu, 2007, Gonzales and Grimm, 2009; Gill et al., 2012).

Significant climate changes also occurred during the Holocene in North America: some, such as the 8.2 ka event (ca. 8,400-8,200 years BP) with a sudden decrease in regional to hemispheric temperature (Shuman et al., 2002). Some had large and long-lasting effects on terrestrial ecosystems while others were less severe, but still had substantial ecological and societal effects, such as the 4.2 ka event marked by widespread aridity (ca. 4,200 years BP) (Stahle et al., 2000; DeMenocal, 2001). Prior paleoclimatic research in middle central North America shows periods of prolonged aridity during the early and middle Holocene accompanied by brief periods of severe droughts and aridity during the Holocene (Ogden, 1966; Williams, 1974; Booth and Jackson, 2003; Miao et al., 2007; Hotchkiss et al., 2007; Booth et al., 2012; Wang et al., 2012). Most of this prior work has focused on the Great Plains and Upper Midwest (Minnesota, Wisconsin, Illinois, upper Michigan) (Miao et al., 2007; Hotchkiss et al., 2007; Gonzales and Grimm, 2009), but the eastern Great Lakes States (Indiana, Ohio, western Pennsylvania) remain understudied (Ogden, 1966; Williams, 1974; Shane, 1987; Gill et al. 2009, 2012).

These past climatic changes offer context for understanding the ecological effects of climate change and developing adaptation strategies. In conservation biology and ecology, paleoecological research provides a way to study ecosystem variability during times of climate change and reduced or no human intervention. Paleoecological data can contribute to present conservation activities, from defining baseline targets for ecological restoration to directing conservation management and policy (Hadly and Barnosky, 2009; Davies and Bunting, 2010; Dietl and Flessa, 2010; Willis et al., 2010). Paleoecological perspectives increase our understanding of the dynamic nature of landscapes and provide a framework of reference for understanding modern patterns and processes (Swetnam et al., 1999). In the 21st century, climatic and environmental variability, especially hydrological variability, likely will exceed historical observations (Cook et al., 2008), and the Holocene is a critical time period for understanding the drivers of regional climate shifts and the sensitivity of ecosystems to abrupt hydrological variability (Williams et al., 2011; Ireland et al., 2012).

In this thesis, I will analyze the environmental history at Spicer Lake, Indiana, to understand the patterns of vegetation and environmental changes in east-central North

America during the late Pleistocene and Holocene. I will analyze the pollen sequence, loss-on-ignition sequence (LOI) and XRF data at Spicer Lake to reconstruct past vegetation history and test hypotheses about the role of past climate variability, mainly drought and aridity events, on vegetation dynamics. As part of this analysis, I develop a Bayesian time series analysis to model vegetation changes as a function of environmental conditions (based on LOI) and prior vegetation state. This work builds upon previously collected lake sediment cores at Spicer Lake, prior LOI by Jeremiah Marsicek, and prior pollen analyses from 13,000 to 9,000 years BP by Jacquelyn Gill. To this work, I add a high-resolution pollen sequence for the middle and late Holocene, new radiocarbon dates, and joint analyses of all data, including time series models of the pollen and LOI data.

Background Literature Review

1. Climate and vegetation history in the north-central United States during the late-glacial period and Holocene

The late-glacial period

The late-glacial period is defined here as 18 to 11.7 ka and represents the transition time from the Last Glacial Maximum to the Holocene interglacial.

Studies from across midwestern North America showed strong vegetation changes indicated by pollen records characterized by decreases in relative abundance of conifers, such as *Picea, Pinus* and *Abies*, and increases in abundance of some deciduous taxa (mainly *Fraxinus nigra*, *Quercus* and *Ostrya*) (Wright, 1964; Cushing 1967; Schweger 1969; King, 1981; Webb et al., 1983, 1993; Shane and Anderson, 1993;

Grimm and Maher, 2002; Grimm and Jacobson, 2004; Gonzales and Grimm, 2009), suggesting a shift from colder to warmer conditions with temperature fluctuations during the Pleistocene to Holocene transition.

Radiocarbon-dated pollen sites from the Allegheny Plateau and the Till Plains document three vegetation zones between 18,000 and 10,000 calendar years BP south of the Great Lakes: ice retreat to ca. 15,800 ± 800 years BP with pollen assemblages dominated by *Picea*, 15,800 ± 800 years BP to 11,400 – 10,300 years BP (Shane and Anderson, 1993). These records include a later return to high abundances of *Picea* that is correlated roughly with the European Younger Dryas; the start of the Holocene is marked by the decline of conifer pollen abundances and the increase of *Quercus* pollen abundances (Shane and Anderson, 1993). These vegetation shifts suggest the climate changed from wetter and colder conditions at the end of the Last Glacial Maximum to warmer conditions with a cold oscillation roughly equivalent to the European Younger Dryas, and then developing to the warm Holocene. However, these sites are dated using bulk sediment radiocarbon, and so the timing may be inaccurate due to hard water contamination (Grimm et al., 2009).

At Crystal Lake, IL, which has the best late-glacial radiocarbon chronology from this region, vegetation shifts are indicated by five recognizable pollen zones: 1) 16,000 – 14,160 years BP characterized by high values of *Picea* indicating a forest with abundant spruce, 2) 14,160 – 12,400 years BP with a sharp decline in *Picea* and increase of *Abies*, *Fraxinus nigra*-type, *Ulmus*, *Ostrya* and *Quercus* that has no modern analog and that is coeval with the Allerød and early Younger Dryas, 3) 12,400 – 11,600 years BP with the increase of *Picea*, especially *P. mariana*, and decrease of *Fraxinus nigra* roughly corresponding to Younger Dryas, 4) 11,600 – 11,100 years BP marked by decrease of *Picea*, and 5) 11,100 – 9,800 years BP marked by an increase in pollen abundances of deciduous tree taxa. The vegetation changes, especially the variability of *Picea* pollen abundance, suggest relatively wet climate before 11,100 years compared to the Holocene, with fluctuations between colder and warmer temperatures, including the warmer trend indicated by the increase of deciduous trees during 14,160 – 12,400 years BP and the cold and wet conditions illustrated by the increase of *Picea* corresponding to the Younger Dryas, between 17,000 and 11,000 years BP in midcontinent of North America. (Gonzales and Grimm, 2009).

These vegetation changes have been interpreted to indicate that late-glacial climates in the Great Lake region were cold in general (Gonzales et al., 2009), with temperature fluctuations that roughly correspond to climate variability suggested by ice core records in Greenland but with a several hundred year offset, attributed to regional climate effects caused by proximity to the Laurentide Ice Sheet. In addition to the influence of climate changes, the interaction of vegetation and megafauna also may have affected past vegetation composition shifts (Gill et al., 2009, 2012). Pollen and dung fungal records in Appleman Lake, Indiana and Silver Lake, Ohio, show that dung fungal spores declined prior to the rise in deciduous tree taxa, which may show the influence of megafaunal population declines and extinction on the formation of novel plant communities during the transition from deglaciation to the Holocene,. The loss of keystone megaherbivores may have altered ecosystem structure and function by release of palatable hardwoods from herbivore pressure and by fuel accumulation (Gill et al., 2009, 2012).

The Holocene

Many paleoclimate records, such as aeolian records of dune activity and lake sediment records of shifting hydrological balance, have shown that the midcontinent of North America experienced a warmer and drier-than-present climate during the early and middle Holocene and relatively humid climate during the late Holocene (Ahlbrandt et al., 1983; Mason et al., 2004; Miao et al., 2007), with several megadroughts spanning much of North America in the past 2,000 years (Cook et al., 2007, 2010). Shifts in the ratio of aragonite/calcite and $\delta^{18}O$ of lake sediments in Minnesota suggest that many brief droughts occurred during the middle Holocene (Nelson et al., 2004). Rates of loess deposition in the Great Plains of North America increased to high levels from 9,400 to 6,500 years BP in the middle Holocene and fluctuated in the late Holocene with indications of droughts at 3,800, 2,500 and 700 years in central North America (Miao et al., 2007). Drought-induced aeolian activity in stabilized dune systems across the mid-continent indicate that there was a severe drought at 4,200 years BP across the midcontinent (Forman et al., 2001; Booth et al, 2005).

The late Holocene was wetter than the early and middle Holocene, but there were still some major century-scale droughts in North America. A network of centuries-long annually resolved tree-ring chronologies has allowed the reconstruction of past drought over North America covering the past 1000 or more years in most regions, revealing the occurrence of past “megadroughts” of unprecedented severity and duration that have never been experienced by modern societies in North America (Cook et al., 2007). Global climate models indicate that these megadroughts were associated with enhanced warming during a time of increased solar irradiance and prolonged La Nina (Cook et al., 2010). These droughts and aridity events during the late Holocene may have exerted important influence on Native American and early colonial agricultural societies (Clark et al., 2003). Increased aridity could be manifested by a shift to periodic droughts, low productivity, declining fire importance, and soil erosion and loess production (Woodhouse and Overpeck, 1998; Clark et al., 2003; Herweijer et al., 2006).

Vegetation variability during the Holocene

Hemlock decline

Eastern hemlock (*Tsuga canadensis*) was one of the last tree species to migrate into the western Great Lake Region during the Holocene, expanding rapidly across the Upper Peninsula of Michigan from 6,500 to 5,500 years BP (Davis et al., 1986). This expansion was interrupted by a sudden decline of hemlock pollen abundance at ca. 5,500 years BP that lasted over 1,000-2,000 years, followed by increases again at about 3,500 years BP and continued gradual expansion to its modern western range limit in northwestern Wisconsin and Minnesota (Davis, 1981; Davis et al., 1986; Fuller, 1998; Parshall, 2002).

There are many hypotheses for the decline of hemlock. According to Calcote 2003, the decline of hemlock throughout the eastern Great Lakes Region may have been affected by regional climate shifts in addition to insect/pathogen outbreaks (Davis, 1981; Calcote, 2003). Climate reconstructions based on fossil pollen records from eight sites inside the western range of hemlock at the time of the decline (5,400 years BP) indicatedlower-than-modern precipitation, which may have reduced hemlock’s tolerance for cold stress and winter desiccation and perhaps increased its susceptibility to insects or pathogens (Calcote, 2003). Work at Irwin Smith Bog in Lower Michigan partially supports this idea (Booth et al. 2012), showing that the terminal *Tsuga* decline was closely proximal toan abrupt and persistent decline in water table depth but preceded it by about 200 years, suggesting that the *Tsuga* decline was not directly driven by an abrupt climate change. Furthermore, this high-resolution (contiguous 1-cm intervals) record also demonstrates large fluctuations in *Tsuga* pollen percentages before the terminal decline, and dates the terminal decline at 5,000 years BP, 400 years later than estimates from other sites. This suggests that the terminal *Tsuga* decline was evidently asynchronous across the eastern North America (Shuman et al., 2005). Further expanded networks of high-resolution pollen and paleoclimatic chronologies are required for understanding the patterns and causes of the hemlock decline.

<u>*Fagus grandifolia* declines</u>

American beech (*Fagus grandifolia*), another mesic temperate tree species with climatic tolerances generally similar to *Tsuga canadensis*, also shows pronounced variability through the Holocene, although these declines are not as well documented anddated as for *Tsuga canadensis*. *Fagus grandifolia* arrived in the eastern Great Lakes region in the early Holocene and became widely abundant around 6,000 years BP with variability at different sites (Bennett, 1985). Several abrupt declines of *F. grandifolia* populations occurred during the middle and late Holocene (Figure 1). At Pretty Lake (41.6°N, 85.3°W, Indiana), there was a decline of *F. grandifolia* pollen abundance lasting for about 2,400 years from 4,800 years BP to 2,400 years BP (Odgen, 1969), with a similar event about 200 years earlier at Hudson Lake (41.7°N, 86.5°W, Indiana) (Bailey, 1972). There were also declines of *Fagus grandifolia* pollen abundance at other sites during this time interval, but with a much shorter duration, such as the decline at 2,000 years BP and from 4,200 years BP to 3,200 years BP ate Silver Lake (Odgen, 1966), the decline at 2,800 years BP at Seider Lake (44.5°N, 87.5°W, Wisconsin) (West, 1961), and the decline starting at about 3,100 years BP to 2,100 years BP at Gass Lake (44.1°N, 87.7°W, Wisconsin) (Webb, 1983). However, *Fagus grandifolia* pollen abundance kept increasing at Ladd Lake (41.4°N, 84.8°W, Ohio) (Shane, 1991) and Kellners Lake (44.2°N, 87.8°W, Wisconsin) (Bender et al., 1978) from 3,700 years BP to 2,200 years BP, a different changing trend from other lakes and bogs. Besides the variability during the middle Holocene, there were also declines of *Fagus grandifolia* pollen abundance occurring at 1,000 years BP at Pretty Lake, Hudson Lake and Kellners Lake, with several abrupt declines and increases during the past 1,000 years. All of these sites, however, have radiocarbon dates based on bulk sediments and so the timing of these events may be inaccurate.

Of these, the most recent *Fagus grandifolia* decline at 1,000 years BP is the best documented (Gajewski, 1987; Campbell and McAndrews, 1993; Booth and Jackson, 2003; Booth et al., 2012), and there are three hypotheses for the abrupt declines of *Fagus grandifolia* pollen during the late Holocene: temperature variability, Native American land use changes, and hydroclimatic variability (Booth et al., 2012). Each hypothesis has some supporting evidences. Campbell and McAndrews (1993) used a FORET-derived model to simulate forest composition over the last 1000 years with an assumed 2 °C decrease in mean annual temperature from 1200 to 1850 AD, predicting increases in

Acer, *Fraxinus*, *Quercus* and *Pinus strobus*, and slowly decreasing *Fagus grandifolia* and *Tsuga* beginning at about 1,400 AD which last for about 400 years. However, FORET predictions were inconsistent with pollen data counted by Clark and Royall from Crawford Lake, Ontario, Canada, in which there is a very abrupt decline in *Fagus grandifolia* pollen abundance at 1,400 AD. This abrupt decline, which is unlike the gradual and >100-year-delayed decline predicted by the model, was coincident with the rises in cultural indicators such as Indian agriculture, early successional tree taxa (e.g., *Populus*, *Acer rubrum*), and charcoal (Clark and Royall, 1998). The disagreement between pollen data predicted from a temperature model and field data argues against the hypothesis that the *Fagus grandifolia* decline was caused by a cooling.

Booth and Jackson reconstructed the late-Holocene surface-moisture history, fire, and vegetation dynamics of Minden Bog in Michigan, with the *Fagus grandifolia* pollen decline centering around 1,000 years BP (Booth and Jackson, 2003). The surface-moisture record based on testate amoebae from Minden Bog suggests that neither climatic cooling nor anthropogenic disturbance were responsible for the regional *Fagus grandifolia* decline. Instead, the inferred decreased in effective moisture at 1,000 years BP and associated increase in wildfires led to regional declines in *Fagus grandifolia* populations and the expansion of *Pinus*, and in some areas *Quercus*. Booth et al. (2012) examined forest response to the Medieval Climate Anomaly (MCA) in the humid western Great Lakes Region with proxy records of vegetation, fire and hydroclimate, supporting the hypothesis that multi-decadal moisture variability during the MCA was associated with a widespread, episodic decline in *Fagus grandifolia* populations. In their research, spatial patterns of drought and forest changes were coherent, with *Fagus grandifolia* declining only in areas where proxy-climate records indicate that severe MCA droughts occurred.

The mechanisms for the climate changes, such as hydrological variability, and abrupt declines of *Fagus grandifolia* thus are still in discussion and so far most work has focused on the late Holocene rather than earlier declines. More work is needed to assess earlier variations in the pollen abundances of *Fagus grandifolia* and to put them in context of the moisture, temperature and other environmental changes during the middle and late Holocene.

