The Biogeography of Biotic Upheaval:

No-analog Plant Associations and the End-Pleistocene Megafaunal Extinctions

By

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Abstract

The late-glacial/early Holocene transition was a period of widespread environmental upheaval, including the arrival of the first humans, the extinction of 34 genera of megafauna, and the individualistic response of plant ranges and abundances to warming temperatures and ice sheet retreat. North American pollen records from this interval are characterized by a high minimum dissimilarity from present, representing plant associations with no modern analog. I tested the hypothesis that megafaunal herbivory played a role in the formation of late-glacial no-analog plant associations, using spores from the dung fungus *Sporormiella* as a lake sediment proxy for the presence of megaherbivores. For this dissertation, I first review research on modern plant-megaherbivore interactions, outlining testable hypotheses about the impacts of the end-Pleistocene extinctions on vegetation. Next, I present a new, multi-proxy record (including fossil pollen, charcoal, and *Sporormiella*) from Silver Lake, OH, a classic no-analog pollen site. The Silver Lake paleorecord supports the hypothesis that a combination of top-down forcings, including novel climates and megaherbivory release, contributed to the formation of the no-analog plant associations and enhanced fire regimes following the local decline of megaherbivores at ca. 13,900 BP. Third, I conducted a modern process analysis of *Sporormiella* at Konza Prairie that links *Sporormiella* abundances to bison presence and grazing intensity (kg/m^2/year), and indicates a very local source area (< 100 m) of spores. Lastly, I conducted a detailed review of late-glacial vegetation dynamics and no-analog plant associations in the Upper Midwest. I described the trajectory of communities in ecological space through time using nonmetric multidimensional scaling, showing how no-analog associations emerged from individualistic taxon-level dynamics. My results suggest that a combination of local site factors and periglacial conditions influenced the response of vegetation to extrinsic abrupt forcing, including megafaunal extinction and climate change, producing novel plant associations that were unique to the Upper Midwest.

CHAPTER 1

ANCIENT EXTINCTIONS & MODERN EXPERIMENTS: THE ECOLOGICAL EFFECTS OF MEGAFAUNAL HERBIVORY IN QUATERNARY NORTH AMERICA

1. *Introduction*

Megaherbivores have been considered keystone species for their role in modifying habitats in modern systems, and have thus been the target of extensive study by ecologists and rangeland managers. For example, large herbivores can alleviate plant competitive exclusion (Dyer et al 1993, Edenius et al 1993), maintain vegetation openness (Olofsson et al 2004, Weigl & Knowles 1995), alter nutrient cycle dynamics (Hobbes et al 1991, Kielland & Bryant 1998, Ritchie et al 1998), facilitate dispersal (Janzen & Martin 1982), as well as either increasing plant diversity by reducing single-species dominance (Parker et al 2006), or reducing it via selective foraging (Anderson & Katz 1993). At evolutionary timescales, megaherbivores are recognized as playing an important role in plant morphology and diversity, including the development of grasslands in the Mid-Miocene of North America (Anderson 2006) and in the evolution of vegetation forms such as thorns (Hanley 2007) and fleshy fruits (Howe & Smallwood 1982, Lorts et al 2008). In spite of these well-documented influences and the recognition of the importance of megaherbivores at both short and deep timescales, there have been comparatively few studies analyzing the influence of megaherbivores on plant ecological dynamics during the Quaternary Period (the last 2.8 million years). This omission is particularly notable given that at the end of the Pleistocene (ca. 13,000 BP), an extinction event resulted in the disproportionate loss of not only a majority of the world's large animals, but (particularly in North and South America) the loss of its very largest (Barnosky et al 2004). Removing guilds of megaherbivores from the landscape may result in changes in vegetation composition and function due to altered fire regimes, seed dispersal and recruitment, competition, or some combination of these (Johnson 2009), and some of these effects may be detectable in the paleorecord (Gill et al 2012, Gill et al 2009). Research on the ecological effects of the megafaunal extinctions is now more possible than ever before, due to a combination of new advances in radiocarbon dating, fossil proxies, analysis of ancient DNA, and modeling techniques, as well as changing paradigms that recognize the potential role of biotic interactions at Quaternary timescales (Craine & McLauchlan 2004, Jablonski & Sepkoski 1996, Jackson & Overpeck 2000, Petit et al 2004).

In this paper, I review modern herbivore-vegetation dynamics to first describe the mechanisms by which megafauna exert measurable influences on vegetation composition, structure, and function. I then review the late Quaternary megafaunal extinctions, with a focus on North America, exploring the nature of the Pleistocene megaherbivore guilds and the current state of the hypotheses for their demise. The dung fungus proxy, *Sporormiella*, is one promising way forward in testing hypotheses of megaherbivore ecology in the paleorecord; I review previous research utilizing this proxy and the factors that influence its interpretation. Finally, I argue that the end-Pleistocene megafaunal extinctions represented a form of a biotic disruption that would have left a signature on the ecology and evolution of Holocene ecosystems, and suggest that this legacy may be detectable both in the paleorecord and on modern landscapes.

A note about definitions

This paper reviews the influence of megaherbivores on North American vegetation in particular, focusing on mammals during the Quaternary unless otherwise specified. The term “megafauna” (from the ancient Greek for *megas* “large” and the New Latin *fauna* “animal”) has varied usage among scientists; for example, Ritchie and Olff (1999) consider any animal with an adult weight of >2 g to be “large,” as opposed to the vertebrate micro-herbivores (lagomorphs, rodents) and insects (birds and reptiles are variably considered, but generally analyses are limited to mammalian herbivores). The most common thresholds applied in the literature for modern herbivores are 44 kg (100 lb; Martin & Steadman 1999) or 100 kg (220 lb; Stuart 1991); however, Owen-Smith (1987) uses 1000 kg specifically in the discussion of extinct Pleistocene megaherbivores, which is a size class that includes no extant taxa in North or South America. In this paper, I use the 100 kg cutoff when referencing “megafauna” or “megaherbivores,” which includes important extant herbivores such as the Cervidae (e.g. deer, moose, elk) and Plains bison (*Bison bison*) that have well-documented influences on vegetation (discussed below). “Keystone” species are those taxa that exert a disproportionately high influence on their habitats relative to their biomass (Paine 1995), such as bison (Knapp et al 1999).

Coevolution of browsers and grazers with North American vegetation

Modern North American ecosystems are existing out of their evolutionary context; plants coevolved with megafaunal herbivores even in temperate regions (as opposed to today, where the very largest herbivores are typically found in the tropics).

Forested regions have supported large mammalian herbivores for the greater part of the last 50 million years, while in today's forests, one may only find one or two taxa (e.g. moose or deer in temperate North America) (Gill 2006). The radiation of ungulates in the Paleocene and Eocene coincided with the development of grasses as atmospheric CO_2 declined and climates became warmer and drier (Cerling et al 1998, Edwards & Smith 2010, Janis et al 2000, Janis et al 2002). Perissodactyls radiated in the Tertiary to become the dominant ungulates; horses predominated in the Oligocene (30-20 Ma BP) and rhinos joined them in the Miocene (20-5 Ma BP). Artiodactyls took over as the dominant herbivores in the Pleistocene, though they were present as early as the Eocene in primitive forms (Eisenberg 1981). The transition to more open habitats in the middle Miocene favored grazers, rather than browsers. The North American grassland biome has been dated to 18 Ma, in the Mid-Miocene; taxonomic diversity of ungulates was greatest from 16 to 14 Ma, but declined as browsers were reduced (without a significant increase in grazers; Janis et al 2002). It has been hypothesized that this reduction in browsers was due to decreased vegetation productivity due to the decline of atmospheric CO2 in the second half of the Miocene; decreased forage quality may have favored the radiation of horses, though only one genus of Equids survived to the Pleistocene. Large herbivores tend to increase with plant moisture availability, independent of soil fertility (unlike small herbivores, which are limited by soil fertility; (Fritz & Loison 2006).

While some taxa, like camels and horses, evolved in North America, others were relative latecomers, migrating across the Beringian land bridge during one of the many glacial cycles of the Pleistocene. Proboscideans arrived in North America much earlier in the Pleistocene (~ 2 million years ago; Graham 2001) than *Bison antiquus*, which arrived from Eurasia 220,00 to 250,000 years ago (Bell et al 2004).

2. *Plant-Herbivore Interactions in Modern Systems*

Modern North America is ecologically depauperate of native megaherbivores when compared to most of the Cenozoic (the last 65 million years); nevertheless, the ecological impacts of modern megaherbivores on plant community structure, function, and composition have been the subject of extensive study by ecologists. Given that the impacts of herbivores on vegetation increase with body size, the largest mammalian herbivores on the landscape are predicted to have the greatest influence on vegetation relative to their biomass, for several reasons (Owen-Smith 1988). First, compared with smaller herbivores, large herbivores are able to eat lower-quality browse, including greater fractions of woody material, due to the longer gut retention times associated with large body size (Wilson & Kerley 2003) and because animal metabolism rates scale to the ¾ power of biomass (i.e., Kleiber's Law; Kleiber 1932) lowering the energetic needs of large animals (Brown et al 2004). As a result, megaherbivores consume a greater proportion of landscape vegetation relative to their biomass than do meso- or micro-herbivores. Secondly, megaherbivores tend to be more general in their foraging habits, and thus exploit resources over a broader range of vegetation types and at larger spatial scales than smaller animals. Third, due to their large size, megaherbivores in particular are more readily able to escape predators, and so are able to build up sufficient populations to have a significant influence on vegetation (Dublin et al 1990, Owen-Smith 1988, Owen-Smith 1989). Landscapes may support one or more species of megaherbivores simultaneously, as a guild, which is a set of animal species (usually closely related taxonomically) that feed on the same species or in the same community, such as the grass-feeding ungulates of the Serengeti in Africa (Sinclair & Norton-Griffiths 1979).

Megaherbivores influence plant community structure and function both directly (e.g., browsing, grazing, trampling) and indirectly (e.g., nutrient cycling, competitive mediation, fire). The effects of herbivory on plant assemblages are dependent in part on the mode of consumption: browsing, grazing, or mowing. Browsing is the consumption of leaves, shoots, fruits, and even twigs or bark from woody plants, and materials consumed are typically from higher-growing plants (Gill 2006). In contrast, grazing and mowing are the consumption of the lower-growing grasses and forbs. Grazing is patchy in space, and different plants may be grazed to different heights, while mowing is spatially homogeneous and uniform in height (Crawley 1983). Large herbivores influence plant community dynamics largely by influencing competition, by increasing or reducing a particular plant’s ability to compete for light, water, or nutrients (and these may interact).

Modern herbivores preferentially browse and graze taxa that are more palatable; that is, those that have higher leaf protein content, softer tissues, and less chemical and physical defenses (Owen-Smith 1988). Even large herbivores, which are adapted to lower-quality browse, require protein and other nutrients, often preferring young shoots and leaves (Gill 2006), or nitrogen-rich post-fire growth (Fuhlendorf et al 2008). Herbivore preference, however, changes depending on the vegetation available for foraging, and will vary both with shifts in composition and among regions, seasons, and herbivore taxa. At Isle Royale, moose have suppressed hardwoods, and now browse heavily on conifers, (Del Giuduce et al 1997, Peterson 1988, Vucetich & Peterson 2004b). In other parts of the Great Lakes region, however, deer browsing has disproportionately affected the regeneration of hemlock, another conifer (Anderson & Katz 1993, Frelich & Lorimer 1985, Mladenoff & Stearns 1993, Waller & Alverson 1997).