Forest-prairie ecotone

The prairie-forest transition in the midcontinent of North America is a major physiognomic boundary and a classic example of climate-driven ecotonal dynamics (Williams et al., 2009). In response to increased midcontinental drying during the Holocene, an east-west ecotone gradient in prairie composition developed during the middle Holocene in the central United States (Graumlich and Davis, 1993; Baker et al., 2002; Nelson et al., 2004; Umbanhowar et al., 2006). The position of this ecotone shifted over time. In Minnesota, southern Manitoba and Iowa, the prairie expanded eastwards from 11 to 7 ka, with the most rapid expansion rate between 10 and 8 ka (Williams et al., 2008). From 8 to 7 ka, the prairie expansion continued but the rate greatly slowed, and the prairie-forest ecotone reached its maximum eastward extent by 7ka, remaining there through 6ka. Then the prairie retreated west and reached its present position from 4 to 2 ka (Williams et al., 2009).

Besides the general trend described by maps of the shifting ecotone, several high-resolution pollen records during the Holocene in the Great Lake Region with precise chronologies have been collected in recent years. These suggest differences in the timing and abruptness of prairie-forest and climate transitions at individual sites (Camill et al., 2003; Nelson et al., 2004, 2006; Umbanhowar et al., 2006; Nelson and Hu, 2008). Nelson and Hu described pollen, stable-isotope ($\delta^{18}O$ and $\delta^{13}C$), mineral and charcoal data from three lakes in Minnesota, showing relatively wet climate with increasing summer temperature before 8,000 years BP and then asymmetric rates of climate change during the middle-Holocene with an abrupt increase in temperature at 8,000 years BP and a gradual, but variable decline from 7,800 to 4,000 years BP. As a response, the conifer forests changed to mixed-grass prairie without an intervening period of tallgrass prairie or deciduous forest during the early Holocene, whereas the retreat is characterized by transitions from mixed-grass to tallgrass prairie to deciduous forest and finally to coniferous forest, indicating that vegetation is more strongly influenced by climatic changes than by fire-regime shifts in the three lakes (Nelson and Hu, 2008). The time-transgressive drying trend in midcontinental North America could indicate a progressive shift in atmospheric drying from west to east, or could be explained as mediation of timing and rate of site responses to regional drying caused by local factors (Williams et al., 2010).

Also multiproxy analyses, including sediment mineral composition, carbonate $\delta^{18}O$, ostracode assemblages, diatom assemblages, pollen and charcoal $\delta^{13}C$ from early and middle Holocene sediments from Chatsworth Bog and Nelson Lake in Illinois were summarized by Nelson et al. in 2006 to infer fluctuations in moisture availability, vegetation composition and fire in Great Lakes Region. They indicate three phases of vegetation composition at the two lakes: fire-sensitive trees (e.g., *Ulmus, Ostrya, Fraxinus*, and *Acer saccharum*) declining and prairie taxa expanding with increased aridity from 10,000 years BP to 8,500 years BP, prairie coexisting with fire-sensitive and fire-tolerant trees (e.g., *Quercus* and *Carya*) with less aridity between 8,500 years BP and 6,200 years BP, prairie taxa dominant although without any increase in aridity around after 6,200 years BP. Connected with the records discussed earlier, the emergence of prairie taxa and aridity in Illinois, changes in forest composition and wetland testate amoebae assemblages in Michigan, and the expansion and retreat of prairie in Minnesota indicate that hydrological variability was a dominant driver of vegetation dynamics during the Holocene. These climatic and vegetation variations appear to have been heterogeneous in time and space, suggesting that such hereogeneity is a characteristic feature of variations on centennial to millennial time scales in midwestern North America. Shifts in fire regime appear to have played an important role in the establishment and maintenance of prairie communities in the eastern Prairie Peninsula (Nelson et al., 2006).

At this review shows, most work about vegetation and climate changes during the Holocene in the middle central United States has been done in Minnesota, Wisconsin, Illinois and Michigan, but Holocene vegetation history further east (e.g. Indiana, Ohio) remains poorly understood. More work is needed to understand the mechanisms behind the abrupt individual shifts in tree taxa and the response of vegetation changes to droughts in the middle central United States. High-resolution and long records such as the one developed here for Spicer Lake, IN are needed to analyze ecological responses to drought events during the Holocene in central North America.

2. Time Series Analysis

Time series analysis

I apply time series analysis to the pollen and loss-on-ignition (LOI) records from Spicer Lake in order to model vegetation responses to climate, the corresponding response of vegetation to environmental changes around the lake, and the influence of antecedent vegetation. I assume that LOI is a proxy for hydrological variability, because variations in the lake control the distribution of coarser-grained mineral sediments versus finer-grained organic-rich sediments in the basin center (Shuman, 2003; Marsicek et al., 2013). The time lags and differences between pollen records, as a proxy for vegetation composition, and LOI records, as a proxy for past proxy hydrological variablity, can suggest whether the vegetation variability around the lake is caused by climate changes or not.

Temporal data have three crucial characteristics (Cleland, 2002). First, temporal data are directional: the past can influence the future, but not the reverse. This critical property can be used to strengthen inference about causality because effects cannot precede causes, and to predict changes. Second, time is one-dimensional, making temporal patterns simpler to analyze than spatial patterns. Third, temporal domains are often unbounded because the beginning and end of a time series are arbitrary. However, often there are natural boundaries to time series, such as colonization of new space, continental glaciations or mass extinctions (Dornelas et al., 2013). For the Spicer Lake time series, the natural boundaries are the post-deglaciation formation of the lake and the date of core collection.

Observed temporal changes in pollen can be modeled as a function of three main factors: the vegetation state at the prior time step, environmental changes driving a change in vegetation, and an error term encompassing measurement error and stochastic processes in the system. Historical influence is represented by temporal autocorrelation in time series of fossil pollen abundances. Environmental changes encompass changes in both anthropogenic drivers – for example, agriculture, population increase, urbanization and industrialization – and climatic drivers – droughts, increase of precipitation, cooling or warming (Dornelas et al., 2013). In this case, we are using a single proxy driver – LOI -- which is sensitive to past changes in lake level and hence the deposition and focusing of fine-grained organic carbon (Shuman, 2003). Errors, including measurement errors, proxy errors and stochastic process errors, can reduce our ability to interpret patterns. In order to draw inferences about how different predictor variables affect these processes and to forecast pollen abundance changes, errors must be minimized or estimated, and historical effects must be understood (Gaston and McArdle, 1994).

Bayesian analysis and likelihood

A Bayesian statistical framework is used to construct the time series analysis and age-depth model building in this thesis.

Models are used to describe relations among data, and these relations are represented by model structure and parameters in the model (Christen et al., 1995). The

Bayesian approach uses probabilities to express the uncertainty in parameters before and after seeing the data. In broad terms, the Bayesian model has three parts:

1) The prior probability density function. This may be read as “how much belief do I attach to possible values of the unknown parameters before observing the data?” A large prior probability indicates that the value of the parameter is thought to be relatively likely based on prior knowledge; a small value indicates that it is relatively unlikely.

2) The likelihood. This may be read as “how well are particular values of the parameters supported by the data?” A large likelihood value indicates that the data strongly support the parameters; a small likelihood indicates that the data weakly support the parameters.

3) The posterior density function. This may be read as “how much belief do I attach to possible values of the unknown parameters after observing the data?” A large posterior density indicates that the corresponding parameter value is relatively likely; a small value indicates that it is relatively unlikely.

If θ is used to represent parameters, x to represent data, $g(\theta)$ to represent the prior probability density function of parameters, $l(x,\theta)$ to represent likelihood of observed data based on the prior parameters, $h(\theta|x)$ to represent the posterior probability of parameters conditioned on the data, then the Bayesian theorem states:

$$h(\theta|x) \propto l(x,\theta)\ g(\theta)$$

This relationship indicates that the posterior probability of parameters is correlated directly with the likelihood and prior probability density function.

This operation combines the two sources of information provided by the prior and provided by the data. An important feature of Bayesian models is that one can incorporate into the analysis coherently and logically relevant prior knowledge about the parameters. The Bayesian approach is highly flexible and allows fitting of complex models, although it often requires sophisticated and computationally intensive techniques to estimate the parameters of interest.

Research Questions, Hypotheses and Study Design

This thesis focuses on reconstructing past vegetation and environmental variations at Spicer Lake during the Holocene and testing hypotheses about whether these variations were caused by past droughts. In this thesis, I will interpret vegetation history around the lake, and analyze the latent relationship between previous and current pollen abundance and the influence of LOI as a proxy for hydrological variability on individual taxa.

Vegetation variations can be inferred from pollen records. For the relationship between previous and current pollen abundance and the influence of LOI, the hierarchical models developed from Bayesian statistics will be used here. My working hypothesis is that the large LOI shifts during the Holocene were caused by moisture changes. I expect that the pollen record, which represents the vegetation composition, should show signs of drought-sensitive taxa (i.e. *Fagus grandifolia*) becoming less abundant during or after the droughts.

H0: The LOI variability was not caused by moisture changes.

Under the null hypothesis, the LOI events were caused by some other unknown factor. Under this hypothesis, the pollen record will either be stable during the Holocene or will show changes that do not correspond to the LOI changes.

H1: The LOI variability was caused by moisture changes, and the vegetation was sensitive to the LOI variability.

In this hypothesis, the LOI signal is in fact a signal of moisture variability around the lake, and these variations triggered changes in forest composition in Indiana during the Holocene.

H2: The LOI variability was partly influenced by moisture changes, and vegetation could be indicated by LOI changes, but not decided by LOI variability completely.

Pollen changes during the Holocene, especially the moisture-sensitive taxa such as *Fagus grandifolia*, correspond to LOI variability, but are not determined by LOI variations completely. Other factors, although unknown, are affecting LOI changes.

Pollen records and LOI records are compared and jointly analyzed in this thesis to test these hypotheses about the relationship between vegetation and hydrological variability. Two hierarchical Bayesian models are used to test whether a) mineral input is an indicator of hydrological variability and b) whether this variability influences on vegetation and pollen abundances.

Study Site

Spicer Lake (41°44'52" N, 86°31'19" W) is located in New Carlisle, St. Joseph County, northern Indiana, near southeastern Michigan (Figure 2). With about five acres of open water remaining in the center of the lake, the lake is surrounded by marsh and swamp forest, illustrating a succession from open water to swamp forest (Figure 2).

Spicer Lake is a kettle lake formed by blocks of stagnant ice embedded in the glacial till left behind when the Laurentide Ice Sheet retreated in Indiana between about 14,000 and 12,000 years ago (Dyke et al., 2003). Since deglaciation the lake has accumulated various forms of organic and inorganic sediments, including pollen, charcoal, mineralogenic sediments, plants macrofossils, and authigenic organic carbon, together providing indicators of the history of vegetation, climate and environment around the lake over the last 14,000 years.

Methods

The Williams Lab collected two 15m gap-overlapped sediment cores, labeled as A1 and A2 from Spicer Lake, in summer 2006. A standard 5cm Livingston corer was used to capture the sediment-water interface from an anchored floating platform. Tubes were capped and stored upright. Livingston cores were extruded, described, and wrapped on deck, then stored in split polyvinyl chloride (PVC) tubes and labeled.

Cores initially were taken to the Limnological Research Center at the University of Minnesota for longitudinal splitting, scanning for magnetic susceptibility (Thompson et al., 1975), and photographing at high resolution. The A1 core was the main core used in this thesis. One half of each core was used as the working half, and the other was reserved as an archive half.

In Madison, the working half was cut into 1cm thick segments to preserve the stratigraphic integrity of the sediments. All samples used here are from these segments.

1. Radiocarbon Dates and Age Model

We sent 14 accelerator mass spectrometry (AMS) radiocarbon samples for dating (Table 1). Six dates were acquired from the Center for Applied Isotope Studies (CAIS) at the University of Georgia, Athens; four dates were acquired from the Woods Hole Oceanographic Institution (WHOI) in Massachusetts; and four dates were acquired from the Keck Carbon Cycle Accelerator Mass Spectrometry Laboratory (Keck-CCAMS) at University of California, Irvine. All dates reported here are in calendar years using calibration with the original ^{14}C age estimates from IntCal09 shown in Table 1. All depths are reported relative to the sediment-water interface.

I used the *bacon* age model, a Bayesian age-depth model developed (Blaauw and Christen, 2011) to infer the time of deposition for sediments not directly associated with a ^{14}C date (Figure 3, Table 2). In *bacon,* sediment accumulation is modeled as a smooth autoregressive time series. Prior parameters include choice of calibrated curve, postbomb curve, minimum year, maximum year, section length and sediment accumulation rate (Table 2) The sedimentation accumulation rate is established based on the rates in other lakes in eastern North America (Goring et al., 2012), and the information provided here is converted into a prior density function of age estimates. *Bacon* determinates maximum likelihood and then calculates the posterior density of the parameters from the prior and likelihood, and uses this posterior distribution to infer the uncertainty of the ages estimated from the model.

Sediment accumulation rate was set as a gamma distribution. The accumulation rate at given depth is related to the previous depth and an independent noise component. This provides “memory” or coherence in accumulation rates along the core and smooths the modeled age-depth curve, thereby reducing extreme variations (Blaauw and Christen, 2011). The prior accumulation rate was set to 10 year/cm based on Goring et al. (2012). Another parameter set in *bacon* is the section length of the core, which is not strictly a prior parameter representing the information about the core, but rather established for controlling computing speed; shorter lengths and more sections in the core allow more flexibility of the model to fit to within-core changes of sedimentation rate, but will reduce the computational speed. The section length in this thesis is set as 20 cm. All parameters are shown in Table 2. All AMS radiocarbon dates are used in the *bacon* age-depth model. *Bacon* assumes continuous accumulation of sediments, and rejects dates results that violate this assumption, so the presence of an outlier date affects model uncertainty but not the maximum likelihood estimates for the age model (Gill et al., 2011). *Bacon* returns estimated calendar ages at a 1cm interval. All ages reported here are calendar years before radiocarbon present (1950 AD).

2. Loss-On-Ignition

LOI is widely used to estimate the organic and carbonate content in lake and mire sediments (Heiri et al., 2001). By heating the sample at 550 °C the organic carbon in the sediment will be completely ignited, then at 900-1000 °C calcium carbonate will be burned off (Dean, 1974). Through careful measurements of weights before and after each burn, LOI can be used to calculate the relative fraction of organic carbon, inorganic carbon, and mineralogenic sediments.

The organic carbon content in lake sediment cores may vary because of temporal changes in: (1) sediment composition controlled by factors such as productivity and decomposition; and (2) the patterns of sediment accumulation controlled by factors such as basin morphology and water level (Shuman, 2003). Mineral inputs can change in response to shoreline erosion (Almquist-Jacobson et al., 1992; Bjorck et al., 1982) and upland inputs caused by erosional events (Brown et al., 2000; Liu and Fearn, 2000), which are related to hydroclimatic events. For sediment accumulation, reduced groundwater recharge caused by low lake level probably increases the dissolved organic content of the lake water by causing a relative increase in the organic-rich over-land flow into the basin (Shuman, 2003). On the other hand, lowered lake level can reduce organic carbon deposition for sites near the shoreline, and a rapid rise in lake level may generate an influx of eroded inorganic shoreline material to shoreward portions of lake sediments, but organic inputs to the center of the basin may or may not change.

Shannon Hernandez, Jeremiah Marsicek and Dominique Alhambra processed all LOI samples in the Spicer Lake core. 1cm^3 samples were taken with volumetric syringes at 1cm intervals throughout the core. All samples were heated in a muffle furnace at 100

°C overnight to dry the samples, at 550 °C for four hours, and at 1000 °C for two hours to calculate the fraction of weight loss from water, organic carbon and carbonates at each temperature. The residue was weighed to calculate the mineral proportion of the samples.

3. Chemical input

The working half of the A1 core, from 471cm to 752cm, was scanned in the Limnological Research Center (LRC) at the University of Minnesota by the Cox Analytical Itrax XRF Core Scanner at the resolution of 0.2mm for elemental composition and x-radiographic images. The elemental composition results were smoothed to 1cm for analysis.