Large herbivores typically experience a wide range of seasonal, climatic and spatial heterogeneity of resource availability (Illius 2006), either due to variability in moisture (in arid regions), temperature (in high-latitudes) or both (in highly seasonal regions). Large herbivores adapt to seasonality by timing breeding to the optimal period of survival (Loudon & Binklow 1992), restricting growth to the period of peak food abundance, and by migrating to follow optimal habitats or climates (Suttie & Webster 1995). An important characteristic of megaherbivores is the density-dependence of many of their life history traits, including mortality and sexual fecundity; this makes migration a common life history strategy in order to track optimal conditions. Herbivores may also track micronutrients, supplementing their diets with salt (which is particularly important in the metabolism of plant secondary compounds used in chemo-defense) or other essentials. Such micronutrient needs may increase the tendency to migration by prompting movement across the landscape to seek out resources like salt licks, or may tie a species to being in proximity to particular limiting resource. Emigration is almost universally a density-dependent behavior, and is often an immediate response of animals to declining food quality or quantity (Fritz & Loison 2006). Animals can migrate thousands of kilometers to track optimal forage or water, or to avoid natural enemies during the breeding season. This has two consequences: first, herbivore influences on plants may be highly seasonal, and secondly, large herbivores may be more resilient to changes in climate or resource availability, provided there are no barriers to migration.

Herbivore populations both limit and are limited by total plant biomass (Owen-Smith 1988). Vertebrate populations are often limited by the availability of high quality food; there is a strong correlation between the biomass of vertebrate herbivores in African grasslands and the rate of plant productivity, for example (Owen-Smith 2002). The rate of vegetation consumption can continue without diminution until the resource is depleted, at which point overcompensatory mortality results in a population crash; however, few such cycles have been observed, except in closed systems like Isle Royale (McLaren & Peterson 1994, Peterson et al 1984, Vucetich & Peterson 2004a), which indicates the importance of either intrinsic (e.g., migration) or extrinsic (resource-independent influences on growth and mortality) regulatory processes (Clutton-Brock et al 1997). Plant-herbivore interactions do not follow “classical predator-prey” cycles (Crawley 1983, May 1973), in part because both plants and herbivore abundances can be influenced by external processes, such as disease, drought, or a reduction in suitable breeding habitats. Herbivores, particularly in the absence of predators or competitors and when resources are abundant, may exhibit eruptive demographics, which may ultimately lead to a crash, such as the reindeer (*Rangifer tarandus*) on the St. Matthew Island in the Bering Sea (Klein 1968) or the moose on Isle Royale (Peterson et al 1984). Such crashes are an important mechanism in maintaining vegetation heterogeneity. For example, in East African woodlands, *Acacia* trees were not able to establish under constant herbivory pressure, but seedling establishment was associated with rinderpest and anthrax outbreaks that depleted ungulate populations, resulting in mosaics of grasslands interspersed with even-aged shrub stands (Prins & van der Jeugd 1993).

The scales of herbivore selection and plant response may be different; changes in community composition may in fact be the result of processes at the species or even individual level, with the potential for cascading indirect effects on community dynamics (Hester et al 2006). The actions of the megaherbivores at one spatiotemporal scale (e.g. local seedling mortality) result in changes at a broader scale (e.g. reduction in a preferred taxon) (Dormann & Bakker 1999). The response of any given vegetation assemblage to herbivory is mediated in part by the relationship between the defensive ability and palatability for a given set of plant species (Augustine & McNaughton 1998, Coley 1987, Pacala & Crawley 1992). The effects of herbivory on an individual plant will depend on the material consumed, which may include leaves, reproductive tissues, roots, seeds, or meristems (Hester et al 2006). The effects of herbivory on an individual may thus take many forms, and may be either positive (e.g. triggering compensatory growth, dispersal) or negative (e.g. meristem damage, mortality), and direct (e.g. seed dispersal, tissue damage, triggers in reproductive strategy) or indirect (e.g. altering competition for resources).

The ability of plants to persist, and thus the stability of any particular outcome of plant-herbivore interactions, depends in part on the existence of refuges for plants from over-exploitation. Such refuges this may take the form of a habitat that herbivores avoid due to a lack of resources, or the high prevalence of structural or chemical defenses in surrounding plants, or there may be patch dynamics driven by a discontinuous distribution of the animal across the landscape (Illius 2006). In general, factors that tend to increase plant equilibrium (i.e., the stability of the available resource for herbivores) have a stabilizing effect on plant-herbivore interactions (and thus herbivore populations), such as seed banks in the soil, or a protected seed source.

Plants may avoid herbivory physically, through location or visibility, or by the production of deterrents such as thorns or thick cuticles. Plant secondary metabolites are effective chemical defenses against herbivores (Palo & Robbins 1991, Rosenthal & Janzen 1979), either because they are toxic to the animal, reduce digestibility, or decrease the rate of foraging (Foley et al 1999). Other plants may mediate herbivore pressures via the adoption of tolerance mechanisms, including protected or numerous meristems, producing large quantities of long-lived seeds, inducing branching or tillering growth forms, and/or evolving a wide distribution of photosynthetic or reproductive tissues across the plant (Hester et al 2006). Plants may also exhibit compensation, which is the alteration of resource allocation and growth patterns in a positive response to plant injury to counteract the negative impacts of damage, such as increased growth rate or seed production. Many of these responses are plastic or inducible, triggered by tissue damage (Hanley 2007) or even chemicals in a herbivore's saliva (Bergman 2002).

There is some question as to whether megafaunal herbivory is a disturbance, per se. According to Krebs' (Krebs 2001) definition, a disturbance is "any discrete event that disrupts community structure and changes available resources, substrate availability, or the physical environment." This definition suggests that disturbance may be measured either directly as a cause—discrete changes in variables (e.g. biomass removal)—or indirectly as effect: changes in population or community composition (Hobbs 2006). In a review of disturbance, White and Jentsch (2001) argued that continuous levels of herbivory should not be considered disturbance because, according to their definition, a disturbance is a discrete event that is abrupt in nature relative to the longevity of an organism and its growth rate, reproduction, and ecology. In that case, changes in the severity of herbivory or the cessation of co-evolved plant-herbivory interactions may be interpreted as a disturbance. Whether megafaunal herbivory (or its disruption) is properly considered disturbance may ultimately depend on the scale of the herbivory regime (e.g., chronic or acute in space and time), the ecological process being studied, and/or the worldview of the ecologist.

Direct effects

In modern systems, the direct effects of megaherbivores on plant community composition are caused by consumption and trampling, which have affect plant tissues throughout their life stages (from seeds to seed production). Trampling is often cited as the most ubiquitous form of disturbance by herbivores (Cumming & Cumming 2003), as it includes all spheres of plant-herbivore interactions, including foraging, traveling, and bedding areas. For some plants, trampling has a higher likelihood of resulting in mortality, because it typically affects plants' basal regions and can thus damage or sever large proportions of above-ground tissue (Gill 1992, Reimoser et al 1999). The effects of foraging differ depending on the material consumed (Hester et al 2006), which may include reproductive tissues, seeds, or meristems. With browsing, for example, the consumption of leaves and shoots is most common (Gill 2006). Herbivory may suppress species (by direct consumption of reproductive tissue or seedling mortality) or may facilitate seedling establishment through gap production (Bullock et al 1994) or the creation of disturbed germination sites (Hobbs 2006).

The removal of flowering stems promotes plants that can reproduce vegetatively over those that can only utilize sexual reproduction, as well as perennials (which invest in below-ground biomass) over annuals (which invest in seeds). Defoliation delays flower production, and so herbivores can also influence the timing of sexual maturation of plants (Fletcher et al 2001, Kettenring et al 2009, Tiffin 2000, West 2012). Grazing effects may be different for annual plants, which have a reproductive cycle characterized by discrete bursts of productivity followed by periods of dormancy. The net reproductive rate in grazed areas is less than in non-grazed portions of grassland systems (Hester et al 1996), though herbivory can promote reproduction by providing disturbed sites for germination.

The removal of apical meristems changes the growth form and physical structure of plants. The loss of leaves reduces photosynthetic material, which, particularly for evergreens in winter, may also cause the plant to lose stores of nitrogen and carbon reserves, inhibiting new growth the following spring (Baker et al 2005, Crawley 1983, Honkanen et al 1999). If flowers are consumed, seed production is prohibited, which may in turn promote cloning and the expansion of perennial plants at the expense of annuals and plants limited to sexual reproduction (though this will be highly dependent on seed bank capacity of a given taxon) (Hester et al 2006). Plants may also change above- and below-ground allocations, though this is highly variable both across and within systems (Holland et al 1996). Tissue damage and/or chemicals in herbivore saliva may induce compensatory growth responses in plants (Bergman 2002, McNaughton 1979, Rooke 2004). Plants that show a compensatory response to tissue damage may actually be more successful, by increasing seed production or vertical growth (which facilitates competition for light) relative to competitors (Agrawal 2000). In some cases, however, foraging can be fatal to even otherwise resilient adult trees, as in bark stripping (Akashi & Nakashuzuka 1999, Kuiters et al 2006, Mitchell & Kirby 1990), rubbing (Coppedge & Shaw 1997, Hygnstrom et al 2009) or the physical destruction of trees by elephants (Anderson 2010, Maisels et al 2002, Pickett et al 2000).

In forests, browsing most strongly affects leaves and upper shoots of young trees, which contain the highest amounts of leaf nitrogen (Gill 2006), resulting in a relatively high amount of damage to saplings in particular. This in turn can slow tree growth for as many as 25 years or more (Roth 1996, Shaw 1974), keeping trees within the reach of herbivores for longer than they otherwise would without browsing pressure. Selective browsing of palatable taxa can facilitate the spread of non-preferred species, such as expansion of *Prunus serotina* and ferns in southern Pennsylvania forests at very high levels of deer browsing (Tilghman 1989). These effects can be seen on the regional scale in boreal forest in eastern temperate forests in North America, such as the decrease in hemlock (*Taxus canadensis*)*,* Canadian yew (*Tsuga canadensis*)*,* and white cedar (*Thuja occidentalis*) due to herbivory by white-tailed deer (Alverson et al 1988) and aspen (*Populus tremuloides*) in the American west due to herbivory by elk (Ripple & Larsen 2000, Romme et al 1995, Suzuki et al 1999). The effects of herbivory on composition may vary with herbivory density. For example, seedlings of *Alnus glutinosa* were found to regenerate only in areas of moderate density of herbivores (cattle), as a function of the trade-off between germination (which was not facilitated at low levels due to competition) and damage of tissues at high densities (Vinther 1983).

Landscape heterogeneity

The influences of herbivores on vegetation can trigger complex feedbacks that are not fully understood, and which may play out at a range of spatial and temporal scales (Hobbs 2006). Megaherbivores respond to the presence of existing patches by selectively feeding in areas of optimal forage or resting (McNaughton et al 1989, Johnson et al 2001), which may amplify heterogeneity by creating patches of consumption and nutrient deposition (Hobbs et al 2003, Zacheis et al 2002). Megaherbivores may increase landscape heterogeneity through the establishment of cyclic patch dynamics, in which unpalatable or highly defended taxa (e.g. thorny, toxic, woody species) facilitate the establishment of palatable ones by protecting seedlings. In some instances, those palatable taxa then shade out or otherwise out-compete protective vegetation, and their recruits are then susceptible to browsing once again (Gill 2006). This can facilitate “shifting mosaics” of vegetation, which is thought to play an important role in tree-grass coexistence in savannas (Olff et al 1999). Such tree-grass mosaics are what define the savanna landscape, and interactions between herbivory, climate, and fire are thought to prevent a shift to either grasslands or forests (Bond 2005, Sankaran et al. 2005). Conversely, herbivores may also reduce landscape heterogeneity; some species of megaherbivore exhibit cyclical grazing patterns by moving amongst patches at regular intervals to optimize foraging conditions across the landscape by preventing the development of unsuitable patches (Danell et al 2006).

Diversity

Megaherbivore mediation of competition among plant taxa is thought to be one of the most common mechanisms for herbivore influences on plant community composition diversity. In fact, selectively reducing competitive ability may be a stronger factor in determining vegetation composition than reducing fecundity or survival directly (Crawley 1983). The associations between herbivory and interspecific competition may be positive or negative for a given plant species, and will vary depending on what other plants are present. In other words, a species may be subjected to increased herbivory intensity due to its proximity to another, more palatable species, or it may be protected from herbivory due to its association with a less palatable or highly defended plant. This can result in increased diversity, if herbivory is selective to a dominant plant type, or decrease richness if a non-palatable taxon can out-compete grazed species, allowing it to dominate instead. Plant species richness increases most often by providing competition-free germination sites, such as wallows, burrows, or mounds (Hester et al 2006). Generalist herbivores are more likely than specialists to reduce species richness, and generalists can in fact reduce suitable forage for specialists. Much more is known about generalists' influences on vegetation than specialists (Hester et al 2006). The relationship between herbivores and vegetation diversity varies across landscapes, possibly due to differences in productivity across sites (Milchunas et al 1998). In modern North American grasslands, for example, herbivory has been shown to increase biodiversity on productive sites, but to decrease it where resources are limited (Bakker et al 2006, Bokdam & Gleichman 2000). In the tallgrass prairie in particular, plant diversity is highest when both fire and bison grazing are present, as bison consumption of grasses increase the diversity of forbs (Fahnestock & Knapp 1994).

Much of the research on megaherbivore influences on plants in general and their impacts on biodiversity in particular have been in rangelands, where shrub encroachment has occurred due to 1) a combination of fire suppression, overgrazing by cattle, and climate change (Brown & Archer 1999, Grover & Musick 1990, Van Auken 2000), or 2) to the loss of megafaunal diversity (Augustine & McNaughton 2004, Sankaran et al 2005). It is important to note that the concepts of “over-“ and “under-grazing” are normative characterizations that are linked specifically to desired rangeland or management outcomes (Crawley 1983). In natural systems, ‘heavy” grazing tends to reduce productivity at a certain point (Frank 2006). The response of vegetation will depend largely on the availability of moisture; where plant growth is water-limited, as in a savanna or short-grass prairie, heavy grazing causes a reduction of perennials in favor of annuals, followed by the establishment of woody species in thickets and the reduction of grasses. After this threshold is passed, shrub dominance may continue for decades after the removal of grazers, and fire or increases in moisture may be necessary to restore the previous grassland condition (Walker et al 1981).

Dispersal

Herbivores are important dispersal agents, either via passage of seeds through the gut (endozoochory; Janzen 1983), adhesion to fur or other body parts (epizoochory; Sorensen 1986), or through scatter hoarding activities (dyzoochory; Vander Wall & Balda 1977). Endozoochory is the most prevalent of these. Both angiosperms and gymnosperms may be dispersed by animals; while gymnosperms do not produce fruits per se, many species generate diaspores with seeds surrounded by nutritious tissues. While large, fleshy seeds are commonly thought of as the primary beneficiaries of endozoochory, Janzen (1984) suggested that herbivores also play an important role in small seed dispersal, as fruits are incidentally consumed along with other plant tissues. For example, Vellend (2003) found that deer play an important role in the post-glacial long-distance dispersal of the herb *Trillium*, which was previously considered to be primarily dispersed by ants. Not only do herbivores physically transport seeds, but they also provide gaps and disturbed patches necessary for many species to germinate; while trampling does kill some seedlings (Milchunas et al 1992), herbivores tend to result in net positive effects to germination (Crawley 1997, Hester et al 2006, Hester et al 1996). I will discuss seed megafaunal seed dispersal in further detail below.

Nutrient cycling

Herbivores alter both the rate and spatial heterogeneity of nutrient cycling (Cech et al 2010, Pastor et al 2006). The ability of megafauna to influence nutrient cycles was only recognized relatively recently, when the first studies showed that megaherbivores could alter rates of nutrient cycling well beyond their proportion of a given ecosystem's nutrient budget (Hobbs et al 1991, McNaughton et al 1997, Ritchie et al 1998). However, herbivores tend to preferentially consume the most nutritious parts and species of plants, reducing litter quality (and even quantity over time (Pastor & Naiman 1992). Herbivores may concentrate nutrients from wide foraging regions into small patches via dung, urine, and even their carcasses, which can in turn persist for many years (Cech et al 2010, Danell et al 2002, Ruess & McNaughton 1987, Ruess & Seagle 1994, Towne 2000). Deforestation by elephants can release the nutrients of long-lived trees as a pulse to the system, which may be lost if nearby vegetation cannot accommodate the influx of nitrogen and carbon.

Relatively little is known about the influence of megaherbivores on ecosystem carbon dynamics, particularly below-ground carbon stores (Tanentzap & Coomes 2011). The outcome of grazers' influence on C may depend on intensity; for example, at low levels of grazing (4.5 sheep/ha), grasslands in China were a net carbon sink, but as intensity increased, carbon sequestration declined to the point where heavily grazed landscapes ultimately became net carbon source (He et al 2011). In a meta-analysis, Tanentzap (2011) found a small positive impact on the mean influence of herbivory on carbon stocks, though the gains were more significant in grasslands, shrublands, and pastures than in forests.

Fire

Fire-prone ecosystems such as grasslands and savannas tend also to support large herbivores (Bond et al 2005, Milchunas & Lauenroth 1993). The strong preference of grazers for recently burned patches indicates a strong evolutionary relationship between herbivores and fire (Allred et al 2011, Fuhlendorf & Engle 2004, Fuhlendorf et al 2008, Vermiere et al 2004). Modern interactions between fire and megaherbivory have received the most attention in rangelands (Fuhlendorf & Engle 2004) and savannas (Holdo et al 2009), where grazers have been shown to alter fire intensity through the reduction of fuels (Fuhlendorf & Smeins 1997). In savannas, grazing lawns create fuel-limited patches that block the spread of fire, protecting forested patches and contributing to tree-grass coexistence. Positive feedbacks between fuel loads and fire intensity, as well as trade-offs between browsers and grazers, can result in alternate stable states; grazers reduce fire and increase woody plant biomass (shrub encroachment), and browsers increase fire by indirectly stimulating grass growth (Van Langevelde et al 2003). In exclusion experiments involving African elephants, shrubs and woody plants expanded in the absence of large herbivores, changing ecosystem function even as ecosystem structure remained largely unchanged (Guldemond & Van Aarde 2008). Much less is known about the influence of megaherbivores on fire dynamics in forests (especially temperate forests), however, largely due to the 1) longer fire return intervals and 2) the comparative lower density of megaherbivores in modern systems. Changes in the distribution of fuels in rainforests can have significant impacts on fire regimes, increasing the severity of fires and triggering the conversion of forest to grassland (Cochrane 2003, Laurance 2003).

3. The Late-Glacial Megafaunal Extinctions: Patterns and Causes

Fifty thousand years ago, megaherbivores were more diverse and widespread than today on all continents. By the early Holocene (~ 11,000 BP), however, dozens of species of large herbivores and their predators had disappeared from North American as part of a a global, time-transgressive extinction wave (Faith & Surovell 2009, Koch &

Barnosky 2006). An analysis of the most robust radiocarbon-dated fossil remains indicates a relatively narrow extinction window of 15.6 ka to 11.5 ka BP for most North America taxa (Barnosky et al 2004). These late-Quaternary extinctions disproportionately targeted large (>10 kg) mammals, reducing diversity by 34 genera in North America alone (Barnosky et al 2004). Extinct North American taxa included five species of Equids, three species of camel (*Camelops*), two species of llama (*Llama*), giant ground sloths (*Megatherium*), at least two species of bison (*Bison*), the stag-moose (*Cervalces scotti*), mastodons (*Mammut*) and mammoths (*Mammuthus*). Two orders, Perrisodactyla and Proboscidea, were totally eliminated from North America (Koch and Barnosky 2006). Most of the large megafaunal predators were also extirpated, including the dire wolf (*Canis dirus*), the short-faced bear *(Arctodus simus*), the American lion (*Panthera leo*) and the genus *Smilodon* (saber-toothed cats). Six genera (*Hydrochaeris*, *Tremarctos*, *Equus*, *Tapirus*, *Bos*, and *Saiga*) survived on other continents. All species >1000 kg were lost in North America, removing an entire functional guild of the largest browsers and grazers. Less than half of the species between 32 kg and 1000 kg survived the extinction (Koch & Barnosky 2006, Lyons et al 2004). Overall, 72% of mammalian megafauna went extinct in North America alone, with only 13 genera surviving as part of a greatly reduced set of functional guilds. The event was geologically unusual in that it disproportionably affected large mammals (Barnosky 1989); indeed, the event was more selective than any in the preceding 65 million years of mammalian history in North America (Alroy 1999, Koch & Barnosky 2006).

Hypotheses for the cause of the extinction include climate-induced vegetation change (Graham & Lundelius 1984, Grayson & Meltzer 2003), Younger Dryas cooling (Berger 1991), rapid ("blitzkrieg") human overkill (Martin 1984), protracted overkill (Fisher 1997), continental drought (Haynes 1991), or some combination of factors. Firestone et al. (2007) hypothesized that an extraterrestrial impact at 12.9 ka BP may have triggered widespread environmental change at the Younger Dryas, making landscapes unsuitable to support megafauna, but this has been widely disputed (Buchanan et al 2008, Marlon et al 2009, Paquay et al 2009) and is not supported by the pattern of radiocarbon dates of megafaunal remains (Faith 2011, Saunders et al 2010). Determining a cause of the LQE has been limited by the fact that fossil remains are discontinuous in space and time, and the fact that the extinctions were contemporaneous with rapid environmental change and the generally accepted timing of human arrival (Koch & Barnosky 2006).

Causal debates have centered largely on climatic versus anthropogenic causes. Evidence in support of human hunting includes 1) the fact that low-level hunting pressure would have been sufficient to trigger a collapse in megafaunal populations (Alroy 2001), 2) the spatiotemporal association (either regionally or globally) between extinction and the timing of human arrival (Surovell et al 2005), 3) fossil evidence of human hunting and butchery (Surovell & Waguespack 2007), and 4) the fact that megafauna survived previous glacial-interglacial cycles (Barnosky et al 2004). Evidence supporting a climate (or, at least, non-human) cause include 1) lack of clear kill sites for most fossil taxa (Grayson & Meltzer 2003), and 2) widespread vegetation change at the Pleistocene-Holocene transition (Graham & Lundelius 1984, Guthrie 1989). Initially, Martin's rapid overkill, or "Blitzkrieg" hypothesis (Martin 1984) was challenged due to the presumed small size of early human populations relative to those of megaherbivores; however, there is increasing evidence that humans were in North America at least by 15,500 BP, which has significantly widened the interval of overlap between humans and megafauna (Waters et al 2011a, Waters & Stafford 2007, Waters et al 2011b). Increasingly, a combination of modeling and proxies, including ancient DNA (aDNA), improved radiocarbon dating techniques, Bayesian modeling, and the dung fungus *Sporormiella* (discussed in greater detail below) suggest that a combination of environmental stress and human hunting pressure was the most likely cause (Lorenzen et al 2011, Nogués-Bravo et al 2008, Ripple et al 2010).

4. Sporormiella: A Coprophilous Fungus Proxy for Paleo-Megaherbivores

While much attention has been devoted to understanding the causes of the late Quaternary megafaunal extinctions, the ecological consequences of those extinctions have received much less attention, hampered in part by limitations in comparing a discontinuous faunal bone record with a vegetation record constructed primarily from lake sediment records that are typically not associated with megafaunal fossils. *Sporormiella* is a coprophilous fungus that produces spores that are preserved in lakes and mires along with pollen, and so can be used to directly interpret the vegetation record in the context of the presence and absence of herbivores. Recently, *Sporormiella* has been applied with increasing frequency in paleoecological analyses to establish local megafaunal presence or absence, and to provide the ecological context and consequences of megaherbivore collapse (Burney et al 2003, Davis & Shafer 2006, Gill et al 2009, Faith 2011, Rule et al 2012, Robinson et al 2005), including the effects of the extinction on vegetation (by comparing spore records with pollen from the same sediment cores) and fire regimes (by analyzing sediment charcoal records). Davis (1987) first noted that *Sporormiella* spores were found in high abundance in mammoth dung (>16%; Mead et al 1986) and in Pleistocene-age sediments in the American southwest, were essentially absent in Holocene sediments, but increased in historic sediments, presumably due to the local introduction of domestic grazers.