The elemental data are analyzed as ratios that have been previously linked environmental variations. The Zr/Al ratio has been suggested to be a proxy for aeolian sedimentary input, because Zr is concentrated in more mobile sandy-silt fractions while Al_2O_3 represents the concentration of terrestrially-derived feldspars (Roy et al., 2006, 2009). Similarly, Rb variability is associated with feldspars and other K-rich minerals, while Sr is enriched in carbonates, so the Rb/Sr ratio is used as a proxy for weathering intensity in the basin (Jin et al., 2005). The ration of V/Cr is used as an indicator for lake anoxia, with high V/Cr ratios indicating anoxic sediments. V preferentially precipitates under anoxic conditions, while Cr is immobile under both anoxic and oxic conditions (Harris et al., 2004; Das et al., 2009). All ratios are smoothed to a resolution of 1cm intervals, in order to reduce noise caused by grain-scale variations in elemental composition.

Because only the part from 752 cm to 471 cm of cores – about 9,000 years BP to 6,200 years BP – in the lake was scanned for XRF, we show the data in this thesis, but do not analyze XRF data.

4. Pollen Analysis

Fossil pollen provides evidence of vegetation changes through time (von Post, 1914; Prentice et al., 1988; Sugita, 1994). The composition of fossil pollen assemblages can reflect the distribution and abundance of plants in the surrounding vegetation. Palynologists identify pollen and spore types by grain size; shape of the exine; the number, position, and shape of apertures in the exine; and the arrangement of sculptural elements on the exine surface. Confident identification of pollen types can be accomplished to the genus and family level; a few pollen types can be identified to species level (McAndrews et al., 1973; Kapp et al., 2000). The inability to identify grains to the species level is not an insurmountable obstacle to the reconstruction of vegetation and climate from pollen records, because these higher taxa tend to have distributions as coherent as species in climate space (Bartlein et al., 2010). This has been confirmed by more recent work that has shown the general tendency for lineages to be evolutionarily conservative in terms of climate preferences (Huntley et al., 1989; Ackerly, 2003; Moles et al., 2005; Wake et al., 2009).

Modern-analog analyses of networks of pollen records have been widely used to reconstruct past vegetation and climate from regional to continental scales (Davis et al., 2000; Calcote, 2003; Williams, 2003; Viau et al., 2006; Bartlein et al., 2011). According to prior research, the main tree pollen taxa in Indiana during the Holocene are *Pinus* (pine), *Picea* (spruce), *Acer* (maple), *Quercus* (oak), *Ulmus* (elm) and *Fagus grandifolia* (beech)(Ogden, 1966; Williams, 1974; Booth et al., 2005; Gill et al., 2009). In terms of plant functional types (Prentice et al. 2000), both *Picea* and *Pinus* are evergreen needleleaf trees and are classified as boreal evergreen conifers and cool temperate conifers. High abundances of *Picea* or *Pinus* in fossil pollen records thus are interpreted to indicate colder-than-present cold climates. *Acer, Quercus, Ulmus* and *Fagus grandifolia* are deciduous broadleaf tree classified as temperate summergreens; thus, the increase of the three taxa indicates rising temperatures. Among these temperature summergreen trees, some species of *Quercus* are drought-tolerant, while *Fagus grandifolia* is the most sensitive to soil moisture changes.

Sediment samples for pollen analysis are taken with $1cm^3$ volume using modified volumetric metal syringes. In some cases where sediments were mineral-rich silts and sands with, $2cm^3$ were taken. I added 1ml of well-mixed polystyrene microspherule solution ($5.0*10^4$ sph/ml) to calculate pollen concentrations and accumulation rates, then added 10% hydrochloric acid (HCl) heated it for 5 minutes in a hot water bath to remove carbonates from the samples. Samples are then treated with a hot 10% potassium hydroxide (KOH) solution for 10 minutes in a hot water bath to break up sediment and to remove humic acids. Between each pair of steps, samples are rinsed with deionized (DI) water two to three times and centrifuged at 3000 rpm. Ethanol (EtOH) is added to the top of each sample to sink any floating particles if necessary.

After KOH treatment, samples are screened through 250 μm sieves to remove large organic particles and coarser sands if they were very organic or fibrous. Then samples are treated with 48% hydrofluoric acid (HF) in a hot water bath for 20 minutes to remove silicates (e.g. sand, silt, clay). Following HF treatment, samples are treated with 10% HCl in a hot water bath for five minutes. This step breaks up siliceous colloidal clumps that form during the silica digestion by HF. Then samples are rinsed with DI two to three times, and twice with glacial acetic acid to remove water. After that, samples are added to Erdtmann's acetolysis solution, composed of 1 part concentrated sulfuric acid and 9 parts acetic anhydride, and heated in a hot water bath for 2 minutes. This step removes organic materials (cellulose), cleans the surface of the pollen grains, and etches the grains to make them easier to identify based on sculptural elements. Following acetolysis, samples are rinsed once with glacial acetic acid to adjust the pH and then with DI two to three times.

Samples in which the organic material remains clumped after these steps are treated with 10% KOH again, then all samples are rinsed twice with 95% EtOH and once Tertiary Butyl Alcohol (TBA) to replace water in the samples, which does not mix with the silicone oil mounting medium. Then samples are transferred to dram shell vials using TBA and centrifuged to remove TBA. I added 3 to 5 drops of silicone oil to each sample to suspend the pollen in the microscope slide, then capped and labeled all the samples.

Jacquelyn Gill previously counted the pollen for the late-glacial and early Holocene portion of the record, from 750cm to the bottom of the core. For the records in the Holocene, pollen samples were taken at 8cm intervals from the top to the depth of 750cm. 93 samples were taken for pollen analysis. All pollen samples were scanned at 400x magnification (1000x magnification with oil immersion was used as necessary) and counted to at least 300 pollen grains. Identification was done according to Kapp et al.

(2000) and McAndrews et al. (1973). Aquatics were rare in this record. Most herbs were identified to the family level, with the exception of *Ambrosia* and *Plantago*, which were identified to genus. Pollen abundance is expressed as percentage of the total pollen grains in the sample, which includes all arboreal taxa and terrestrial herbs. I searched for and was able to discriminate all pollen types that Jacquelyn Gill identified, but did not identify all spores that she searched for. The spore types that she discriminated and I did not were: moss type, *sphagnum*, black mold, *aureobasidium*, *coprinus*, *podospora*, *hemicolsporium*, *helicoma*, *botryococchus*, *pediastrum* and egg type. Hence any apparent absence of these types above 750cm may be due to non-discrimination rather than true absence.

After the initial round of counting pollen from the top to 744cm, a discrepancy in the pollen records was found between my counts and Gill's counting results: the *Acer* pollen percentage in the sample at 750cm which was counted by Gill was apparently higher than the *Acer* pollen percentage in the sample at 744cm which that I counted, while the *Quercus* pollen percentage in Gill's result was much lower than in mine. In order to see whether the discrepancy is caused by vegetation changes or miscounting either by me or by Gill, I examined *Acer* and *Quercus* references in the lab again, then recounted Gill's samples at the depths of 750cm, 756cm, 774cm and 846cm. The differences between my recounting results and Gill's results for each taxon were smaller than 5%, indicating that I had originally miscounted the *Acer* and *Quercus* pollen grains in the samples from the top of the core to the depth of 744cm before. To correct the miscounting, I recounted the *Acer* and *Quercus* pollen in all the samples from the top of the core to the depth of 744cm later. The pollen percentages shown in this thesis are from the second round of counting results.

5. Pollen Synthesis

I obtained other regional pollen records (from Ohio, Indiana, and Wisconsin) with *Fagus grandifolia* from the Neotoma Paleoecology Database (www.neotomadb.org), which I accessed in April, 2013 I used the Neotoma default chronologies, which were in radiocarbon years. I converted these to calendar years by using the Neotoma-estimated radiocarbon ages for each sample and then converting that radiocarbon age to calendar years using *Calib* and the IntCal13 calibration curve (http://calib.qub.ac.uk/calib/calib.html).

6. Time Series Analysis

Three forms of a Bayesian hierarchical model were created (Figure 4). Model 1 is a simple autoregressive model of pollen abundance in which the current pollen abundance depends only on pollen abundance at the previous time; model 2 is also a simple model of LOI variability in which the current pollen abundance depends only on mineral content; while model 3 adds the mineral abundance from LOI data and pollen abundance at the previous time as parameters, thus testing whether pollen abundances can be predicted from LOI and implicitly whether vegetation is a function of climate. If the results from model 2 and model 3 are not better than model 1, it indicates that pollen shifts are less related to LOI variability than auto-correlation, suggesting that the LOI from a single core is not a good proxy for hydrological variability or that hydrological variability had no influence on past vegetation changes. If model 2 and model 3 have more explanatory power than model 1, this implies that past vegetation dynamics (as signaled by pollen) were influenced by climate variability (based on LOI). The model structure was developed at the PalEON boot camp in summer of 2012 under the guidance of Chris Paciorek, who is a statistician at the University of California Berkeley and one of the teachers at the PalEON boot camp.

Model 1: pollen abundance in current time and previous time

The basic model for the pollen abundance is:

$$y_t \sim f\ (\theta_t, \sigma^2) \qquad \text{equation (1)}$$

$$\theta_t \sim f\ (\theta_{t-1}, \tau^2) \qquad \text{equation (2)}$$

where y_t is the pollen percentage of individual taxon i at time period of t. The first line of the model simply states that the pollen percentage of taxon i is related to the probability θ_t that taxon i can be found in time period t. The second line of the model means that the probability that taxon i can be found in time period t is related to the probability that taxon i can be found in time period t-1. This creates a simple first-order auto-regressive model. Parameters σ and τ are error terms representing uncertainties in the relationship: τ is the systematic uncertainty caused by environmental factors other than the vegetation in the previous period; σ is the systematic and analytical uncertainty produced during pollen accumulation in the lake sediments and during pollen processing and counting.

For the probability that pollen can be found in the sample, I use the binomial distribution: the pollen found in the samples is either taxon i or not, and the probability for pollen being taxon i is θ. The equation, developed from equation (1) above, is:

$$y_t \propto \theta_t^x (1-\theta_t)^{n_t-x} \qquad \text{equation (3)}$$

n_t is the total number of pollen grains in the sample of time period t. x is the number of pollen grains of taxon i in the sample. Pollen percentage of taxon i is a binomial distribution with the probability that pollen taxon i can be found in the sample of time period t.

The probability that pollen taxon i is found in time period t is normally distributed with the probability that taxon i was found in the time period t-1. Because θ is the probability ranging from 0 to 1, but normal distributions are centered on zero, I log-transform θ_t, creating a new parameter λ_t that can range from –∞ to +∞ and meets the requirement for the normal distribution.

$$\lambda_t = \log(\theta_t/(1-\theta_t)) \qquad \text{equation (4)}$$

$$\lambda_t \sim N(\lambda_{t-1}, \tau^2) \qquad \text{equation (5)}$$

These equations are directly analogous to equation (1) and equation (2), but with the transformations of θ_t to λ_t.

I then modify equation (4) to use λ_t to represent θ_t. Combined with the binomial distribution, the model for pollen abundance in the current and previous time periods is:

$$y_t \propto \theta_t^x (1-\theta_t)^{n_t-x} \qquad \text{equation (3)}$$

$$\theta_t = e^{\log \lambda_t}/(1+e^{\log \lambda_t}) \qquad \text{equation (7)}$$

$$\lambda_t \sim norm(\lambda_{t-1}, \tau^2) \qquad \text{equation (8)}$$

Equation (8) means that the probability that pollen taxon i is found in the sample is determined by the probability in the previous time period with a normal distribution. Equation (3) indicates that the pollen abundance of taxon i found in the sample is a binomial distribution determined by the probability from equation (7) that is the transform of equation (8).

Model 2: pollen abundance with mineral abundance

This replaces the pollen abundance at the previous time in model 1 with mineral content from LOI variability to include the hypothesized influences of climate on vegetation via the proxies LOI. The initial formulations are the same as Model 1:

$$y_t \propto \theta_t^x (1-\theta_t)^{n_t-x} \quad \text{equation (3)}$$

$$\theta_t = e^{\log \lambda_t}/(1+e^{\log \lambda_t}) \quad \text{equation (7)}$$

$$\lambda_t \sim norm(\lambda_{t-1}, \tau^2) \quad \text{equation (8)}$$

Equation (7) can be transformed to:

$$\lambda_t = \log(\theta_t/(1-\theta_t)) \quad \text{equation (7)}$$

Then I used z_t to replace λ_{t-1} in equation (8):

$$\lambda_t \sim norm(z_t/(1-z_t), \tau^2) \quad \text{equation (9)}$$

Equation (9) shows the probability that pollen of taxon i is found in the sample is related with mineral content in the core. In Model 2, this probability is only determined by the mineral input change in the sample. z_t represents the mineral abundance in the sample at the time period t. The model 2 about mineral input is:

$$y_t \propto \theta_t^x (1-\theta_t)^{n_t-x} \quad \text{equation (3)}$$

$$\theta_t = e^{\log \lambda_t}/(1+e^{\log \lambda_t}) \quad \text{equation (7)}$$

$$\lambda_t \sim norm(z_t/(1-z_t), \tau^2) \quad \text{equation (9)}$$

In model 2, equation (3) and equation (7) are the same as model 1, while equation (9) indicates that the probability that pollen of taxon i is found in the sample is only determined by the the mineral input changes in this time period.

Model 3: pollen abundance with mineral abundance

Model 3 combines model 1 and model 2 to include the hypothesized influences of climate on vegetation via the proxies LOI and pollen and the autoregressive model of vegetation change. The initial formulations are the same as Model 1:

$$y_t \propto \theta_t^x (1-\theta_t)^{n_t - x} \qquad \text{equation (3)}$$

$$\theta_t = e^{\log \lambda_t}/(1+e^{\log \lambda_t}) \qquad \text{equation (7)}$$

$$\lambda_t \sim norm(\lambda_{t-1}, \tau^2) \qquad \text{equation (8)}$$

Equation (7) can be transformed to:

$$\lambda_t = \log(\theta_t/(1-\theta_t)) \qquad \text{equation (7)}$$

Then I used θ_t to replace λ_t in equation (8):

$$\log(\theta_t/(1-\theta_t)) \sim norm(\log(\theta_{t-1}/(1-\theta_{t-1})), \tau^2) \qquad \text{equation (10)}$$

Equation (10) shows how the probability that pollen of taxon i is found in the sample is determined. In Model 3, this probability is not only determined by the pollen abundance in the previous time period, but is also related to the mineral input change in the sample. I combined equation (9) and equation (10), such that the probability that taxon i can be found in the sample at time period t is determined by the pollen abundance at the previous time period and the mineral input change.

$$\log(\theta_t/(1-\theta_t)) \sim norm(\log(\frac{\theta_{t-1}}{1-\theta_{t-1}} * (\frac{z_t}{1-z_t})), \tau^2) \qquad \text{equation (11)}$$

z_t represents the mineral abundance in the sample at the time period t. The parameter in the normal distribution is composed of the probability that taxon i was found in the sample at the previous time period and the change of mineral input to the sediment. I use λ to replace θ again to simplify the equation:

$$\lambda_t \sim norm(\lambda_{t-1} + \log \frac{z_t}{1-z_t}, \tau^2) \qquad \text{equation (12)}$$

The model 2 about pollen abundance and mineral input is:

$$y_t \propto \theta_t^x (1-\theta_t)^{n_t - x} \qquad \text{equation (3)}$$

$$\theta_t = e^{\log \lambda_t}/(1 + e^{\log \lambda_t}) \qquad \text{equation (7)}$$

$$\lambda_t \sim norm(\lambda_{t-1} + \log \frac{z_t}{1-z_t}, \tau^2) \qquad \text{equation (12)}$$

In model 3, equation (3) and equation (7) are the same as model 1, while equation (12) indicates that the probability that pollen of taxon i is found in the sample is not only determined by the probability in the previous time period, but also the mineral input changes in this time period.