Sporormiella requires digestion by herbivores to complete its life cycle (Wicklow 1981, Wicklow & Angel 1980); newly-defecated spores produce fungi, often 6 weeks or more after the dung has been deposited (Ebersohn & Eicker 1997, Richardson 2002). The fungus then sporulates, releasing new spores onto surrounding vegetation, where they may be consumed by herbivores or transported into sedimentary basins via slopewash, saltation, or short-distance airborne transport. Spores have occasionally been found in pollen traps, usually in association with agriculture, zoos, or urban horses (Gonianakis et al 2006, Mallo et al 2011, Mitakakis & Guest 2001), but are generally not transported long distances (see Chapter 3 of this dissertation for discussion of *Sporormiella* transport, which is supports a source area <100 m). The ascus releases ascosopores with four or more spore cells; in the fossil record, *Sporormiella* is typically found (and counted) as subspores. Spores are brown in color and resist staining, and have thick, distinct walls. Intact spores are notable for having divided septa, and most, but not all, species have a distinct sigmoid aperture, or slit, which may vary in the degree of curvature. Subspores can often be identified as rectangle-shaped mid-cells or bullet-shaped end cells. Doveri (2004) provides an extensive guide to the variety of *Sporormiella* morphotypes.

Sporormiella spores are found in association with a wide range of faunal taxa, including megaherbivores (e.g., bison, cattle, horse, moose, elephant) and smaller animals, including mammals and birds (e.g., rabbit, geese, porcupines) (Ahmed & Cain 1972, Richardson 2001); however, coprophilous ascomycota in general are seldom reported on reptile or amphibian dung (Richardson 2001). High abundances of *Sporormiella* in sediments is often—but not always (Cordova et al 2011)—found in association with modern domestic herbivores (Davis & Shafer 2006, Graf & Chmura 2006, Raper & Bush 2009). It is currently unknown why spores are absent from some grazed locations, though one possibility is the patchiness of herbivory and the short dispersal distance of spores (see Chapter 3). While some megafaunal taxa did survive into the Holocene (e.g. bison, moose, elk, bighorn), the low abundances of *Sporormiella* in Holocene sediments is assumed to be because megafaunal biomass was not sufficient to produce volumes of the dung necessary to generate a noticeable signal in lake sediment records. Currently, no *Sporormiella* records exist from sediment records from the Great Plains, a region that has relatively fewer lakes than the more mesic regions of eastern North America; this region is a critical target for future research (see also Chapter 3 of this dissertation for further discussion of bison and the Holocene paleoecology of the Great Plains).

Sporormiella has been used in a range of geographic settings and time periods to indicate megafaunal presence or the timing of decline, including the presence of Pleistocene megafauna in Siberia (Schirrmeister et al 2011, Wetterich et al 2012), the end-Pleistocene extinctions in eastern North America (Gill et al 2012, Gill et al 2009, Robinson et al 2005) and Australia (Rule et al 2012), late-Holocene extinctions in Madagascar (Burney et al 2003) and New Zealand (Wood et al 2011), the presence and/or effects of pastoralism (Connor et al 2012, Schofield & Edwards 2011), agriculture (Ballut et al 2012, Mudie et al 2011, Urrego et al 2011), butchery (Bos et al 2012) or site function in human settlements (Bosi et al 2011, Florenzano et al 2012) in the archaeological record, grazing impacts in the historic record in Europe (López-Merino et al 2011a, López-Merino et al 2011b), evidence of coprophagy in mammoth young (Fisher et al 2012), and even as indicators of lake level (Williams et al 2011) or terrestrial sediment input in marine systems (Shumilovskikh et al 2012).

Given its increasing usage as a proxy, understanding the factors governing *Sporormiella* spore production, dispersal, taphonomy, preservation, and linkages to herbivore hosts and biomass are essential to critically evaluating its suitability and limitations as a proxy. Feranec et al (2011) raised several key concerns, namely that spores may be indicators of aridity (given the fact that fungi are often moisture-limited) or may reflect densities and cycles of non-megafaunal herbivores. *Sporormiella* may differ from pollen transport in that spores are not (primarily) anemophilous, but instead are washed or blown into lakes from the surrounding ground surface (see Chapter 3 of this dissertation). As a consequence, spores may be more concentrated in near-shore sediments than in the deepest part of the lake sediment basin, and so variations in Sporormiella abundances in a single core may be sensitive to fluctuations in lake levels and shoreline position (Raper & Bush 2009). However, a recent study by Parker et al. (Parker & Williams 2011) found a positive relationship between distance-to-shoreline and *Sporormiella* abundances. Parker et al. also found that aridity was a significant influence on spore relative abundances, but not concentrations, concluding that *Sporormiella* is influenced by environmental factors, in addition to the presence of herbivores. The fact that spores have been found in association with herbivores on all continents, including Antarctica (possibly in association with horses and other animals from early Antarctic expeditions; Bridge & Spooner 2012), and on islands as remote as the Azores (Connor et al 2012), as well as in a range of habitats, from the Negev Desert (Anderson et al 2006) to the lower Yangtze wetlands of China (Zong et al 2011), suggests that *Sporormiella* is able to reproduce in a wide range of habitats and climate types, and any particular set of climates may not necessarily preclude using *Sporormiella* as a proxy. The absence of spores from modern sites where herbivores are known to be present (Davis & Shafer 2006) has yet to be explained, but it indicates that the lack of a spore record at a given site may be less meaningful than the presence of spores that fluctuate through time.

5. Ecological Consequences of the End-Pleistocene Extinctions: Data, Hypotheses & New Directions

While the causes of the North American megafaunal extinctions have inspired both research and debate, their ecological consequences have received considerably less attention, due in part to the limitations of comparing the fossil plant and animal records mentioned previously. For this reason, tests of the direct impacts of Pleistocene megafauna on vegetation have been few until recent developments in vegetation modeling and lake sediment proxies such as *Sporormiella*. What does the paleorecord say about the impacts of the end-Pleistocene megafaunal extinctions? Research on megaherbivore influences on vegetation has been limited, but is increasing with the development of statistical and proxy tools, including *Sporormiella* and other indicators of herbivory.

Whether the subject is of interest to paleoecologists may also rely on the causal factors of the extinctions; Johnson (2009) argued that if vegetation change was the primary cause of the megafaunal declines (Guthrie 1989), there would be no reason to suspect an ecological response to the extinction, as a breakdown in animal-plant dynamics would itself have triggered the extinction. However, if human hunting (or some other non-vegetation factor) played a role, there may have been a response in the vegetation to the removal of the Pleistocene megaherbivores. Regardless, there are some herbivore influences, such as on seed dispersal, which may have been notable regardless of the cause of the demise of the mammoths, mastodons, and other megaherbivores. Given the strength of the modern megaherbivore-plant interactions, and the evidence that (in North America) human hunting contributed to the extinctions, for the purposes of this paper I am operating under the assumption that the megafaunal extinctions left an impact on Holocene vegetation.

Olff and Ritchie (1998) predicted that body size may explain the direction, magnitude and scale of the effects of herbivores on plant density in modern systems; given the documented effects of modern megaherbivores on contemporary plant communities, it has been hypothesized that ancient landscapes would have been likely been similarly influenced (Craine & McLauchlan 2004, Owen-Smith 1987). Johnson (2009) hypothesized three general landscape responses to the end-Pleistocene extinctions: a loss of open vegetation and habitat mosaics, increased fire, and the decline of co-evolved plants that thrive with the assistance of megafaunal dispersers. Herbivores influence the physiology, form, and growth of plants, and the paleorecord may not capture the full range of the effects of vegetation-herbivore interactions. Some effects, like influences on species coexistence and competitiveness, may only be inferred as a potential mechanism driving changes in community composition, though such inferences may grounded with modern experimentation and observation to identify mechanistic linkages between pattern and process. Others, such as megaherbivore effects on seed dispersal could be modeled in migration, demography, or species distribution models (Lorenzen et al 2011) The pollen record is biased to anemophilous plants, and particularly trees and shrubs, while herbs are both underrepresented and are often only distinguished to the genus or family level, which limits inferences of the effects of megaherbivores on understory communities. Charcoal analyses, particularly when combined with Sporormiella records from the same lake, may provide one of the best opportunities to study linkages between herbivore extinctions and cascading effects on plants by examining the lead-lag dynamics of changes in megafaunal abundances and fire regimes in tandem. Terrestrial paleo-biogeochemistry is an emerging field (McLauchlan et al 2008, McLauchlan et al 2007), with the potential to test the effects of herbivore reductions on nutrient cycling by studying the elemental composition of lake sediments.

One advantage of paleoecology is the ability to study broad spatiotemporal scales, but this comes with a limitation in the realms of direct observation and experimental manipulation. In other words, paleoecology is inherently a descriptive science (with the exception of modeling), and requires that events be recorded with a material that is preserved until it can be analyzed and interpreted in the present. While not all consequences of the late-Quaternary extinctions may be tested empirically, or even modeled, the wealth of modern data on megaherbivore influences on vegetation allow us to make several predictions about the long-term ecological consequences of this biotic upheaval event. I have limited discussion to those effects that may be most readily observed in or inferred from the paleorecord.

H_0: The extinction of the Pleistocene megafauna did not result in any measurable ecological change in the paleorecord.

There may be no observed effect of the megafaunal extinctions in paleorecords, either due to 1) the actual lack of an effect of herbivores on their environment, 2) the absence of evidence for the effect of herbivores in the paleorecord (no evidence for an effect), or 3) indeterminacy due to a multiplicity of causal factors that cannot be disentangled (i.e., the inability to distinguish an effect). In other words, the lack of an observed effect may be a limitation of the paleorecord's ability to record or distinguish an effect of the megafaunal extinctions, or it may reflect an actual lack of a measurable impact due to the extinction due to the resilience of plant communities to changes in herbivore densities.

H_1: Community composition would have been altered by the release of palatable taxa from herbivory.

Several pollen records from eastern North America show an increase in hardwood deciduous taxa immediately following the *Sporormiella* decline, including an increase in *Fraxinus nigra*-type and *Ostrya*-type pollen at Appleman Lake, IN (Gill et al 2009) and Silver Lake, OH (Gill et al 2012), and an increase in *Acer* in upstate New York (Robinson et al 2005). These shifts took place during an interval of high climate dissimilarity relative to present (see Chapter 4), and so may reflect the response of vegetation to non-mammalian drivers. However, pollen and *Sporormiella* records from Australia (Rule et al 2012) during the penultimate glaciation and from late-Holocene Madagascar (Burney et al 2003) also record major shifts in community composition immediately following the decline in megafauna, in the presumed absence of major climate change. A future challenge for paleoecology will be to disentangle the causal mechanisms (e.g., climate change, plant migrations, changes in CO_2 concentrations) of changes in community composition. Two potential ways forward include 1) including megaherbivore effects in dynamic global vegetation models (Allen et al 2010), and 2) further analyses of *Sporormiella* records, particularly from regions that experienced megafaunal declines during periods of relative climatic stability. It will be especially difficult to disentangle whether vegetation change was a cause or an effect of the observed changes in composition, but this may be resolved in part with high-resolution sampling to determine lead-lag dynamics, as well as the analysis of *Sporormiella* records from regions where the cause of the extinctions are known to be anthropogenic, such as Pacific islands (Wood et al 2011).

H_2: Fire regimes in Pleistocene ecosystems were reduced compared to the Holocene.

Fire is considered the primary mechanism for consumer control of vegetation today (Bond & Keeley 2005), but was this necessarily the case throughout the Quaternary, and for all biomes? Joint analyses of fossil charcoal records and *Sporormiella* records indicate that the loss of Pleistocene megaherbivores may have increased fire in Madagascar (Burney et al 2003), upstate New York (Robinson et al

2005), Indiana (Gill et al 2009), and Ohio (Gill et al 2012). Megafaunal consumption of biomass likely reduced litter and fuel loads during the Pleistocene, just as herbivores have been observed to do today (Bond & Keeley 2005); when megaherbivores went extinct, this may have allowed for the buildup of landscape fuel loads, and a reduction in landscape heterogeneity would have facilitated the spread of fires (Waldram et al 2007). In Australia, the loss of megaherbivores (inferred from a 130,000-year *Sporormiella* record) was followed by a shift from rainforest to sclerophyllous vegetation, due to a combination of relaxed herbivory pressure and ensuing enhanced fire regimes (Rule et al 2012).

An increase in fire activity following herbivory release would not necessarily have represented a one-for-one substitution of one vegetation consumer for another, however. Bond (2005) noted that while both fire and herbivores convert complex organic molecules to simple organic and mineral products, fire differs from herbivory in that it regularly consumes dead material and is not limited by requirements for protein or other nutrients. Fire and megafaunal herbivory operate at different spatial and temporal scales, and are likely to have had different influences on community composition, structure, and ecosystem function (Bond et al 2001). The effects of a fire differ depending on characteristics of the fire regime (Gill 1975), including the type (i.e., ground or crown), season, spatial extent, intensity, severity, so the effects of changes in fire regime are likely to be significant (Bond & Keeley 2005). I hypothesize that both fire frequency, severity, and spatial extent may have been greater during the Holocene following the loss of herbivores. This hypothesis could be tested both by examining the post-extinction fire regimes (including charcoal morphotype analysis to determine material burned), particularly in comparison with previous interglacials (where such records are available), but also by modeling interactions between grazers, fire, and vegetation, particularly as CO_2 concentrations changed during glacial-interglacial cycles.

H_3: Pleistocene ecosystems were more open and/or patchy than present.

Given the role that megafaunal grazers in particular play in maintaining tree-grass coexistence, the end-Pleistocene extinctions may have resulted in a reduction of open vegetation in favor of closed canopies, which may in turn have resulted in a decrease in landscape heterogeneity (Johnson 2009). Vera (2000, 2006) suggested that the early Holocene mosaics of grassland, thicket, and forest in Europe were maintained by herbivores, and that the closing of mid-Holocene forests were potentially due to the reduction of Europe's last remaining megafauna, including the aurochs (*Bos primigenius*), moose (*Alces alces*), and European bison (*Bison bonasus*). In the absence of herbivores, light-demanding woody taxa, including oak (*Quercus*) and hazel (*Corylus*), were out-competed by shade-tolerant beech (*Fagus*), elm *(Ulmus*), hornbeam (*Carpinus*), lime (*Tilia*), and hophornbeam *(Ostrya*) as canopies closed. Mitchell (2004) tested this hypothesis by comparing pollen records from Europe with Ireland, which lacked mid-Holocene megafauna, and found that hazel and oak were abundant even in the absence of browsers. In testing the impacts of herbivores forest dynamics, is important to note that pollen records may not be accurately reflecting landscape heterogeneity, due to 1) the integration of pollen from multiple patches in the source area, and 2) the fact that late glacial pollen abundances tend to overestimate the regional leaf area index (Williams et al 2008). Mitchell (2004) attempted to circumvent this issue by analyzing pollen from forest hollows. However, Ireland also lacked shade-tolerant lime and beech, and so herbivory may not have been necessary to promote landscape openness that allowed for the expansion of those shade-intolerant taxa (Hodder et al 2009). Fossil beetle evidence does support that regions of Europe were more open than present, particularly in the lowlands, presumably due to both herbivory and (possibly anthropogenic) fire (Svenning 2002).

Graham (1984) hypothesized that a shift from mosaic to zonal vegetation gradients was a primary cause of the megafaunal extinctions in North America, but in modern studies, megaherbivores have been found to maintain landscape heterogeneity. Therefore, closing landscapes and the development of more continuous vegetation may have been a consequence, rather than a cause, of the end-Pleistocene extinctions. Bakker et al. (2004). tested whether modern European thorny and light-demanding taxa, including English oak (*Quercus robber*) and blackthorn (*Prunus spinosa*) were “ecological anachronisms,” adapted to now-extinct aurochs (*Bos primigenius*) and tarpans (*Equus ferus ferus*). They tested the response of vegetation to cattle and horse grazing, and found that extensive grazing in floodplains established a shifting mosaic of grasses, shrubs, and trees similar to conditions during the Pleistocene.

Ultimately, the question remains as to the role of megafauna in maintaining openness or landscape heterogeneity in Europe, and has yet to be tested in North America, which supported a greater diversity of megafauna than Eurasia at the time. Pollen analyses that are corrected for biases in arboreal pollen productivity may help to resolve this question, and some regions may be especially well-suited for such tests. For example, Weigl and Knowles (1995, 2006) hypothesized that the now-endangered grass balds of the southern Appalachian mountains may be remnants of past herbivory (later maintained by Native American burning) though this has yet to be tested with paleoecological analysis. Dynamic global vegetation modeling that incorporates megaherbivores may also be used to test drivers of changes in ecosystem structure for a range of habitats and climates.

H_4: Megafaunal influences on vegetation will vary with landscape position.

Megafaunal communities are not uniformly spread across landscapes, but can exhibit spatial patterning due to ties to resources or landscape barriers. I would therefore predict greater effects of the megafaunal extinction in those areas that are most suitable for megaherbivore habitat, such as lowlands with ample water sources and soil nutrients (Bakker et al. 2004). Svenning (2002) examined non-arboreal pollen abundances from the last interglacial of Europe, and found evidence for open vegetation in the lowlands, while uplands remained closed (“high forests”). In the early Holocene, however, non-arboreal pollen abundances were reduced in both upland and lowland sites, suggesting that our current interglacial is more dominated by closed forests in Europe than during the penultimate glaciation. Svenning (2002) also found increased dung beetle fossils in the riparian samples from last interglacial than in Holocene sediments, suggesting that megaherbivores played a role in maintaining open habitat. Tests of this hypothesis could include targeting pollen analyses to sites across a variety of landscape positions, as well as the analysis of other indicators of herbivory such as dung beetles (Craine and McLauchlan 2004). The effects of herbivores on vegetation may also differ in high-altitude environments, where megaherbivores have been shown to influence tree line dynamics in modern settings (Speed et al 2010).

H_5: The end-Pleistocene extinctions affected both the rate and spatial distribution of nutrient cycles.

Very little is known about the role of Pleistocene megafauna on nutrient cycles, though recent advances in lake sediment proxies of ecosystem function may shed light on the role that extinct megaherbivore played on the nitrogen and other dynamics (McLauchlan 2008, McLauchlan et al 2007). One major challenge will be to differentiate allochthonous from autochthonous processes governing lake sediment records of biogeochemistry. Additionally, any proxy will likely integrate processes at the watershed level, and so differentiating spatial heterogeneity will likely not be possible using lake sediment records.

H_6: Many Holocene plants are more dispersal-limited than during the Pleistocene.

If megaherbivores were important agents of dispersal—at least for some taxa—

then plants that relied on (or at least benefited from) zoochorous dispersal should be expected to exhibit reduced gene flow increased population structuring due to increased clumping, and reduced geographic ranges and/or rates of migration (Guimaraes et al 2011). Dispersal vectors may have been completely different in the Holocene than in the Pleistocene, perhaps even altering migratory pathways away from pervious megafaunal migration routes along waterways or lowlands, or increasing the influence of dispersal barriers. Plants that previously relied upon herbivory to generate gaps or open canopies for germination or to light availability may show different habitat preferences (i.e., a shift to edges, association with fire or ruderal areas), which may in turn result in different species associations during the Holocene than the Pleistocene. Similarly, plants that may have been able to take advantage of megafaunal inputs of nitrogen or other limiting nutrients may no longer be able to compete as effectively.

Dispersal limitation has likely affected some taxa more than others; those plants with large fruits may have been particularly affected, as until the expansion of humans or the arrival of domestic herbivores such as cattle, sheep, and horses, plants with the very largest fruits would have had no alternative modes of dispersal (thus limiting their postglacial rates of migration). In North and South America, several taxa of large-fruited trees may be “ecological anachronisms,” with adaptations to megafaunal dispersers that vanished from the landscape millennia ago (Janzen & Martin 1982). In addition to bearing large, nutritious fruits, trees like the papaya (*Cerica papaya*), avocado (*Persea americana*), honey locust (*Gleditsia triancanthos*), Kentucky coffee tree (*Gymnocladus* *dioicus*), pawpaw (*Asimina triloba*), persimmon (*Diospyros virginiana*), and Osage orange (*Maculra pomifera*) all show adaptations to megafaunal herbivory and dispersal, including clonal growth, root suckers, and/or large thorns (Barlow 2002). These taxa are often cited as classic examples of the ecological implications of lost megafaunal dispersers, but the effects of the megafaunal extinction on their modern ranges and rates of dispersal has yet to be tested. Changes in plant dispersal would not necessarily have been limited to large-fruited plants (Janzen 1984, Vellend et al 2003), and so should be tested for other taxa as well, including slow-dispersing forest herbs. Tests could include comparisons between modern ranges and that of previous interglacials, tests for migration lags using species distribution models, plant dispersal models that incorporate animal dispersers, or measuring patterns of gene flow in modern and ancient populations.

H_7: The breakdown of plant-megaherbivore interactions at the end of the Pleistocene would have had cascading effects to meso- and microfaunal communities.

Megafaunal-induced changes to vegetation composition and structure would theoretically cascade to meso- and microfauna (Blois et al 2010), which are more tied to high-nutrient forage and are often less selective than megaherbivores (Crawley 1983). Small mammals would also affected to changes in landscape openness and/or the availability of herbaceous taxa for seed. Thus far, effects of the megafaunal influences on small-mammal habitats has been largely untested in the paleorecord. It will be especially difficult to discriminate megafaunal effects from changes in climate, but multi-proxy paleorecords (e.g. packrat middens, cave deposits) that record small mammal communities, changes in animal diets (such as those measured in stable isotopes in tooth enamel), and independent records of climate (speleothems) may provide useful inferences.

Vegetation-Herbivore interactions and the cause of the end-Pleistocene extinctions

Extending the study of vegetation-herbivore interactions to the Quaternary may have important implications for understanding the mechanisms of the end-Pleistocene extinctions. Climate and climate-driven vegetation changes are some of the most important mechanisms of extinction on geological timescales. Researchers often cite late Pleistocene diets of fossil herbivores as being different from the available forage in the provenance region during the Holocene (Teale & Miller 2012, Yansa & Adams 2012), but these conclusions often do not take into account megafaunal capacity for migration. Vegetation change is one of the primary mechanisms for a climate-only hypothesis for the megafaunal extinction, but such work often assumes a unidirectional influence of vegetation on megafauna, and such studies have typically interpreted any vegetation change associated with the extinctions as a cause of the extinctions. In modern systems, the vegetation-megafauna relationship is more accurately described as a feedback system than a hierarchy, which indicates that there is likely much that is unresolved about plant-herbivore interactions in the past.