MCMC and JAGS

Markov Chain Monte Carlo (MCMC) is a computational technique used to create a posterior distribution by sampling from the prior distribution and observational data. The strategy here used is called Gibbs sampling – it involves cycling through parameters and sampling from

$$g(\theta_1 | \theta_2, \ldots, \theta_p, y)$$

$$g(\theta_2 | \theta_1, \theta_3, \ldots, \theta_p, y)$$

$$\cdots$$

$$g(\theta_p|\theta_1, \theta_2, \ldots, \theta_{p-1}, y)$$

In this cycling, θ includes all unknown parameters in the process. JAGS is a package in R (Plummer, 2013) , as the interface to run the MCMC chains.

Four common pollen types in the middle and late Holocene – *Fagus grandifolia, Quercus, Acer* and *Ulmus* – are separately modeled, using Models 1, 2, and 3, to analyze the influence of pollen abundance at the previous time period and mineral abundance from LOI data. Results are compared to test hypothesis H0, H1 and H2.

Results

1. Age-Depth Model

Fourteen radiocarbon dates are used for the *bacon* age model (Figure 3). I also used the *Ambrosia* increase at 32.5 cm as an age control (Figure 6), which is interpreted to indicate European settlement in Indiana in 1820 AD. Four radiocarbon dates were identified as outliers in the *bacon* age model due to their too-young ages. The top 10 meters of the core extend back to about 15,000 years ago, with a sharp increase of accumulation rate at 950 cm, and a decrease to the rate as before again at about 900 cm. This peak of accumulation rate occurs just before the increase of minerals and decrease of organic carbon at about 900 cm. Above 900 cm, the accumulation rate is near 10 cm/year.

2. LOI analysis

Organic carbon percentages in the lake sediment were low during the late-glacial period, then increased and remained high during the Holocene except when interrupted by brief drops (Figure 5). Mineral input changed in the opposite trend. The general increase in organic carbon content during the Pleistocen-Holocene is consistent with other sites in Great Lake Region and is interpreted to indicate an increase in lake productivity as temperatures rose (Shane and Anderson, 1993). The LOI curves are not stable during the Holocene (Figure 5). There are seven sharp increases in mineral content and decreases of organic carbon: 1) around 8,500 years BP; 2) around 8,000 years BP; 3) around 6,800 years BP; 4) around 5,800 years BP; 5) (the largest) from 4,500 years BP to 3,500 years BP; 6) the most recent one was around 1,300 years BP and 7) after European settlement. Increases in mineral content occurred at 700 cm, 650 cm, 550 cm, 410 cm, 200 cm, 115 cm and 5 cm depth below sediment surface. These drastic changes may be signals of hydrological changes at the lake. To my knowledge, no other Holocene LOI records from this region have been analyzed at the resolution necessary to discover the abrupt changes observed here.

3. Pollen analysis

86 pollen and spore types were identified in the Spicer Lake sediments (Table 3). Only pollen types that reached the maximum percentage of at least 5% are included in the pollen diagram (Figure 6-8). A table with counts for all taxa is in Appendix I.

Five zones are identified from the pollen abundances (Figure 7):

Zone 1: *Abies-Picea*, conifer forest, from about 13,000 years to 11,800 years BP. This zone has high abundance of pollen from conifer trees such as *Abies* and *Picea.* Among them *Picea* was the most abundant, with pollen percentage close to 30%. Pollen from deciduous trees was rare: only *Acer*, *Fraxinus nigra* type and *Ostrya/Carpinus* type were relatively abundant, although the percentages were lower than for conifer trees. *Poaceae* is abundant during this time period, with pollen percentage close to 10%. This zone is interpreted to represent a conifer forest or woodland with deciduous elements under mesic conditions.

Zone 2: *Pinus-Abies-Picea-Ulmus*, a mixed forest, from 11,800 years to 10,200 years BP. Conifer pollen types that were abundant during the previous interval, *Abies* and *Picea*, declined abruptly during this time period. *Pinus* pollen increased rapidly from less than 5% to near 40%, becoming the most abundant type. For deciduous trees, pollen taxa that were relatively abundant during the previous interval – *Acer*, *Fraxinus nigra* type and *Ostrya carpinus* type – decreased during this time period, while *Betula* and *Ulmus* increased, especially *Ulmus*, reaching to about 20% of the total terrestrial taxa. *Quercus* increased abruptly near 10,800 BP. *Poaceae* decreased to less than 5%. According to the pollen data, vegetation composition changed a lot compared to the previous interval, with declines of previously abundant taxa and increases of previously uncommon taxa for both conifer and deciduous trees.

Zone 3: *Acer-Quercus-Ulmus-Ostrya/Carpinus-Abies-Picea-Pinus*, interpreted to represent a mixed conifer-deciduous forest, from 10,200 years BP to 9,200 years BP. Pollen abundance of conifer trees – *Abies*, *Picea* and *Pinus* – decreased to a relatively small component with less than 5% of the total terrestrial pollen sum, indicating fewer conifer trees during this time period. *Acer*, *Quercus* and *Ulmus* pollen abundances increased and gradually became the most abundant tree pollen taxa on land with *Ostrya/Carpinus* type remaining relatively stable. Herbaceous pollen remained rare.

Zone 4: *Acer-Quercus-Ulmus*, interpreted to represent deciduous forest, from 9,200 years BP to 6,800 years BP. Pollen records were mainly composed of deciduous pollen from this interval, while conifer pollen declined to a very small component. *Acer*, *Quercus* and *Ulmus* were the three main abundant pollen types; each of them increased to near 20% of the total terrestrial taxa. *Ostrya/Carpinus* type decreased gradually to less than 5% on land. Herbaceous pollen was still rare. This zone is inferred to represent deciduous forests with abundant *Acer*, *Quercus* and *Ulmus* around the lake.

Zone 5: *Acer-Fagus grandifolia-Quercus-Ulmus*, deciduous forest, from 6,800 years BP to the present. The rapid increase of *Fagus grandifolia* pollen was the most important change in this interval, from less than 5% before 6,800 years BP to near 20% at the maximum, with several abrupt changes during the period. Deciduous pollen types were still abundant, and *Acer* and *Quercus* pollen abundance remained high. *Ulmus* pollen declined slowly at about 6,000 years BP, and became relatively few, near 5%, to the present. Herbaceous pollen remained rare. The pollen record indicates that the main vegetation type on land is deciduous forest with *Fagus grandifolia* becoming an increasinnly important but variable constituent component.

The increases and decreases of *Fagus grandifolia* pollen are the most notable feature of vegetation dynamics during the middle and late Holocene. To illustrate this, I added six subzones to Zone 5, using the original CONISS output (Figure 8) from to 6,800 years BP to the present. These subzones closely match to changes in *Fagus grandifolia* pollen abundances.

In summary, the pollen abundance data show that the sequence of vegetation composition around Spicer Lake is: conifer forest dominated by *Picea* and *Abies* before 11,800 years BP; conifer forest dominated by *Pinus* from the start of the Holocene to 10,200 years BP; conifer and deciduous forest in the next 1,000 years until 9,200 years BP; deciduous forest dominated by *Acer*, *Quercus* and *Ulmus* in the early and middle Holocene; deciduous forest dominated by *Acer*, *Quercus*, *Ulmus* and variable *Fagus grandifolia* abundance from about 6,800 years BP until the expansion of pastures and farmland after European settlement in 1820 AD.

4. Pollen accumulation rate

Pollen relative abundances can only show the relative abundance shifts among different pollen types in fossil assemblages, but not the absolute increases and decreases of a single pollen type, which may complicate interpretations of vegetation composition and climate changes. Here pollen accumulation rate will be analyzed in the next part to give a better understanding of the environment around the lake.

The pollen accumulation rates (PAR) during the past 7,000 years are much more variable than pollen percentages, with more distinguishable peaks (Figure 9). In general, the pollen accumulation rates of almost all taxa show five large peaks during the past 7,000 years – around 5,500 years BP, 3,400 years BP, 1,600 years BP, and two around 1,000 years BP – Among them the peak near 3,400 years BP is the most abrupt compared with the other two peaks. The PAR variations appear to correspond to changes in sedimentation rate. The first three peaks match the mineral increases shown in the LOI data. The similarity between pollen accumulation rates and LOI variations indicate that pollen accumulation rates are likely influenced by variations in sedimentation rates.

For *Fagus grandifolia*, the peaks in pollen percentage from 6,700 years BP to 5,300 years BP and from 1,900 years BP to 1,000 years BP correspond to the peak of pollen accumulation rate around 6,000 years BP and from 2,000 to 1,000 years BP, indicating that relatively high abundance of *Fagus grandifolia* pollen corresponds to high pollen accumulation rates. For *Acer*, *Quercus* and *Ulmus*, their pollen percentages are not as well as correlated to pollen accumulation rate as for *Fagus grandifolia*. This suggests that *Fagus grandifolia* is the most abundant taxon when the pollen accumulation rates highest, due to either high forest pollen production or low background sedimentation rates.

5. Sedimentology and Elemental Geochemistry

XRF and LOI results from 9,000 to 6,200 years BP are shown together in Figure 10. Although Rb/Sr ratio and V/Cr ratio were low with little variability in this time interval, V/Cr increase and Rb/Sr decrease from 8,400 to 7,800 years BP, when there was a peak of mineral sediments as indicated by LOI. The lower weathering intensity indicated by Rb/Sr ratio and anoxic environment suggested by V/Cr may be caused by higher precipitation and more river input to the lake.

For the Zr/Al ratio, the relatively higher ratio from 9,000 to 8,200 years BP and from 6,800 to 6,200 years BP may indicate higher aeolian sediment input during the these time intervals. However, the LOI data indicate lower mineral proportions during the 9,000 to 8,200 years BP, and higher during the 6,800 to 6,200 years BP. The reason for the discrepancy between the changing trends of mineral and Zr/Al ratio in the two time intervals is unclear.

6. Hierarchical models of *Fagus grandifolia*, *Acer*, *Quercus* and *Ulmus* pollen percentages and LOI data

Fagus grandifolia, *Acer, Quercus* and *Ulmus* were the most abundant pollen types during the middle and late Holocene (Figure 6, Figure 7, Figure 8), and the variances of their pollen abundance changes are the highest four in all pollen types (Table 4), so they can represent most environmental changes around the lake. The pollen abundances of the four taxa seem to have some relationships with mineral component (Figure 11): the increase of *Acer* and *Quercus* may correspond to the decrease of minerals, while the increase of *Fagus grandifolia* and *Ulmus* may match the increase of minerals.

In order to test the statistical relationships between the four taxa and mineral content, the three Bayesian models – model 1, model 2 and model 3 – were run separately for the four taxa (Figures 12-14).

In Figure 12, the estimated results for *Fagus grandifolia* differ from the results for *Acer*, *Quercus* and *Ulmus*. For *Fagus grandifolia*, the trend between data and estimated pollen abundance are similar; while for *Acer*, *Quercus* and *Ulmus*, the estimated pollen abundance changes are smoother than the observed shifts. In general, an autoregressive model is able to fit many trends in these time series, suggesting that the abundances of these four pollen types are influenced by previous vegetation and pollen composition.

For Model 2, the modeled and observed pollen results are also similar (Figure 13). Model 3 produced similar results (Figure 14). Especially for *Acer, Quercus* and *Ulmus,* the estimated distributions from model 2 and 3 (which consider mineral inputs) are less smooth than the results from model 1. For *Fagus grandifolia*, the changes between the two estimated distributions from the two models are not as obvious as for the other three taxa. But in general model 2 and 3 are also able to fit the trends of observed data in these time series.

The similarity of results for *Fagus grandifolia, Acer, Quercus* and *Ulmus* pollen abundance to the observed pollen data suggests that model 1, model 2 and model 3 can all fit the trends of the four pollen types from 7,000 years BP to the present. In order to formally assess which model has the best goodness of fit to the data, the deviance information criterion (DIC) is used to compare the three models.

DIC is an approximation to a penalized loss function based on the deviance, combining a measure of model fit, the expected deviance, with a measure of model complexity, the effective number of parameters (Plummer, 2008). The DIC is defined by Spiegelhalter et al. (2002) as:

$$DIC = \overline{D} + p_D$$

where $\overline{D} = E(D|Y)$ is considered to be a measure of model fit based on the observation data Y, and p_D is the "effective number of parameters", a measure of model complexity related with the number of parameters in the model. DIC is straightforward to calculate using MCMC simulation and is routinely implemented in the JAGS package in R software. The smaller the DIC, the better the model fit.

For *Acer*, *Quercus* and *Ulmus*, the DIC of model 2 and 3 are larger than DIC of model 1, with a smaller mean deviance and a larger penalty (Table 5). This suggests that generally model 1 is better than model 2 and model 3 for *Acer*, *Quercus* and *Ulmus*; the lower deviance from model 2 and model 3 cannot make up the larger complexity of more parameters in the model. However for *Fagus grandifolia*, the DIC for model 2 and model 3 is slightly lower than for model 1, indicating that for *Fagus grandifolia*, the influence of pollen auto-correlation and mineral content are similar. Hence, only for *Fagus grandifolia* pollen does the influence of mineral content result in a slight improvement in model fit; for *Acer*, *Quercus* and *Ulmus*, the model without the consideration of mineral content works better.

Discussion

1. Temperature and moisture changes during the late-glacial period inferred from pollen analysis

Before 10,300 years BP, conifer forests were dominant around the Spicer Lake. This vegetation type reflects the relatively cold climate during the deglaciation period and the early Holocene. During this time period, conifer forest changed from *Abies-Picea* dominant forest to *Pinus*-dominant forest at about 11,800 years BP, mainly *Pinus banksiana/resinosa* which is well fire-adapted and drought-adapted (Figure 6). The shift of dominant conifer trees suggests a moisture change at this time: the environment changed from wet and cold conditions to dry and cold conditions. This moisture shift and vegetation composition changes correspond well to pollen data from the Allegheny Plateau and the Till Plains (Shane and Anderson, 1993). Both results suggest that there was a shift from wet climate to dry climate during the cold late-glacial period in the Great Lakes region.

From 10,300 years BP to 9,800 years BP conifer forests declined and deciduous forests expanded, suggesting a transition to warmer climates. After that interval, deciduous forest was the dominant vegetation type on land, indicating warm climate during the Holocene (Shane and Anderson, 1993; Gonzales and Grimm, 2009).

2. LOI variability, vegetation composition shifts and climate changes during the Holocene

During the Holocene, the pollen assemblages were dominated by *Acer*, *Quercus*, *Ulmus* and *Fagus grandifolia,* which are the most common deciduous trees in the Great Lakes region. However, the four pollen types have different responses to LOI variability in the lake, indicating that different taxa may have responded differently to climate changes during the Holocene.

The pollen abundances of *Fagus grandifolia* is more correlated to mineral input to the cores compared with other three pollen types, as indicated by the same estimated pollen abundance from models considering mineral inputs based on the DIC test (Table 5). In this way, the H0 hypothesis, that LOI variability was not caused by aridity, is rejected. The shifts of minerals input and LOI variability at the Spicer Lake are inferred to have been caused by climate and moisture changes, with responses of vegetation types shifts around the lake.

For Acer, Quercus, and Ulmus, there is no improvement from model 2 and model 3 compared to model 1. Thus the H1 hypothesis, that the LOI variability was caused by moisture changes, and the vegetation was sensitive to the LOI variability, is rejected for these taxa. Either these taxa were insensitive to past hydrological variations or the LOI signal from this single core is a too noisy signal of moisture variability around the lake.

The H2 hypothesis is supported for Fagus grandifolia by the modeling of the pollen and LOI data. The LOI variability was caused by aridity, and the vegetation varied during the Holocene. The unimproved model with smaller deviance but larger penalty indicates that for the three pollen taxa, pollen abundance is less influenced by mineral input than by the pollen abundance in previous time interval. This indicates that pollen changes during the Holocene, especially the moisture-sensitive taxa such as *Fagus grandifolia*, correspond to LOI variability, but not determined by LOI variations completely.