Atmospheric CO_2 concentrations change the quality and palatability of vegetation by influencing leaf protein abundance, soluble carbon concentrations, fiber content, and plant secondary compounds used for defense. Generally, as CO_2 increases, protein content decreases, and animals respond with slower growth rates and reduced effectiveness of allocation to reproduction (Agrell et al 2000, Arnone et al 1995, Körner 2000). Nitrogen and fiber contents affect the digestive efficiency of ruminants in particular; as nitrogen concentrations in forage are reduced and fiber components increase, the amount of assimilated ingesta (ingested material) relative to egesta (waste material) declines (Owensby et al 1996). As CO_2 concentrations increased during the late-glacial/early Holocene transition, the C:N rations of vegetation would likely have increased, reducing the quality of available forage (Ehleringer et al 2002). Conversely, lower CO_2 concentrations during glacial intervals would have promoted the expansion of C_4 grasses, which tend to have reduced protein and increased C:N ratios and are thus less nutritious than C_3 grasses (Ehleringer & Monson 1993). Modern megaherbivore diets today are diverse, and large body size is an adaptation to poor-quality forage. Faith (2011) suggested that lower nutrient quality in the Holocene was a contributing factor to the megafaunal declines in North America, while Allen et al. (2010) modeled a reduction in vegetation net primary productivity, which they linked to the extinction of the megafauna in northern Eurasia. Vegetation response to changes in CO_2 concentrations at glacial-interglacial cycles would also have interacted with changes in moisture availability (Policy et al 1993), temperature, and growing season length, which must all be taken into account in future analyses of the effects changing megafaunal diets during glacial-interglacial cycles.

The late Holocene survival of dwarf mammoths in the Arctic islands has been interpreted as both due to a refuge from human hunting pressure (Koch & Barnosky 2006) and as an indicator that optimal habitats were drastically reduced (Vartanyan et al 1993). There is conflicting evidence as to whether Pleistocene megafaunal populations were under environmental stress leading up to the arrival of humans in North America. For example, fossil evidence from Beringia indicates that horses (Guthrie 2003) and possibly Cervids (Rivals et al 2010) experienced dietary stress during the Pleistocene/Holocene transition, while physiological evidence is lacking to support dietary-driven declines in Floridian Proboscideans (Koch et al 1998) or Shasta ground sloths in California (Thompson et al 1980) and Nevada (Hofreiter et al 2000). Physiological species distribution modeling of megafaunal distributions across glacial-interglacial transitions (particularly those that are informed by changing nutritional availability), analysis of forage quality from macrofossils, experimental tests of the impacts of forage grown under low CO_2 conditions, and *Sporormiella* records from the last interglacial may help to clarify the relationship between herbivores, humans, climate, and vegetation change at the Pleistocene-Holocene boundary.

6. Conclusions

Modern and paleoecological analyses have much to contribute to one another; future directions include a better understanding of direct and indirect effects herbivores on of nutrient cycling (including feedbacks), trophic cascades resulting from the megafaunal extinctions (including on insects, birds, and arthropods), the role of fire in forested landscapes, factors influencing palatability and preference through time, density-dependent effects, the evolutionary consequences of changing defense needs, and trade-offs between browsing and grazing guilds. Given the importance that modern megaherbivores play in a range of ecosystems, in spite of greatly reduced diversity and biomass, it is intuitive that the end-Pleistocene extinctions were significant not only for their own sake, but for cascading effects to the ecosystems that megaherbivores and their predators inhabited. Growing evidence, including this dissertation, supports the hypothesis that the loss of megaherbivores—particularly in tandem with changes in climate—resulted in regime shifts that spanned North American biomes. What were the long-term legacies of this event? Do modern ecosystems still bear the genetic, functional, or compositional signature of the megaherbivore extinctions? Linking megafaunal herbivory and vegetation at Quaternary timescales is not a trivial task, but an interdisciplinary approach that combines proxy records and modeling grounded by modern studies will help to link pattern and process in the paleorecord. Modern megaherbivores are among some of the most threatened species today; like their Pleistocene counterparts, megafauna face the combined threats of anthropogenic land use and climate change. The ecological consequences of the end-Pleistocene extinctions may thus have relevance not only to understanding the dramatic vegetation changes of the early Holocene, but may help to understand and manage ecosystems in the Anthropocene.

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CHAPTER 2

CLIMATIC AND MEGAHERBIVORY CONTROLS ON LATE-GLACIAL VEGETATION DYNAMICS: A NEW, HIGH-RESOLUTION, MULTI-PROXY RECORD FROM SILVER LAKE, OHIO

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Abstract

Novel plant assemblages are a long-recognized feature of late-glacial North America, but identifying their causes has been hampered by inaccurate radiocarbon chronologies and the multiplicity of ecological and climatic events during the late Pleistocene. Recently we reported that the formation of no-analog vegetation may have been linked to declines in Pleistocene megafaunal communities, based on pollen and spores from the coprophilous fungus *Sporormiella* at sites in Indiana and New York. We present a new, multi-proxy analysis from Silver Lake, OH, which 1) updates the radiocarbon chronology of a classic pollen record with a well-established zone of no-analog vegetation, 2) combines a new sub-centennial pollen record with charcoal, *Sporormiella*, and x-ray fluorescence (XRF) spectroscopy analyses for an integrated record of landscape change before, during, and after the period of no-analog vegetation, and 3) replicates both the absolute and relative temporal patterns of landscape change at Appleman Lake, IN. At Silver Lake, the decline in *Sporormiella* at 13.9 ka BP was immediately followed by the formation of novel plant assemblages, as well as the highest-magnitude charcoal peak in the record. Increased Ca and Sr concentrations during the no-analog interval indicate either increased moisture, increased input of nutrients from deciduous litter, or both. The duration of the no-analog assemblages (13.9–11.8 ka BP) roughly corresponds to the period of peak insolation dissimilarity, but is more temporally constrained than previously reported in subcontinental-scale syntheses (17–11 ka BP). We propose a hierarchy of controls on

late-glacial plant communities, where biotic interactions such as megaherbivory mediate climate-driven vegetation change.

1. Introduction

Pollen assemblages with no modern analog are a long-recognized feature of late-glacial paleoecological records in eastern North America (Wright et al., 1963; Cushing, 1967; Jackson and Williams, 2004). Relative to modern pollen samples, no-analog assemblages include unusual combinations of boreal (e.g. Picea, Larix) and temperate deciduous taxa (e.g., Quercus), low abundances of other taxa common to modern boreal forests (e.g. Pinus, Betula, Alnus), anomalously high abundances of certain deciduous taxa (e.g. Fraxinus, Ostrya-type), and low to moderate abundances of herbaceous taxa such as Artemisia and Ambrosia (suggesting parkland-like conditions) (Winter, 1962; McAndrews, 1966; Ogden, 1966; Davis, 1967, 1969; Wright, 1967). The lack of modern analogs has complicated the interpretation of these assemblages. Early explanations invoked the differential rates of response among taxa (migration lags), but these hypotheses have been discarded (Jackson and Williams, 2004), due to 1) evidence that at a sub-continental scale the formation of no-analog communities preceded the period of fastest climate change (Williams et al., 2001) and 2) the presence of macrofossil evidence for temperate hardwoods in the late-glacial upper Midwest (Jackson and Williams, 2004). Most recent explanations for the formation and maintenance of late-glacial no-analog vegetation invoke various climate factors (Williams et al., 2001; Grimm and Jacobson, 2004; Jackson and Williams, 2004; Gonzales and Grimm, 2009), but new evidence from lake-sediment records from Appleman Lake, IN, and sites in New York links the development of no-analog vegetation to declining megafaunal population abundances and altered fire regimes, indicating that top-down trophic processes also may have shaped novel plant communities (Gill et al., 2009). In this paper, we improve understanding of the late-glacial no-analog communities and their primary drivers by comparing temporal changes in pollen assemblages with other physical and biological changes, including fire regimes, megafaunal population change, chemostratigraphy, and physical characteristics of lake sediments. Our study updates previous work at Silver Lake, OH (Table 1), a site with a classic record of late-glacial vegetation history and formation of no-analog plant associations (Ogden, 1966).

Late-glacial and early Holocene climates were strongly influenced by higher-than-present insolation, lower-than-present CO2 concentrations, and the effects of the nearby Laurentide Ice Sheet (LIS) on regional radiative budgets and surface atmosphere circulation patterns (Ruddiman, 2007). Early climatic hypotheses for late-glacial no-analog vegetation invoked lower-than-present seasonal temperature ranges to allow for the co-existence of temperate and boreal taxa. Bryson and Wendland (1967) proposed that the LIS blocked the southern incursion of Arctic air, and adiabatically warming air off the ice sheets resulted in warmer and drier winters. However, Williams et al. (2001) reported that periods of no-analog community formation corresponded to increased temperature seasonality and dryer-than-present climates during the late-glacial to early-Holocene transition, based on paleoclimatic simulations. The high abundance of pollen from Fraxinus nigra (black ash), which grows in mesic to hydric conditions today (Wright and Rauscher, 1990), indicates that conditions in the Midwest were much wetter than present (Grimm and Jacobson, 2004). Gonzales et al. (2009), using an expanded response surface method, argued for wetter-than-present winters with no change in temperature seasonality. However, the expanded response surface method is based on the assumption that the distribution of pollen abundances along environmental gradients are stable over time, when in fact they may have varied at glacial–interglacial timescales (Veloz et al., in press). Amidst these differing explanations, perhaps the most plausible climatic interpretation for the no-analog communities of the upper Midwest is that insolation regimes and temperatures were more seasonal and moisture availability was regionally higher than at present, either due to enhanced precipitation (Gonzales and Grimm, 2009) or because these landscapes were newly deglaciated and poorly drained (Yansa, 2006).

In addition to novel climates and plant associations, late-glacial and early Holocene landscapes also experienced unprecedented disruptions to their faunal communities. While the causes of the extinction of 34 genera of megafaunal browsers, grazers and their predators have been much-discussed (Koch and Barnosky, 2006), the influence of Pleistocene megaherbivores in shaping late-glacial vegetation dynamics remains poorly understood. A recent paleovegetation record from Appleman Lake, IN, (Gill et al., 2009) suggests that the increased abundances of broadleaved deciduous trees during the interval of peak no-analog vegetation may have resulted from herbivory release following the collapse of megaherbivore populations. The Appleman Lake study combined traditional pollen and charcoal records with the analysis of spores from the dung fungus *Sporormiella*, which was used as a qualitative proxy for the functional extinction of megaherbivores (Davis and Shafer, 2006). The results at Appleman indicated that megaherbivores influenced vegetation composition, ecosystem structure, and ecosystem function, and that their local extinction allowed for the expansion of broad-leaved deciduous trees and the buildup of landscape fuel loads. These findings are consistent with the results of modern megaherbivore studies, such as hardwood suppression by moose (Alces alces) on Isle Royale (McInnes et al., 1992), documented impacts of megaherbivores on sapling recruitment (Hester et al., 2000), and effects of herbivores and fire on tree-grass coexistence in savannas (Sankaran et al., 2005).

The data at Appleman Lake, however compelling, represent a single site that may be complicated by age-model errors and sedimentological variations, including sand and gravel layers in the deeper horizons (Gill, 2008; Gill et al., 2009). Here, a new multi-proxy, well-dated, high-resolution record from Silver Lake presents an opportunity to test the hypotheses raised by Gill et al. (2009). Silver Lake, OH (Ogden, 1966) is located in the heart of the no-analog communities (Shane, 1987; Williams et al., 2001; Grimm and Jacobson, 2004) (Fig. 1), with a previously identified no-analog interval (Table 1); Ogden (1966) concluded that for Zone 2, “no modern equivalent vegetation type has been found.” Our new Silver Lake record improves upon Ogden's chronology, which utilized widely spaced bulk-sediment 14C dates that may have had millennial-level offsets due to carbon sourced from Paleozoic carbonates (Ogden, 1966). We analyzed the Silver Lake sediments for pollen, *Sporormiella*, macroscopic charcoal, loss-on-ignition, and X-ray fluorescence (XRF) spectroscopy analyses to better understand the ecological and climatic history of the landscape around Silver Lake before, during, and after the megafaunal declines and formation of the no-analog plant associations. This record contributes to a new generation of high-resolution, well-dated records from the upper Midwest (e.g. Nelson et al., 2006; Umbanhowar et al., 2006; Gonzales and Grimm, 2009) that can be used to study species responses to abrupt climate change, map spatiotemporal patterns of the rise and decline of the no-analog plant communities, and study the interacting effects of climate change, human arrival (Waters et al., 2011), and megafaunal declines on late-glacial vegetation dynamics (Johnson, 2009).

2. Material and methods

2.1. Site description

Silver Lake (Fig. 1) (Logan County, OH, 40°21’15“ N, 83°48’45”W, 332 m MSL) is a compound kettle located on the Central Lowland Till Plain, and was formed when the Miami Sublobe of the Lake Erie Lobe of the Laurentide Ice Sheet retreated from what is now the Farmersville Moraine (Ogden, 1966; Ekberg et al., 1993). The lake is bordered by YMCA Camp Willson to the east and a raised railroad bed to the north. Silver Lake has an apparently man-made outlet channel on the west side (steep sides, uniform, <1 m deep). Marl benches (∼30 cm above the lake surface) are present on the south and southwest sides, and the lake's beaches are marly with abundant gastropods and clams.

2.2. Core acquisition, initial description & sampling

During July 13–16, 2007, three overlapping sediment cores (A, B and C) were collected within a few meters of each other in the deepest portion of Silver Lake (Fig. 1), using a modified Livingstone piston corer from an anchored floating platform. The sediment–water interface was captured using a Bolivian adapter and polycarbonate tubing (0–100 cm below the sediment–water interface); we then cored with a 7.62 cm diameter Livingstone (100–500 cm depth) and finally with a 5.08 cm diameter Livingstone steel barrel (500–1380 cm depth). Depth from water surface to the sediment–water interface was 10.06 m, based on Secchi disk measurements. Cores A (13.8 m total length) and B (12.8 m) were taken as full overlapping stratigraphies; Core B drives were offset 50 cm from Core A drives. Core C began at 600 cm sediment depth as a third overlap of the early Holocene and late-glacial sediments. Sediment recovery was >95% (1 m) for each drive, except for the basal drives, which ended in coarse-grained and poorly sorted sediments mixed with pieces of wood, interpreted as a meltwater "trash layer" (Wright and Stefanova, 2004). Core segments were measured and described in the field, then wrapped with plastic wrap and aluminum foil and encased in split PVC tubes.

Cores were split longitudinally into two halves at the National Lacustrine Core Facility at the University of Minnesota, where they were subsequently imaged with high-resolution photography and scanned for magnetic susceptibility. One half of each core was archived at the Lacustrine Core Repository, and the other half was brought to the University of Wisconsin for further analyses. Both halves were kept in cold storage (>0 °C). Markers were placed in the archive half every 10 cm to monitor changes in core length during storage. The working half of each core was sliced into 1 cm-thick “cookies,” which were individually packaged in Whirl-pak bags for sub-sampling. All analyses were conducted on Core C, which was the richest in terrestrial plant macrofossils of the three cores and hence the most suitable for radiocarbon dating.

2.3. Chronology

We submitted 13 wood and other terrestrial plant macrofossil samples to the Woods Hole Oceanographic Institution's NOSAMS facility for AMS radiocarbon dating (Table 2). Dates were calibrated using IntCal09 (Reimer et al., 2009) and the Bacon software for Bayesian age modeling in R (Blaauw and Christen, 2011) (Fig. 2). Bacon repeatedly samples from the full probability density function of each calibrated age to fit many possible splines to the age controls, and discards fitted splines that result in age reversals. A posterior probability density function for each depth in the sediment core is generated from the population of the retained splines. Bacon requires a prior estimate of the mean sedimentation rate throughout the core. We estimated a mean sedimentation rate of 30 years/cm based on previously collected late-glacial/early Holocene records from the region (e.g. Appleman Lake, Crystal Lake; Gill et al., 2009; Gonzales and Grimm, 2009). Another parameter in Bacon is the section length of the piecewise-calculated spline, which we set to 30 cm. Section length is not a prior parameter per se, but rather affects computational speed (more segments allow more flexibility of the model to adapt to within-core changes in sedimentation rate, but increases calculation time). All dates were used in the model, including an obvious outlier at 741.5 cm (OS-7984; Fig. 2, Table 2). Because Bacon assumes stratigraphic ordering of dates and a linear sedimentation process, it rejects age models that violate these assumptions, so the presence of an outlier date affects model uncertainty but not the maximum likelihood estimates for the age model (Blaauw and Christen, 2011). Bacon returns a maximum probability age estimate at 1 cm intervals; ages were linearly interpolated between 1 cm intervals to proxy sample depths using the Approx function in R. All ages are reported in thousands of calendar years (ka) before radiocarbon present (1950 AD).

2.4. Pollen & charcoal analyses

Subsamples (1 cm3, or 2 cm3 when pollen concentrations were low) were taken for pollen analysis at 4, 8, or 16 cm intervals using a volumetric sampler. Samples were processed for pollen using a modification of the protocols reported by Faegri and Iverson (1989), including treatments with hot 10% HCl and 10% KOH, hot 55% HF (successive hot HF treatments were used if necessary to remove all silicates), sieving (250 µm), and acetolysis for two minutes. Three tablets containing exotic Lycopodium tablets (batch #483216; 18,583 ± 764 spores/tablet) were added to each sample before processing to calculate pollen concentrations (Stockmarr, 1971); see online Supplemental material for accumulation rates (Fig. S1). Pollen samples were mounted on microscope slides using 1995 cs silicone oil. At least 300 arboreal pollen grains were counted per sample using a Zeiss Axio Imager. Pollen abundances are represented as percent of the upland pollen sum; *Sporormiella* is ratioed against the upland pollen sum, but is not included in that sum. To be consistent with previous studies (Davis, 1987; Robinson et al., 2005; Gill et al., 2009) we report the relative abundances of *Sporormiella* in percentage terms, although strictly speaking we are reporting a pollen ratio, not a percentage.

Subsamples (1 cm3) were taken for macroscopic charcoal analysis at consecutive 1 cm intervals using a volumetric sampler. Charcoal samples were processed with a modified version of the protocols described by Whitlock and Larson (2001). First, samples were treated with 6% H2O2 at 50 °C for 24 h. Ethanol was added to clay-rich samples to prevent clay and charcoal particles from sorbing up the sides of the flasks and adhering during heating. Samples were screened through nested 125 µm and 250 µm sieves; the >250 µm portion of each sample was counted wet on the sieve and then discarded, and the 125-to-250 µm portion was rinsed with 6% H2O2 into plastic Petri dishes and placed in the drying oven at 50 °C until all liquid was evaporated and charcoal particles adhered to the dish surface. Petri dishes were placed on a gridded platform for counting. Each charcoal fragment was identified as one of nine possible morphotypes based on reference burns (Jensen et al., 2007): dark (likely source: woody plant matter), graminoid cellular (source: grass), branched (source: deciduous leaf veins), bordered pits (source: conifer wood), fibrous, spongy, lattice, porous, or “other.” The most diagnostic morphotypes are reported here: dark (woody), graminoid cellular (grass), and bordered pit (conifer wood) (see Supplemental material for other morphotypes, Fig. S2). Charcoal data were counted as pieces, rather than total charcoal area, based on prior studies linking fires with high concentrations of particles, and showing a high correlation between total charcoal area and number of pieces per sample (Whitlock and Millspaugh, 1996; Higuera et al., 2005; Peters and Higuera, 2007).

2.5. LOI & elemental analyses

Subsamples (1 cm3) were taken for loss-on-ignition analysis at 10 cm intervals with a volumetric sampler; samples were weighed in crucibles. Crucible lids prevented cross-sample contamination, and two replicates of reference standards (two sets of two crucibles containing ashless filter paper and dry calcium carbonate) were included in the front and back of the ovens during all sample runs to ensure complete combustion throughout the oven. Samples were heated in the muffle furnace at 100 °C for 24 h, 550 °C for 4 h, and 1000 °C for 2 h (Heiri et al., 2001), and weighed after each treatment to calculate the percent weight lost during each burn.

The unsampled archive halves of Core C were shipped to the x-ray fluorescence spectroscopy (XRF) facility at Woods Hole Oceanographic Institution, where they were scanned for high-resolution elemental intensity using an ITRAX model XRF Corescanner. XRF scanning was conducted at 1 mm resolution with 10 s exposure time using a Mo X-ray source set to 45 kV and 30 mA. Scanning XRF is a non-invasive, whole-core analysis that measures elemental intensity as counts per second (cps) (Croudace et al., 2006). We smoothed the XRF data by calculating a running mean for a moving 1 cm window. To calibrate the smoothed XRF intensity data into estimates of elemental concentration, samples (1 g dry-weight) were taken at 10 cm intervals in Core C, dried and ground, and sent to the ALS Chemex Reno Minerals Lab for inductively coupled plasma atomic emission spectroscopy (ICP-AES) analysis, which provided elemental concentrations (either ppm or % w/w). The ICP-AES concentration data and the XRF smoothed intensity measurements from the same depths were used to calibrate linear regression models that then were applied to estimate elemental concentrations for the entire smoothed XRF time series. The lists of elements measured by XRF and ICP-AES analyses are not identical, so some values are expressed as cm-resolution ppm based on the XRF and ICP-AES regression (V/Cr, Sr, Ca), others as uncalibrated XRF cps (Al/Zr, Rb/Sr), and some (Mg/Ca) were available as low (10cm) resolution ICP-AES concentrations (ppm or %) only. For several lithogenic elements, including Fe and Ti, ICP-AES and XRF values had low correlations, so these elements were not analyzed further (see Supplemental data, Fig. S3).

We report here a subset of the elemental data, using elements and elemental ratios that have been previously established to reflect paleoenvironmental conditions. Zr/Al ratios are used as a proxy for aeolian sedimentary input, because Zr is concentrated in more mobile sandy-silt fractions while Al2O3 reflects the concentration of terrestrially-derived feldspars (Huag et al., 2003; Roy et al., 2006, 2009). Similarly, Rb tends to be associated with feldspars and other K-rich minerals, while Sr is enriched in carbonates, so Rb/Sr ratios are used as a proxy for weathering intensity in the catchment basin (Jin et al., 2005; Roy et al., 2009). The ratio of V to 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 (Rosenthal et al., 1995; Harris et al., 2004; Das et al., 2009). Mg is associated with the clastic fraction of sediments, and Ca is associated with carbonates, so Mg/Ca ratios indicate the relative abundance of clastics to carbonate-evaporites and are thus interpreted as a proxy for moisture (Roy et al., 2009).

Several biophilic elements are used as proxies for the amount and type of plant litter inputs into the lake. Biotic uptake and mobilization of Ca from soils tends to be higher beneath deciduous trees than conifers (Dijkstra and Smits, 2002); while peaks in calcium are generally associated with endogenic carbonate minerals in lacustrine sediments, such peaks have also been interpreted as originating from deciduous-mobilized Ca (Calanchi et al., 1996; Willis et al., 1997). Here, we interpret endogenically precipitated Ca as the stronger signal, but there may be evidence for the litter-derived Ca as well. Sr is mobilized from soils by vegetation and concentrated in litter (leaves, twigs, and roots), so as soil acidity increases (e.g., due to an increase in needle-leaved litter), Sr is preferentially taken up over Ca (Bowen and Dymond, 1955). Peaks in Ca and Sr are thus interpreted in both climatic and vegetation terms.