3. Interpreting the LOI data

The shifting inputs of mineral and organic sediments can be due to many climatic and hydrological causes, and it is difficult to infer moisture trends indicated by increases or decreases of minerals just from LOI variability at a single core. The increases of minerals in the LOI data either indicate increasing water table caused by wet climate or more mineral input to the lake due to aridity events in the past (Shuman, 2003). When the lake level is lower and the core is near the shore, less dilution of organic-rich runoff and increased mineral sediment focusing by erosion of the shoreline may contribute to an increase in the mineral content of LOI. When the lake level is lower but the core is deep in the basin, the lower sediment input limit may decrease the mineral input into the core.

As the climate indication of LOI variability in one core is ambiguous, vegetation composition must be considered together with LOI variability to infer climatic and environmental shifts around the lake. The declines of mineral inputs usually correspond to increases of *Pinus*, increases of *Quercus*, decreases of *Ulmus* and declines of *Fagus grandifolia* (Figure 11). Considering that the declines of *Fagus grandifolia* usually indicate drought events in other lakes in the north central United States, the declines of mineral inputs at this coring location in Spicer Lake during the Holocene can be illustrated as a signal of aridity events and droughts, while the increases of minerals can be treated as a signal of relatively wetter climate.

The first period of high mineral content appeared from 8,500 years BP to 8,000 years BP, when the *Acer-Quercus-Ulmus* deciduous forest was dominant on land. Although the forest composition did not change much, *Ulmus* increased with about a 100-years time lag. *Acer* also decreased slightly, although the decrease was not as large as that of *Quercus*.

The second period of high mineral content is between 6,800 years BP and 6,000 years BP; an abrupt increase of *Fagus grandifolia* occurred during this interval while *Acer*, *Quercus* and *Ulmus* remained dominant in the deciduous forest. This transition of sub-zones of vegetation-pollen composition corresponded well to moisture changes in this time period.

The peak of minerals during the third period of high mineral content was the largest in the core and lasted for a long time, from 4,500 years BP to 3,500 years BP. The increases of *Fagus grandifolia* and *Ulmus* with tens of years' time lag to the LOI rise period were the most important responses to the inferred moisture changes. *Acer* decreased slightly during this period.

The last period of high mineral content was around 1,300 years BP, during which *Fagus grandifolia* increased from near 1,200 years BP as a response to the wet climate. After this wet period, deciduous forest around the lake changed from *Acer-Quercus* dominant forest to *Acer-Fagus grandifolia-Quercus-Ulmus* dominant forest.

In summary, the LOI records are suggested of hydrological variability during the Holocene. Vegetation composition changes in response to the inferred moisture shifts with tens of years time lag, featuring increases of *Fagus grandifolia* and *Ulmus* and decreases of *Quercus* and *Acer* during the wet periods. Deciduous forest was the dominant vegetation type during most of the Holocene. Deforestation only occurred after 1820 AD by the influence of European settlement.

4. Fagus grandifolia shifts in the north central United States

The increases and declines of *Fagus grandifolia* are the largest signals of vegetation change at Spicer Lake during the middle and late Holocene. High variability in Fagus grandifolia pollen appears to be a general phenomenon in this region; many other pollen records from the north central US also show substantial variations of *Fagus grandifolia* pollen abundance during the Holocene (Figure 15). Some of these events may correspond to events seen at Spicer Lake, although age uncertainties make it difficult to confidently correlate events.

The 5,200 years BP decline at Spicer Lake appears to occur at Ladd Lake in Ohio and Hudson Lake in Indiana. And at East Twin Lake the *Fagus grandifolia* pollen started a gradual decline at about 5,000 years ago. This *Fagus grandifolia* decline may temporally correlate to the hemlock decline around 5,400 years BP in the eastern North America, which has been attributed to drought events (Davis, 1981; Davis et al., 1986; Fuller, 1998; Parshall, 2002). Renewed dune activity in western Illinois (Figure 14) (Wang et al., 2012) suggests that there might be a dryer condition in western Illinois between ca. 6 ka and 5 ka, perhaps preceding the *Fagus grandifolia* declines, or possibly co-eval, given the uncertainty in the OSL dating.

The second decline around 4,100 years BP seems to correlate to *Fagus grandifolia* declines in Ladd Lake, Pretty Lake and Kellners Lake pollen records, and may correlate to the 4.2 ka drought reported elsewhere (Stahle et al., 2000; DeMenocal, 2001; Booth et al., 2012). There is also dune activity roughly centered at 4 ka in western Illinois (Figure 14) (Wang et al., 2012).

The prolonged period of low *Fagus grandifolia* abundances from 3,300 to 1,900 years BP at Spicer Lake has no clear counterpart to the other lakes in the Great Lakes region (Figure 14). There are similar period of prolonged low *Fagus grandifolia* abundances lasting more than 1,000 years at Pretty Lake, but about 1,500 years earlier, and even lasting 1,500 years longer and 1,800 years earlier at Hudson Lake, starting at about 5,200 years BP, closer to the first decline of *Fagus grandifolia* pollen at Spicer Lake around 5,200 years BP. The long-time decline of *Fagus grandifolia* may be caused by a lasting regional aridity event, with different starting time and variability at local sites. More researches about hydrological variability in the middle United States during this time interval are still needed for this event.

The *Fagus grandifolia* decline around 1,000 years BP is seen at several sites, which may be also caused by drought events during the late Holocene (Miller, 1973; McAndrews, 1973; Webb, 1973; Booth et al., 2012). The widespread nature of the *Fagus grandifolia* declines and the model simulation together suggest that *Fagus grandifolia* variability is related to hydrological variability in the north central United States in the middle and late Holocene.

Conclusion

Conifer forest was the main vegetation type at Spicer Lake before 11,800 years BP. The change of *Abies-Picea* conifer forest to *Pinus* conifer forest is interpreted to indicate a shift to dryer conditions near 11,800 years BP. After 10,300 years BP, conifer forest decreased and deciduous forest expanded during this time, ending with deciduous forests dominant with *Acer*, *Quercus*, *Ulmus* and *Fagus grandifolia*, among which *Fagus grandifolia* increased and became dominant after about 6,800 years BP. Several relatively wet climate periods occurred during the middle and late Holocene, indicated by peaks of minerals in the lake sediment. *Fagus grandifolia* and *Ulmus* increased, and *Acer* and *Quercus* decreased in response to the wet periods with a time lag. After 1820 AD, deciduous forest decreased abruptly and savanna or grassland was dominant around the lake. This transition is mainly due to the land use changes brought by European settlement.

LOI variability in the lake sediment can reflect the moisture changes, but the exact reasons for the increases or decreases of minerals may change according to the different relative position of lake level and core position.

Fagus grandifolia pollen declines at Spicer Lake may be associated with *Fagus grandifolia* pollen declines at other lakes in north central United States, although with some time lags and variability among lakes. The 5,200 years BP and 4,100 years BP decline may be connected with dune activity in western Illinois, partly supporting the hypothesis that *Fagus grandifolia* decline is caused by drought events. The long-time decline from 3,100 – 1,900 years BP may be associated with *Fagus grandifolia* decline at two other lakes in Indiana, with different staring times among the three lakes. The decline at 1,000 years BP is also related with *Fagus grandifolia* pollen declines at other lakes and drought events. Bayesian hierarchical models also indicate that *Fagus grandifolia* pollen abundance changes are related to LOI variability at Spicer Lake. Both pollen evidence and models suggest that *Fagus grandifolia* variability is related to drought events during the middle and late Holocene.

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Tables and Figures

Table 1 Radiocarbon Dates

Lab ID Number	Sample ID	Composite Depth (cm)	Sample Material	Lab*	^{14}C Age (years before 1950AD)	Calibrated Median Age (years before 1950AD)	Full Calibrated Age Range (years before 1950 AD)
UGAMS-12651	SPIC06-A-228	228.5	charcoal	CAIS	3,770 +/- 45	4,150	3,843 – 4,308
UGAMS-12652	SPIC06-A-443	443.5	*Ulmus* seed	CAIS	5,170 +/- 25	5,985	5,769 – 6,089
NOSAMS-65291	SPIC06-A-494	494.5	wood	WHOI	5,370 +/- 35	6,321	6,127 – 6,357
NOSAMS-65872	SPIC06-A-498	498.5	wood	WHOI	5,270 +/- 130	6,355	6,130 – 6,375
NOSAMS-65292	SPIC06-A-583	583.5	wood	WHOI	6,210 +/- 35	6,933	6,874 – 7,319
UGAMS-4653	SPIC06-A-861	861.5	*Pinus* seed	CAIS	9,470 +/- 60	10,818	10,377 – 11,237
UCIAMS-56655	SPIC06-A-887	887.5	charcoal	Keck	5,060 +/- 160	5,813	5,570 – 6,207
UGAMS-4654	SPIC06-A-887	887.5	charcoal	CAIS	6,730 +/- 300	7,599	6,971 – 8,177
NOSAMS-65862	SPIC06-A-888	888.5	wood	WHOI	10,100 +/- 140	11,207	10,936 – 11,501
UGAMS-4655	SPIC06-A-914	914.5	charcoal	CAIS	7,620 +/- 280	8,464	7,918 – 9,135
UCIAMS-56656	SPIC06-A-914	914.5	charcoal	Keck	8,940 +/- 80	10,040	9,744 – 10,237
UGAMS-4656	SPIC06-A-915	915.5	wood	CAIS	10,090 +/- 60	11,669	11,392 – 11,975
UCIAMS-56652	SPIC06-A-957	957.5	pollen	Keck	12,410 +/- 35	13,723	12,884 – 14,234
UCIAMS-56653	SPIC06-A-1056	1056.5	pollen	Keck	12,740 +/- 35	15,272	14,853 – 15,728

*CAIS=Center for Applied Isotope Studies at the University of Georgia
WHOI=Woods Hole Oceanographic Institution
Keck=W. M. Keck Carbon Cycle Accelerator Mass Spectrometry Laboratory

Table 2: Bacon age modeling parameters.

Parameters	
Radiocarbon Calibration curve	IntCal09
Post-bomb Calibration curve	NH1
Minimum year	-56 BP
Maximum year	50,000 BP
Accumulation rate	10 yr/cm
Section length	20 cm

Table 3: List of pollen and spore types identified in this study.

Arboreal pollen types	Herb pollen types	Spore types
Abies balsamea	*Sarcobatus* (Amaranthaceae)	*Botrychium*
Picea glauca	Amaranthaceae undiff	*Drypoteris*
Picea mariana	*Ambrosia*-type (Asteraceae)	*Isoetes*
Picea undiff	*Artemisia* (Asteraceae)	*Lycopodium*
Pinus banksiana/resinosa	*Eupatorium* (Asteraceae)	*Osmunda*
Pinus strobus	*Iva* (Asteraceae)	*Polypodium*
Pinus undiff	*Xanthium* (Asteraceae)	*Pteridum*
Acer negundo	Asteraceae undiff	*Fern* undiff
Acer pennsylvanicum	Balsaminaceae	
Acer rubrum	Commenlinaceae	
Acer saccharinum	Cyperaceae	
Acer saccharum	*Shepherdia* (Eleaegnaceae)	
Acer undiff	Ericaceae	
Alnus	Fabaceae	
Betula	*Mentha* (Lamiaceae)	
Carya	*Stachys* (Lamiaceae)	
Castanea	Oxalidaceae	
Celtis	*Hippuris* (Plantaginaceae)	
Cornus	*Plantago* (Plantaginaceae)	
Corylus	Poaceae	
Cupressaceae/Taxaceae	*Rumex* (Polygonaceae)	
Fagus grandifolia	Polygonaceae undiff	
Fraxinus americanum-type	*Thalictrum* (Ranunculaceae)	
Fraxinus nigra-type	Ranunculaceae undiff	
Ilex	*Potentilla* (Rosaceae)	
Juglans cinerea	Rosaceae undiff	
Juglans nigra	*Cephalanthus* (Rubiaceae)	
Larix	*Galium* (Rubiaceae)	
Morus	Saxifragaceae	
Myrica	Urticaceae	
Nyssa	Violaceae	
Ostrya/Carpinus-type	Vitaceae	
Platanus	*Nuphar* (Pontederiaceae)	
Populus	*Nymphaea* (Pontederiaceae)	
Quercus	*Typha* (Pontederiaceae)	
Rhamnus	*Equisetum* (Pontederiaceae)	
Rhus glabra		
Salix		
Sambucus		
Tilia		
Tsuga		
Ulmus		

Table 4: Variance and standard deviation of pollen abundance from 7,140 BP to the present for main pollen types at Spicer Lake. The top three (*Fagus, Quercus, Ulmus*) are highlighted in bold.

Taxa	Variance	Standard Deviation
Abies balsamea	0.595	0.772
Picea	0.290	0.539
Pinus	0.147	0.384
Acer	**12.731**	**3.568**
Betula	0.354	0.595
Carya	2.767	1.663
Corylus	0.758	0.871
Cupressaceae/Taxaceae	2.748	1.658
Fagus grandifolia	**36.316**	**6.026**
Fraxinus americana/penn type	1.929	1.389
Fraxinus nigra/quad type	5.886	2.426
Juglans	0.566	0.753
Larix	1.382	1.176
Ostrya/Carpinus type	1.118	1.057
Quercus	**26.612**	**5.159**
Tilia	1.602	1.266
Tsuga	1.463	1.209
Ulmus	**18.209**	**4.267**
Asteraceae ambrosia type	9.881	3.143
Cyperaceae	1.178	1.085
Plantaginaceae plantago	0.448	0.670
Poaceae	1.0717	1.035
Polygonaceae	2.118	1.455
Urticaceae	1.208	1.099

Table 5: DIC of model 1, model 2 and model 3 for *Fagus grandifolia*, *Acer*, *Quercus* and *Ulmus*. Model 1 only considers the influence of the pollen abundance from the previous period, and model 2 only considers the influence of the mineral input, while model 3 considers the influence of both pollen abundance and mineral input. Mean deviance is the measure of model fit, representing the expected deviance. Penalty is the measure of model complexity, related with the effective number of parameters. The DIC is the penalized deviance. For all models, model 1 has the best goodness of fit (lowest penalized deviance), but the goodness of fit is most similar among models for *Fagus*.

	Model 1			Model 2			Model 3		
	Mean Deviance	Penalty	Penalized Deviance	Mean Deviance	Penalty	Penalized Deviance	Mean Deviance	Penalty	Penalized Deviance
Fagus	421.7	56.03	477.7	415.9	67.16	483.1	414.9	63.50	478.4
Acer	465.8	28.42	494.2	460.1	65.54	525.7	456.1	59.10	515.2
Quercus	462.6	39.39	502.0	457.1	65.40	522.5	453.0	59.26	512.3
Ulmus	410.8	32.34	443.1	406.5	66.95	473.5	404.1	63.17	467.3

Figures

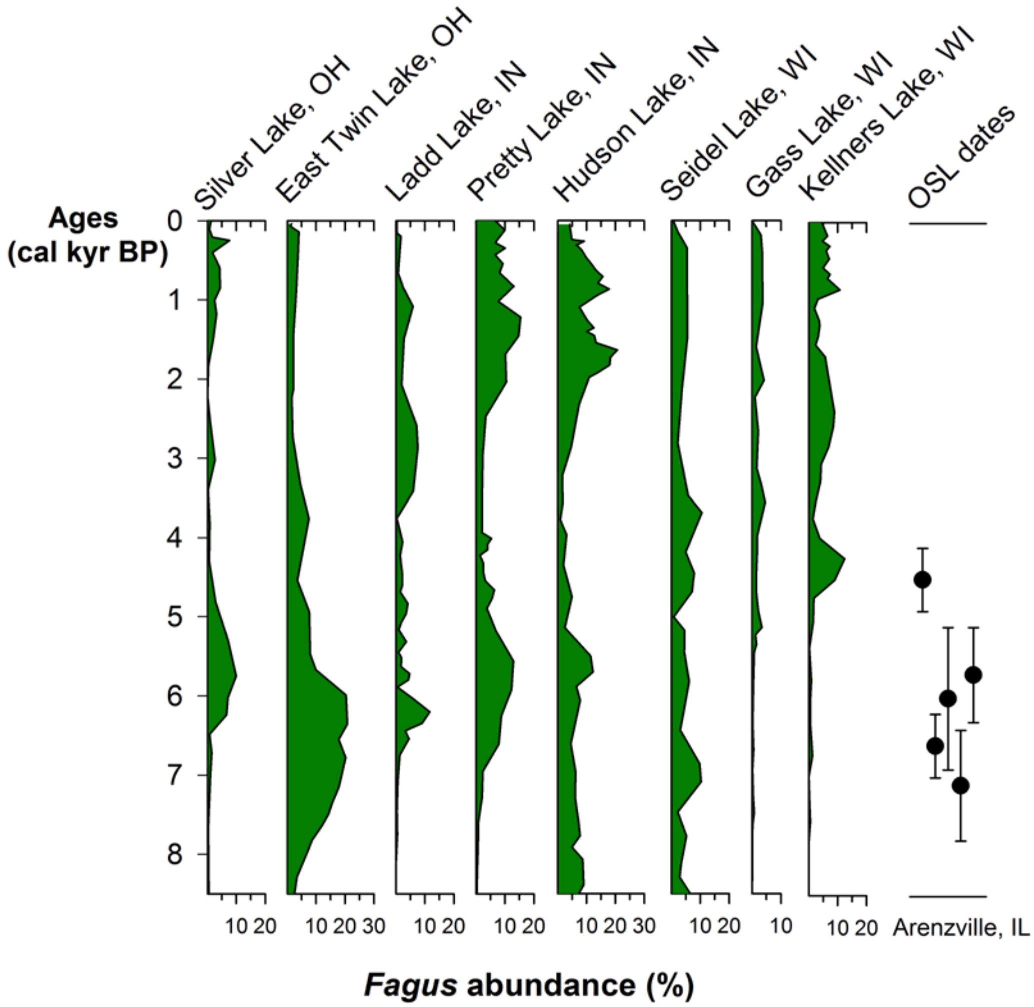

Figure 1: ***Fagus grandifolia*** **pollen abundances from Holocene records in the east-central United States. Pollen data were obtained from Neotoma database; the original citations are from researches in Silver Lake (Ogden, 1966), East Twin Lake (Shane, 1989), Ladd Lake (Shane, 1991), Pretty Lake (Ogden, 1969), Hudson Lake (Bailey, 1972), Seidel Lake (West, 1961), Gass Lake (Webb, 1983) and Kellners Lake (Goodwin, 1976). Dots and whiskers on the right represent OSL dates for dune activities in the middle Illinois River Valley (Wang et al., 2012). Whiskers indicate 2σ certainty of ages.**

Figure 2: Image of Spicer Lake, Indiana from from Google Earth. The inset figure shows the position of Spicer Lake in Indiana.

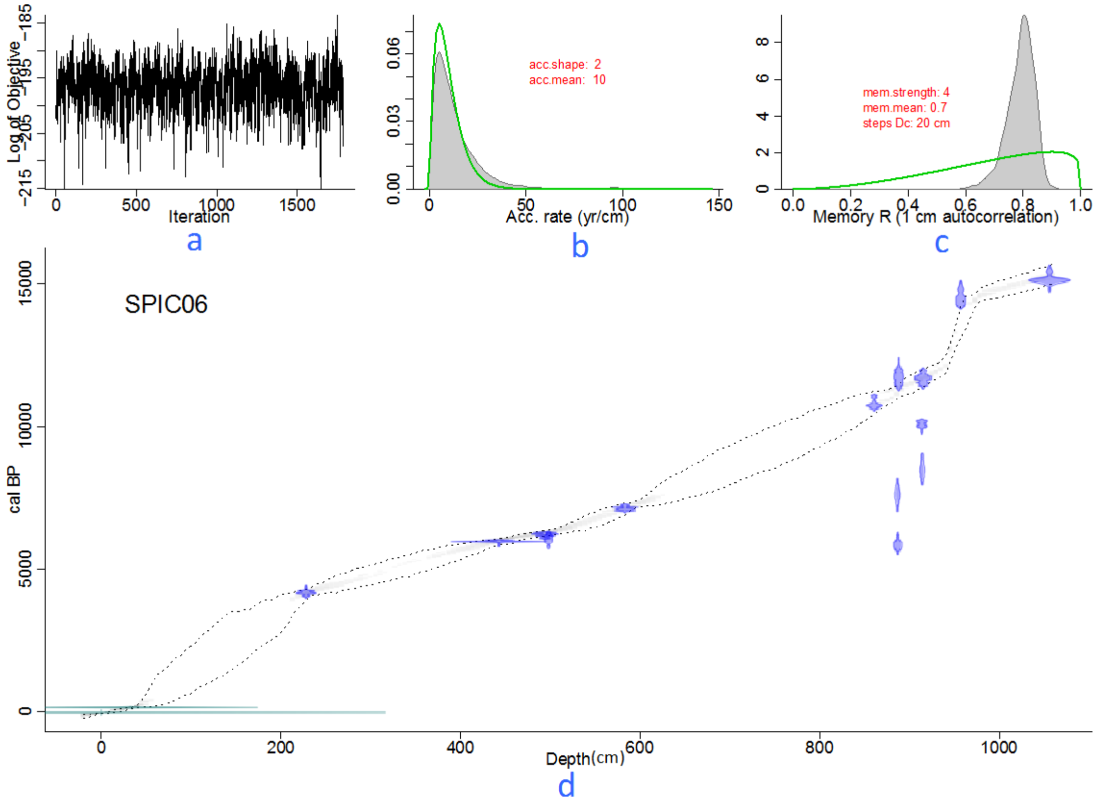

Figure 3: Age-depth model for Spicer Lake based on *bacon* (Blaauw and Christen, 2011). (a): the MCMC iterations, good runs showing a stationary distribution with little structure among neighboring iterations. (b): distribution of accumulation rates. The green line shows the prior distribution while the filled grey curves show the posterior distribution. In Spicer Lake, the mean accumulation rate is set as 10 yr/cm. (c): the probability density for memory (i.e. the autocorrelation strength at 1cm). As for (b), the green line shows the prior distribution while the filled grey curves show the posterior distribution. (d): age and depth. Individual radiocarbon dates are shown in blue as probability density functions of calibrate ages. The grey area is the uncertainty area with dashed lines indicating 95% confidence intervals.

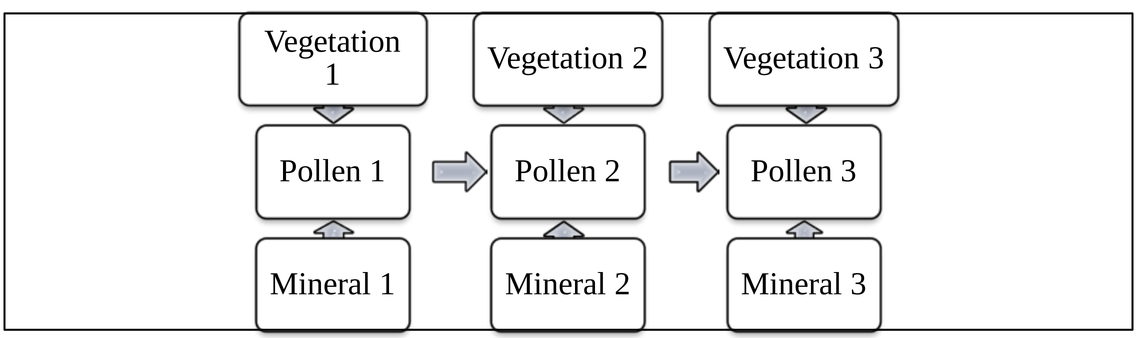

Figure 4: Vegetation, pollen and mineral relationships across time. From left to right is from older to younger samples. Pollen abundances at each time step are partially determined by vegetation community around the lake at that time step, and by pollen abundances at the previous time step. Input of mineralogenic sediments is used as a proxy forenvironmental conditions, which also affects the pollen abundance at the same period. Model 1 is essentially an autoregressive model in which pollen abundances are mainly determined by pollen abundances at the prior step plus an error term. Model 2 uses mineral input as a predictor of pollen abundances.

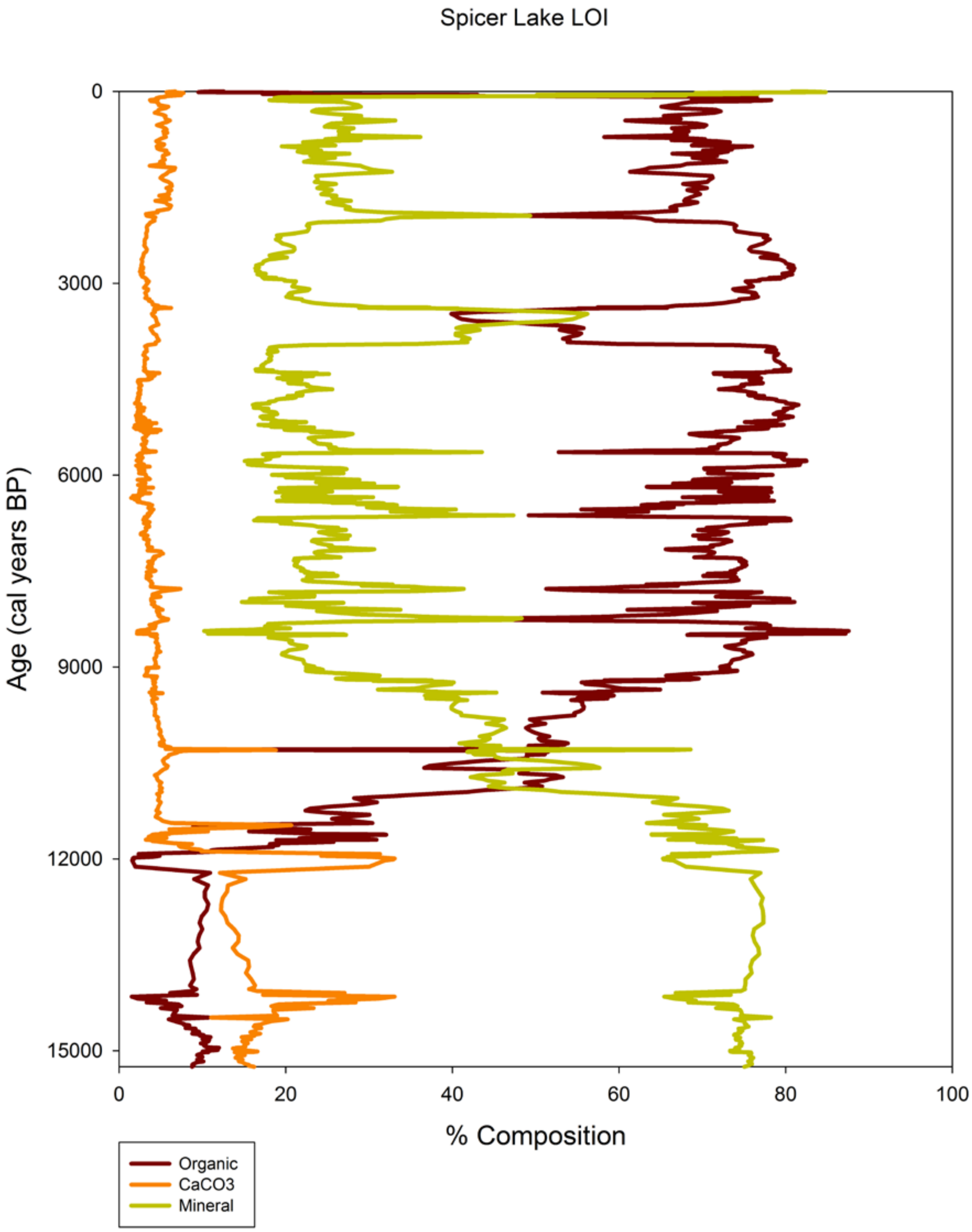

Figure 5: Loss-on-ignition (LOI) data at Spicer Lake showing the relative fraction of the organic carbon, inorganic carbon, and mineral components. Analysts: Shannon Hernandez, Jeremiah Marsicek and Dominique Alhambra.

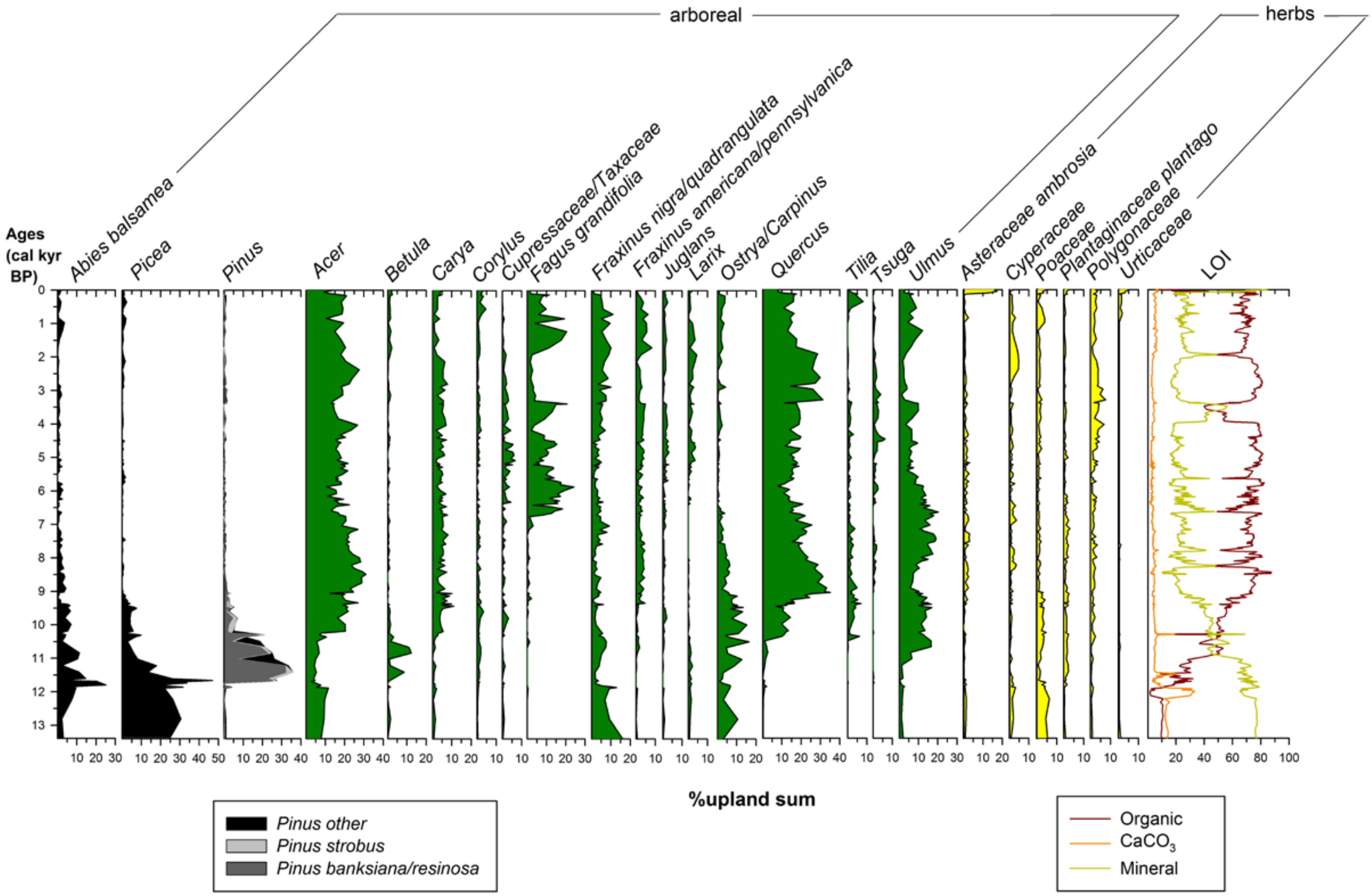

Figure 6 Pollen abundance and LOI variability during the past 13,000 years at Spicer Lake. Analysts: Yue Wang and Jacquelyn Gill.

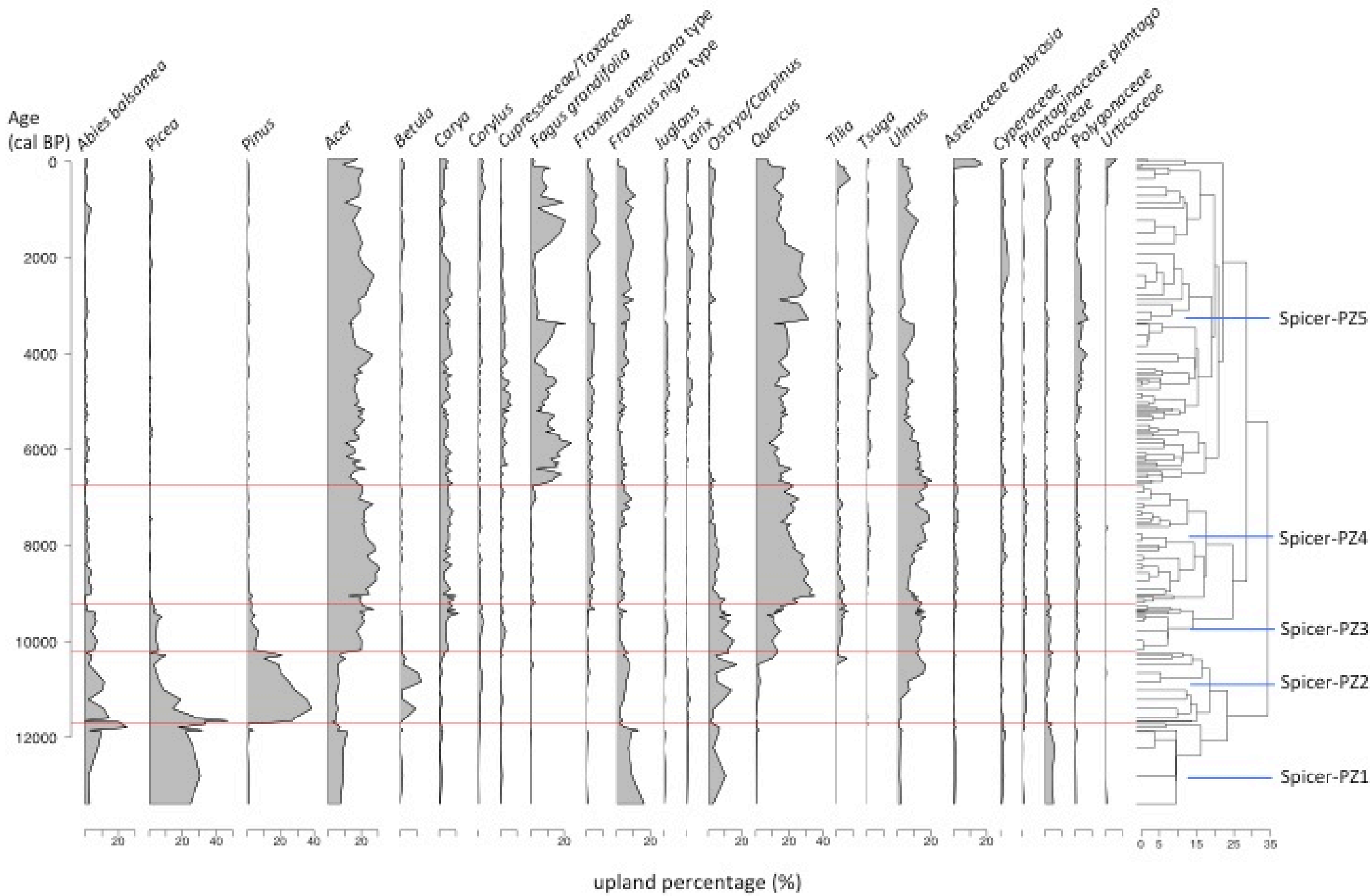

Figure 7: Stratigraphically constrained zonation of pollen percentages at Spicer Lake during the deglaciation and the Holocene, based on using CONISS by the package *rioja* in R. Only pollen taxa with maximum abundances larger than 5% are shown. Five zones were identified during the past 13,000 years.

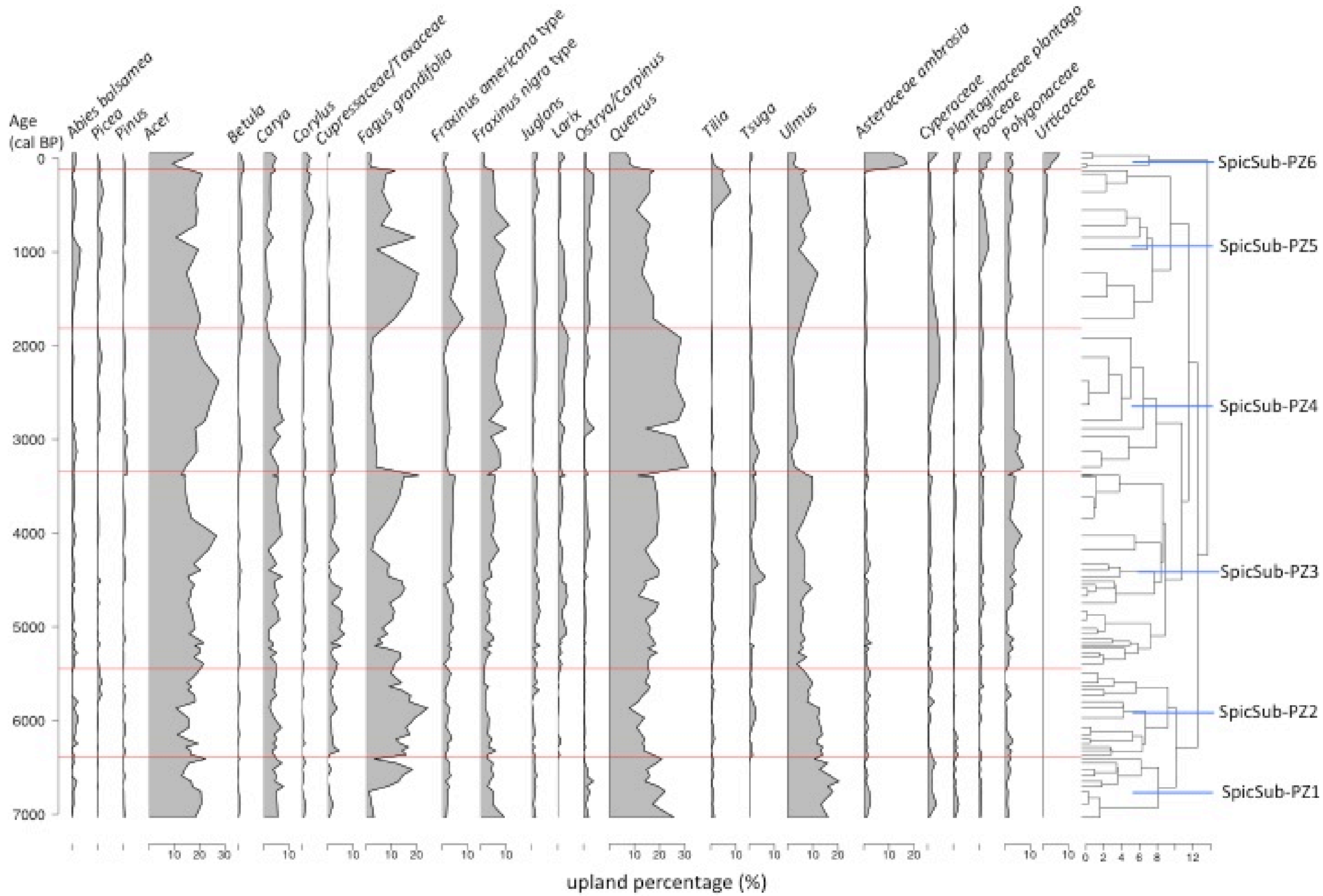

Figure 8: Stratigraphically constrained zonation of pollen percentages at Spicer Lake during the middle and late Holocene when *Fagus grandifolia* was abundant. The zones were categorized using CONISS by the package *rioja* in R. Only pollen taxa with maximum abundances larger than 5% are shown. Six zones were identified for the past 7,000 years; the placement of these zones is primarily determined by variations in *F. grandifolia*.

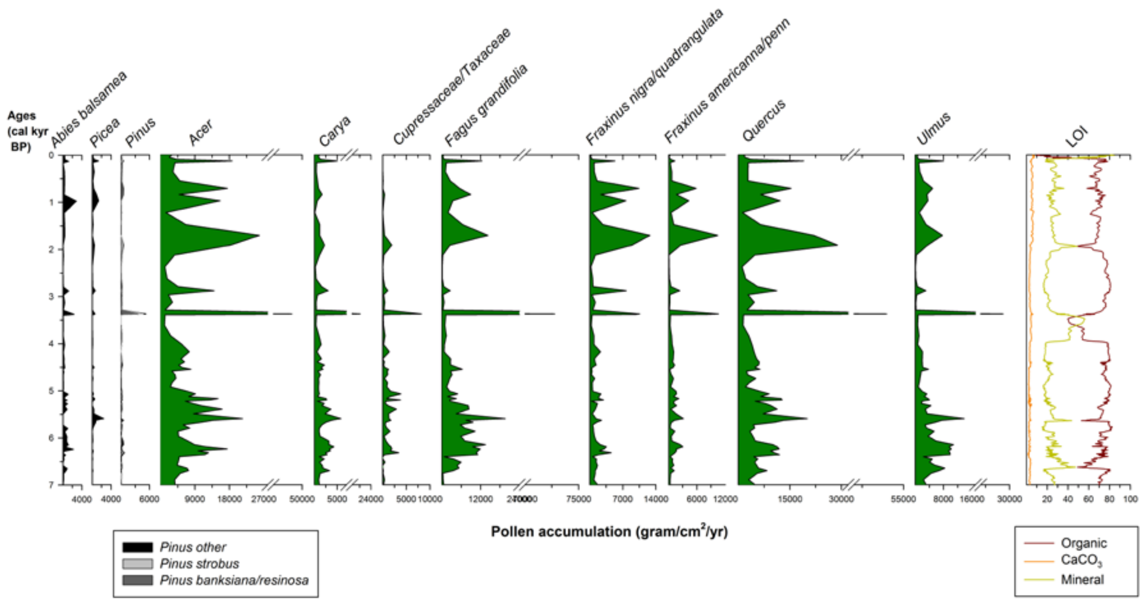

Figure 9: Pollen accumulation rates and LOI data at Spicer Lake during the Holocene. Except for the conifer trees, only taxa with a maximum pollen accumulation rate > 10,000 grains cm^{-2} yr^{-1} are shown here.

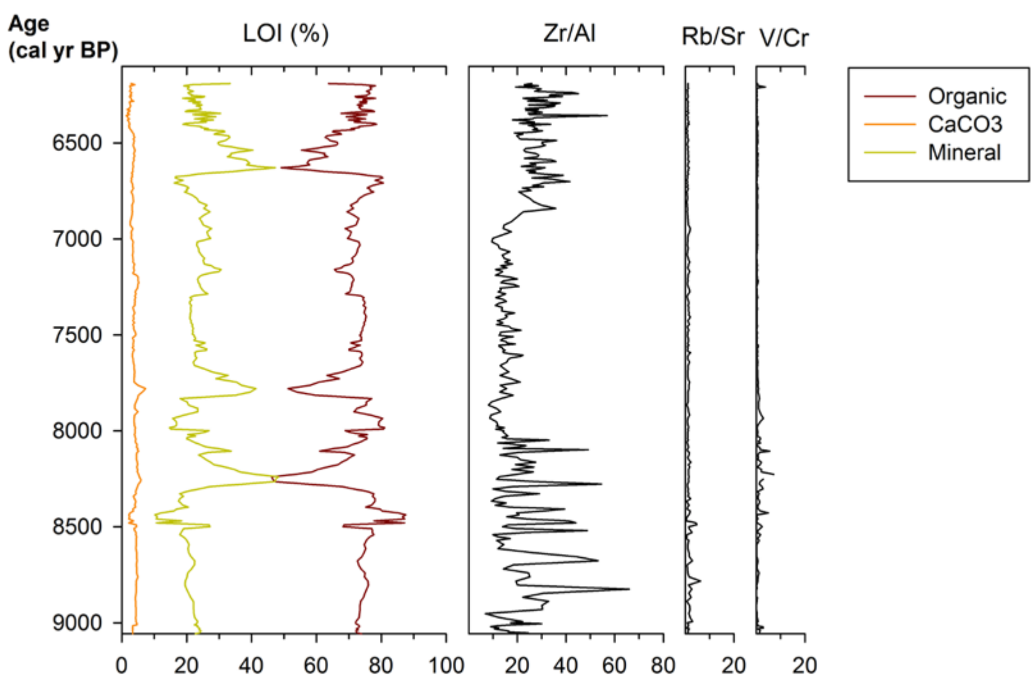

Figure 10: XRF and LOI data from 9,000 to 6,200 years BP

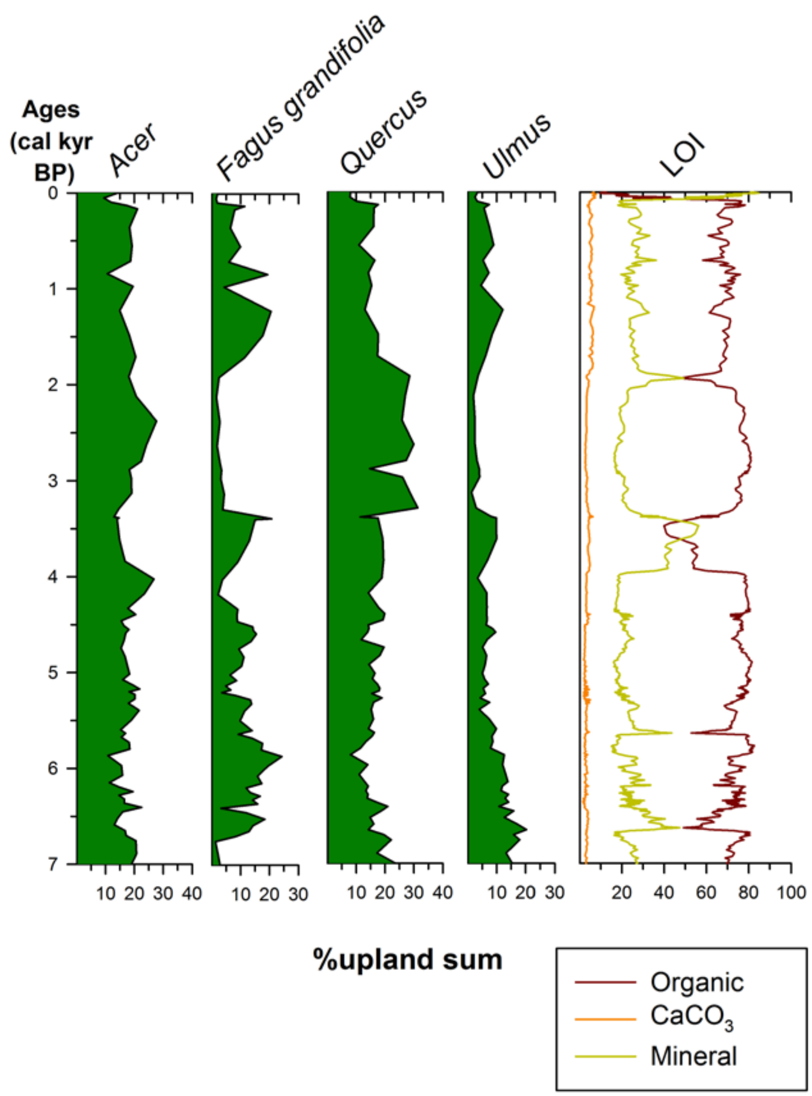

Figure 11: ***Acer, Fagus grandifolia, Quercus*** **and** ***Ulmus*** **pollen abundance with LOI data at Spicer Lake during the middle and late Holocene.**

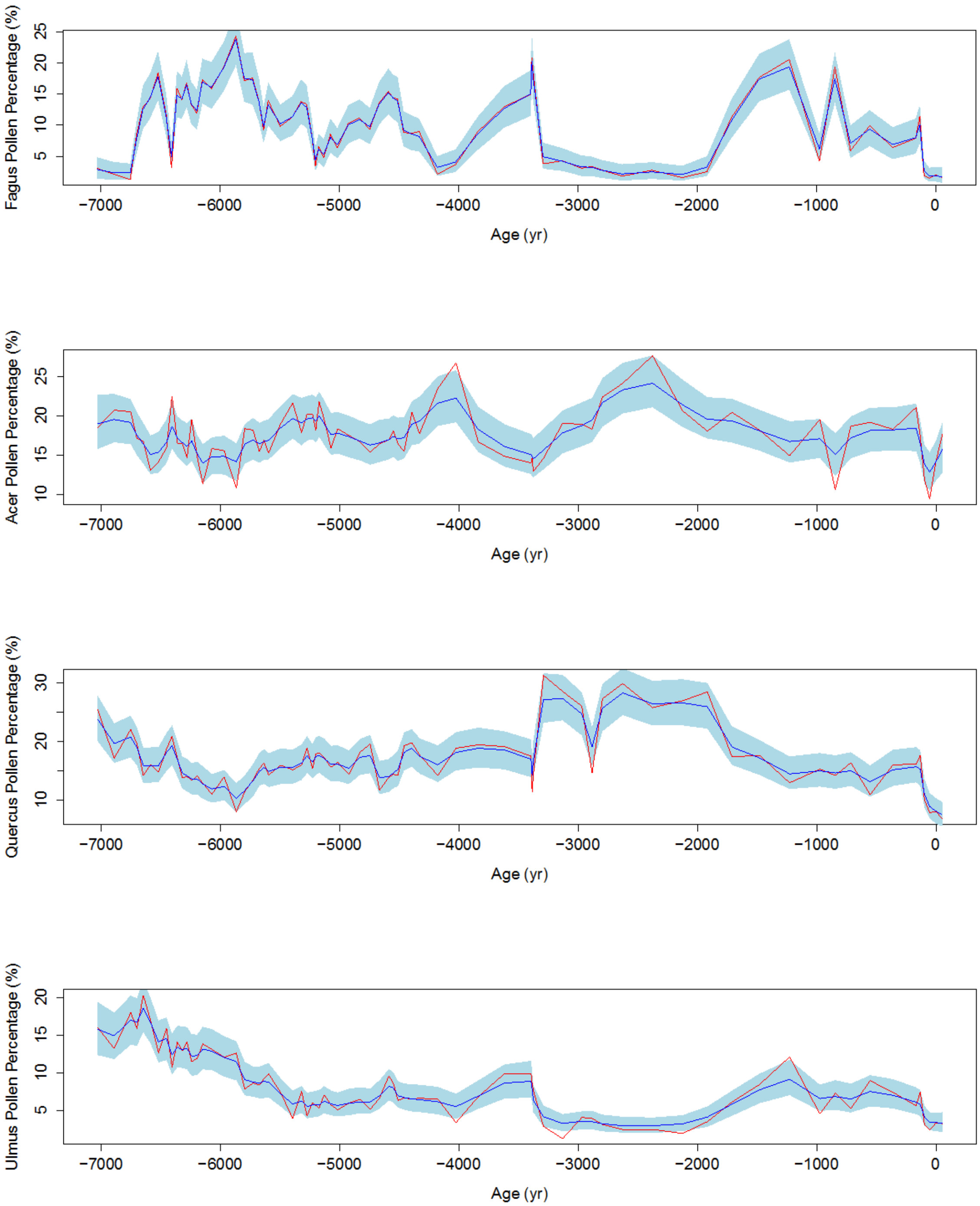

Figure 12: *Fagus grandifolia, Acer, Quercus* and *Ulmus* pollen abundance in hierarchical model 1. Red lines are the observed distributions of pollen abundance; blue lines are the posterior distribution estimated from the model; light blue areas are estimated distribution with 95% confidence.

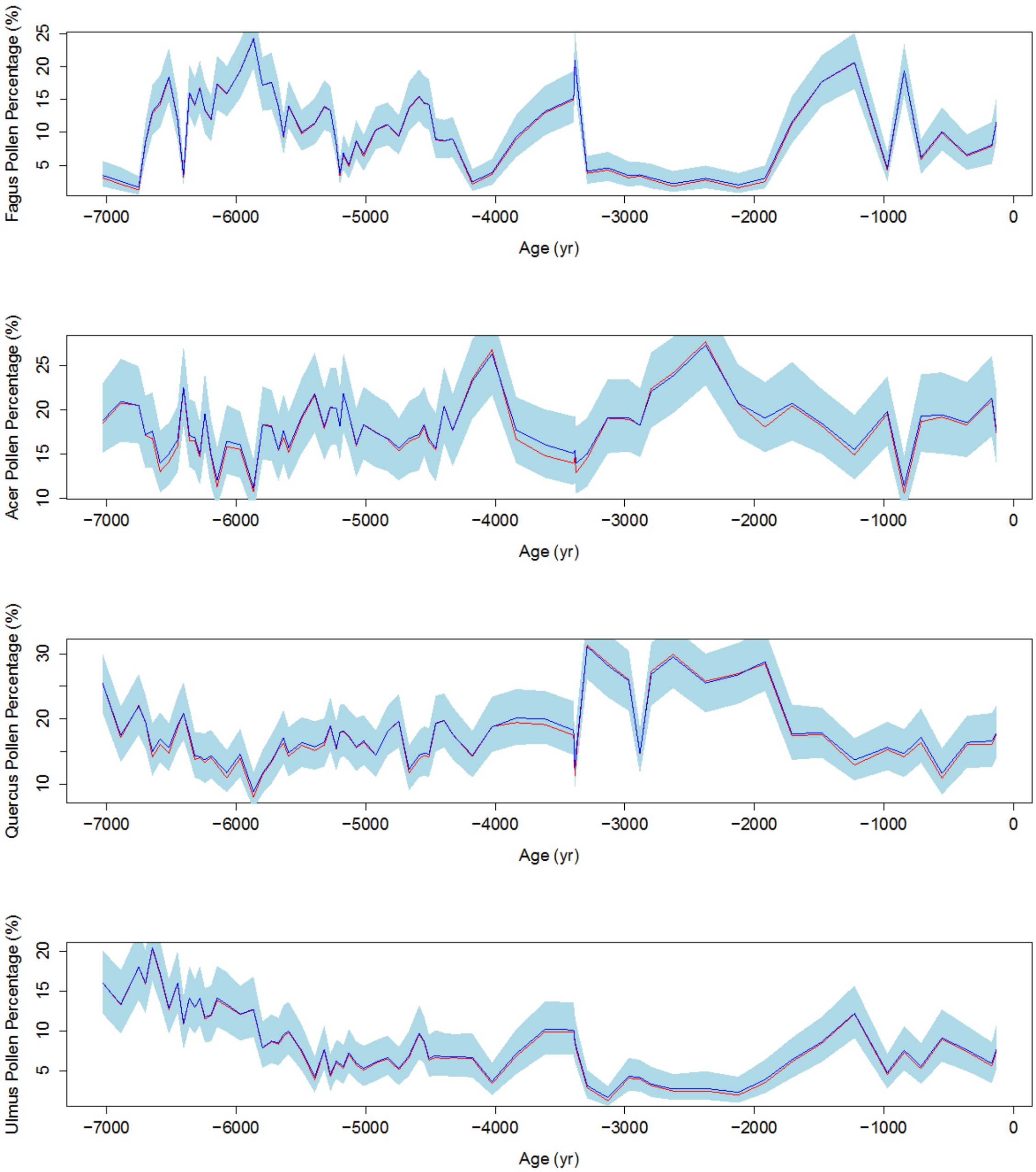

Figure 13: *Fagus grandifolia, Acer, Quercus* and *Ulmus* pollen abundance for hierarchical model 2, which includes a parameter of mineral input. Figure design follows Figure 12.

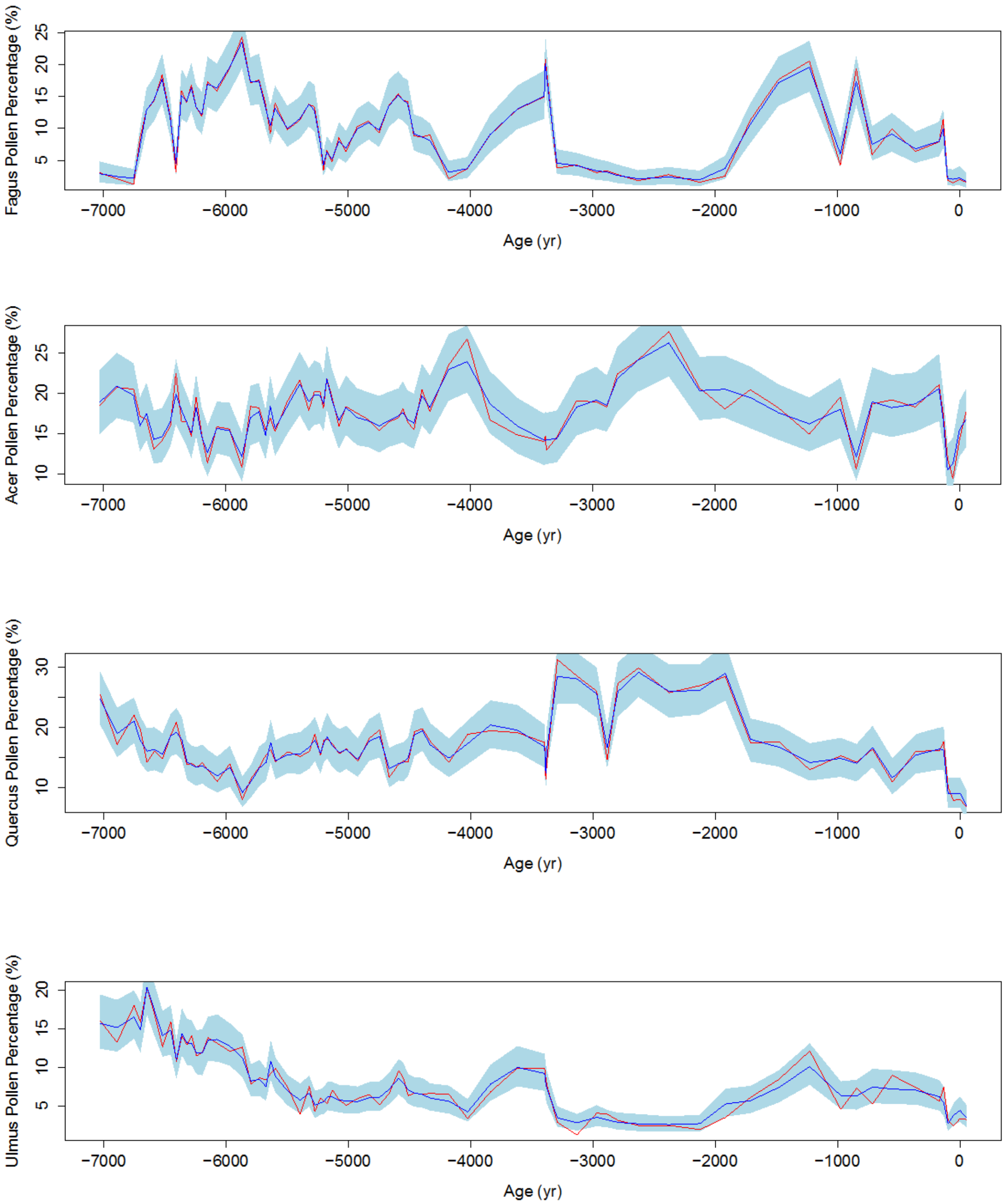

Figure 14: ***Fagus grandifolia, Acer, Quercus*** **and** ***Ulmus*** **pollen abundance with the parameter of pollen abundance at the previous time and mineral input in hierarchical model 3. Figure design follows Figure 12.**

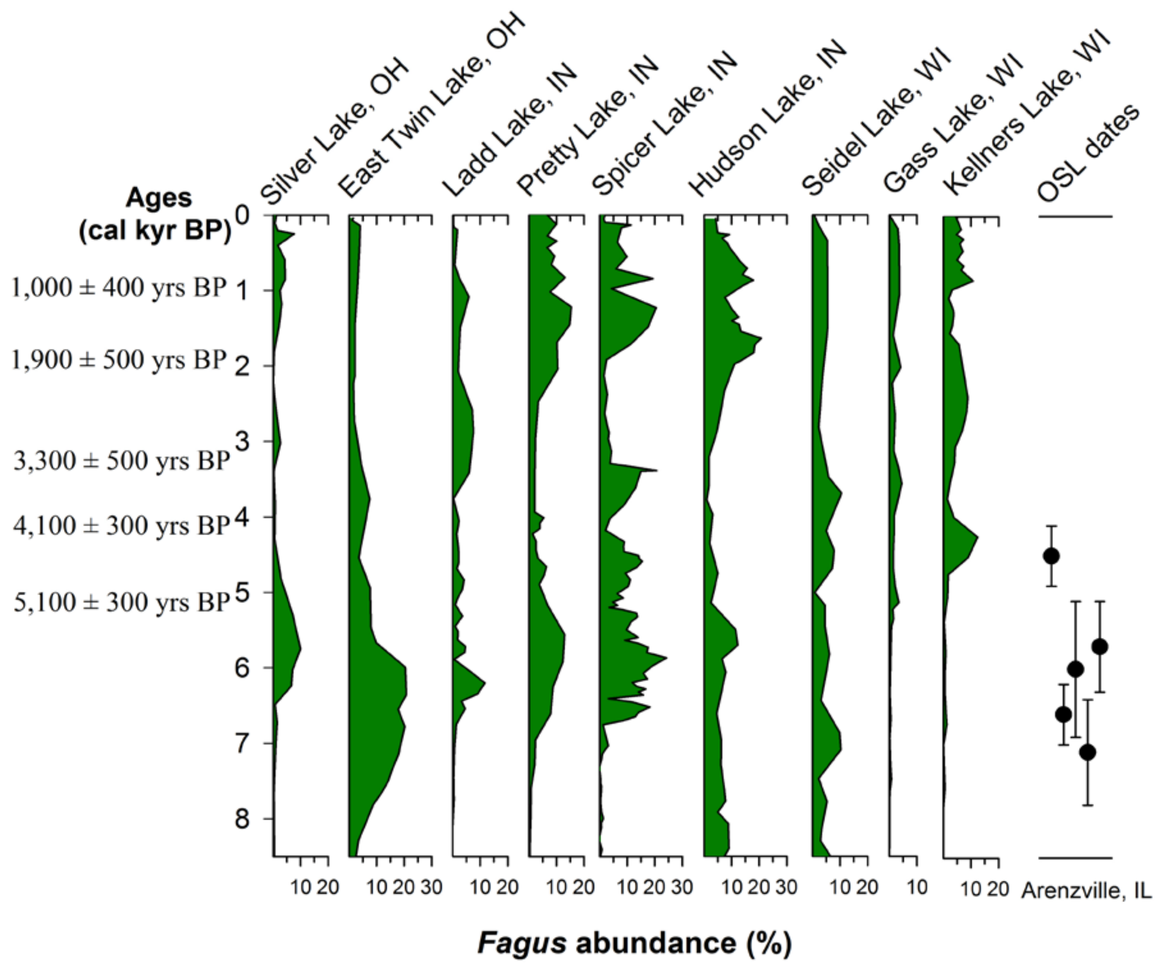

Figure 15: As Figure 1, with Spicer Lake added. Dates at left indicate cal