2.6. Numerical analyses

Minimum vegetation dissimilarity from present was calculated with the analog (Williams and Shuman, 2008) program in Matlab (MathWorks, 2010) using the squared-chord distance (SCD) metric (Overpeck et al., 1985; Gavin et al., 2003). For this analysis, the relative abundances of 41 taxa in each fossil pollen sample from Silver Lake were compared to 4837 modern pollen assemblages from the North American Modern Pollen Database v. 1.7 (Whitmore et al., 2005). Samples with minimum SCD scores >0.3 were determined to have no modern analog (Williams and Shuman, 2008). Vegetation zones were identified using incremental sum-of-squares analysis as calculated by the CONISS program in Tilia v. 1.4.10 (Grimm, 1987), using all non-aquatic pollen types with percentages at or above 1% at any point in the record. *Sporormiella* was not included in the dissimilarity or CONISS analyses.

We used Bayesian change point analysis (BCP) to determine the last significant decline in the *Sporormiella* time series (Barry and Hartigan, 1993), using the bcp function in R (Erdman and Emerson, 2007). We used BCP as a test of the widely used 2% threshold reported for *Sporormiella* time series (Davis, 1987, 2006; Burney et al., 2003; Robinson et al., 2005; Gill et al., 2009). Whether and how the declines of *Sporormiella* spore abundances reflect the functional or final extinctions of megafaunal species remains a larger question, which we return to in the discussion.

Charcoal data were separated into background and peak components using CharAnalysis v. 1.1 for Matlab (Higuera et al., 2009, 2010). First, charcoal data were converted to charcoal accumulation rates (CHAR) by multiplying concentrations (particles per cubic centimeter) by the estimated sedimentation rate for each sample. CHAR values were then interpolated to 15-year time steps to account for uneven sampling intervals caused by variations in sedimentation rates and differential time-averaging of samples. The CHAR time series was then decomposed to isolate charcoal peaks (interpreted as fire events within the Silver Lake watershed) from the background influx of charcoal (Clark et al., 1996). Background CHAR was estimated using a LOWESS smoother with a 700-year moving window. Peaks above background are interpreted as signatures of one or more adjacent fire events. CharAnalysis identified peaks using a locally fitted Gaussian mixture model, then screened individual peaks to test whether each flagged peak differed significantly from the smallest non-peak sample in the preceding five samples (or 75 years) using a modified two-sample Poisson test (see Higuera et al., 2009 Appendix A) based on the pre-smoothed charcoal concentrations (particles/cm3).

3. Results

3.1. Paleovegetation

In basal Pollen Zone A (18.7–13.9 ka BP), Picea pollen dominates (>70%), although deciduous taxa (including Acer, Alnus, Salix, Betula, and Populus) were present at low (<3%) pollen abundances (Fig. 3). Abies, Pinus (predominantly Pinus sub. Strobus), and Larix pollen were also present at low abundances. Larix pollen is poorly dispersed and therefore typically under-represented in pollen records (Jackson, 1990), and thus its presence at values up to 5% of the upland sum likely indicates that Larix was a substantial component of the late-glacial vegetation local to Silver Lake. Trace values of Ulmus, Carya, Fraxinus, and Ostrya-type pollen may indicate small local populations near their northern range limits, or long-distance pollen dispersal. Grimm and Jacobson (2004) suggested that some pollen in samples corresponding with the Bølling-Allerød period may be long-distance derived because pollen concentrations in Eastern North American samples during the late Allerød are low, which indicates low pollen productivity of local vegetation. Under such circumstances, long-distance pollen may be disproportionately represented. Upland herbaceous pollen was composed primarily of Asteraceae, Artemisia, Cyperaceae, and Poaceae; non-arboreal pollen (NAP) values are ~10% throughout the zone, indicating spruce-larch parkland vegetation. SCD values remained just below <0.3, with closest modern analogs drawn from boreal forests and woodlands in western Newfoundland (Fig. 3).

A sharp decline in Picea pollen abundances from >60% to 20% marks the transition to Zone B (13.9–12.7 ka BP); this decline coincides with an increase in abundance of several deciduous taxa, particularly F. nigra-type (~16%) and Ostrya-type (~18%) pollen, as well as Quercus, Corylus, Acer, and Ulmus. Non-pollen palynomorphs (Filinia longiseta-type eggs, Pediastrum colonies, and Botryococcus; see Supplemental material, Fig. S4) are also most abundant during this interval. A sharp increase in SCD scores to >0.3, resulting from the co-occurrence of moderate abundances of Picea pollen with deciduous hardwood pollen types (particularly F. nigra-type and Ostrya-type), indicates the development of no-analog plant associations. Abundances of herbaceous pollen taxa (especially Ambrosia, Artemisia, Asteraceae, and Cyperaceae) remained steady during this interval, but herb diversity increased, including the addition of Brassicaceae, Ericaceae, Plantago, and increased abundances of Rumex, Ranunculaceae, and Rubiaceae; Poaceae values remain ∼10%. Aquatic types are rare throughout the record in general, with the exception of Typha, which was most abundant during Zone B. Pollen Zone B is interpreted to represent a no-analog mixed parkland or forest; i.e., with a composition unlike any modern vegetation (Williams et al., 2001).

Zone C (12.7–10.9 ka BP) is marked by a second peak in Picea from 12.4 to 10.9 ka BP, coincident with a rise in Abies and reduced abundances of Fraxinus and Ostrya-type pollen. We have chosen to subdivide Zone C into two sections, C1 (12.7 ka BP–11.8 ka BP) and C2 (11.8 ka BP–10.9 ka BP), to highlight ecologically important variation within this zone that was not captured by the cluster analysis, particularly the peak in Pinus (predominantly subgenus Pinus) pollen from 11.8 to 10.9 ka BP. The division between Zones C1 and C2 at 11.8 ka BP is also marked by a decline in NAP and a decline in Abies. A large peak in Equisetum co-occurs with the peak in Abies, immediately following the decline in other non-pollen palynomorphs. Elsewhere, Equisetum has been interpreted to indicate the increased extent of marginal lake vegetation due to changing lake levels (Digerfeldt et al., 1997). Tsuga and Tilia pollen also first appear during the Pinus interval and Ulmus abundances increase. SCD values decline throughout Zone C but remain >0.3 (and thus represent no-analog assemblages). The transition from Zone C1 to C2 is interpreted to indicate a closing forest, primarily consisting of conifers, in which the dominant species shifted from Picea spp. to Pinus banksiana or Pinus resinosa. Picea species likely included both Pinus glauca and Pinus mariana, as per the macrofossil evidence at the Christensen (Whitehead et al., 1982) and Kolcharik (Jackson et al., 1986) sites.

Zone D includes the youngest samples analyzed in this record (10.9–8.2 ka BP), and is marked by rising abundances of Quercus and Carya pollen and low to trace abundances of conifer pollen. An increase in herbaceous pollen, particularly Ambrosia, Poaceae, Rumex, Amaranthaceae, and Ranunculaceae, along with a decrease in Ulmus pollen, indicates the beginnings of the formation of a Quercus savanna in response to warming and drying of the North American mid-continent during the early Holocene.

3.2. Sporormiella & other coprophilous fungi

Sporormiella percentages were highest during Zone A, varying from 2 to 6% of the upland pollen sum. The transition to Zone B was marked by a decline in *Sporormiella* to <2% of the upland pollen sum, and percentages remained low (<2%) throughout the rest of the record. This decline is reproduced in the time series of *Sporormiella* accumulation rates (grains/cm2/yr; see Supplemental material Fig. S1) so the decline is not a percentage artifact. BCP analysis (Fig. 4) identified possible change points in the *Sporormiella* time series at 14.0 ka BP and 13.9 ka BP, which corresponds to when *Sporormiella* at Silver Lake drops below 2% of the upland pollen sum. The change-point identified by the BCP analysis is therefore consistent with prior usage of the 2% threshold for *Sporormiella* (Davis, 1987; Davis and Shafer, 2006). Other possible change points were identified at 17.9 ka BP (0.7 probability) and 16.7 ka BP (0.5 probability), which are within a period of fluctuating *Sporormiella* abundances (>2%). These earlier change points may indicate variation in *Sporormiella* abundances attributable to changes in basin morphology or lake level (Raper and Bush, 2009), or may indicate real variability in megafaunal populations, grazing intensity, or biomass. Other coprophilous types identified (Fig 3; "Other dung fungi") including Coprinus-type and Aureobasidium-type were less abundant.

3.3. Charcoal analysis

From 18.3 to 15.5 ka BP, charcoal accumulation rates (CHAR) were low (<2 particles/cm3), suggesting low-intensity fires and/or low landscape fuel loads (Fig. 5A). Between 15.5 and 11.9 ka BP, the charcoal record at Silver Lake alternates between periods of high and low background CHAR, with a roughly millennial-scale quasi-periodicity. An increasing trend in background charcoal is superimposed on this series of peaks; each successive peak in CHAR increases in magnitude, and the spacing between peaks increases through time. Background CHAR is strongly influenced by the amount of biomass burned (Marlon et al., 2008, 2009), so these variations in background CHAR reflect both changes in fire frequency and variations in available fuels.

The temporal variations in reconstructed peak frequency (number of peaks per 1000 years, Fig. 5B) differed from background charcoal. Peak frequency was higher (>10 peaks per thousand years) during the late-glacial portion of the record (∼17 ka BP), declining to <3 peaks per thousand years during Zone C1, and finally increasing to 5–6 peaks per thousand years during Zone D, the early Holocene portion of the record. The combined trends in reconstructed background charcoal and peak frequency could represent a transition from more frequent, lower-intensity fires to less frequent, higher-intensity fires. There are few charcoal reconstructions from late-glacial no-analog sites, and most studies of charcoal processes and data have been conducted on mid-to-late Holocene samples with organic-rich sediments. Interpretations of fossil charcoal samples from late-glacial, mineral-rich sediments associated with structurally and compositionally novel plant associations may be limited by a lack of analogs in modern landscapes. However, shifts in CHAR and peak frequencies at Silver Lake are not associated with any changes in sediment lithology (e.g., LOI and magnetic susceptibility) and are consistent with climatic and vegetation shifts. Note that reconstructions of fire frequency are sensitive to the parameterization of the peak-finding algorithm (Higuera et al., 2010), and so must be interpreted with caution.

Dark (woody material) charcoal particles were the most abundant morphotype throughout the record (Fig. 5D). Graminoid cellular (grass) particles were present in trace amounts from 18.3 ka BP to 11.9 ka BP, and became more abundant after 11.9 ka BP. Graminoid cellular charcoal was typically present at higher abundances in each initial peak in the high-background intervals, but was present at much lower abundances by the end of each peak interval. This may indicate trends towards forest closure within each period of high background charcoal accumulation, or may represent the time-transgressive breakdown and in-wash of larger wood fragments. Bordered pit (conifer wood) particles composed the majority of the first large peak at 15.5 ka BP, and a significant portion of the second large peak at 13.4 ka BP. The increase in bordered pit CHAR at 11.9 ka BP coincides with the period of increased Pinus abundances (Fig. 5D). However, the majority of the charcoal during this interval is dark (Fig. 5).

3.4. Loss-on-ignition, sedimentary and & geochemical results

The organic fraction of the sediments was low during Zone A (<10%) (Fig. 6), likely indicating both low within-lake productivity and increased mineral inputs due to dusty atmospheric conditions during the late Pleistocene (Dean, 1974; Bengtsson and Enell, 1986). Magnetic susceptibility is highest in the basal sediments as well, which may be due to the influx of unsorted terrestrial sediments following the collapse of the ice block that formed the kettle. This interpretation is supported by the presence of a presumed trash layer (Wright and Stefanova, 2004), including abundant wood fragments (1140–1180 cm) with overlapping radiometric ages. A peak in the carbonate fraction and Ca concentrations at ∼18.5 ka BP may indicate erosion of sediments from carbonate-rich tills in the Farmersville moraine deposits. A second peak in the carbonate fraction is accompanied by an abrupt peak in Ca and Sr between 13.5 ka BP and 13.9 ka BP and coincides closely with pollen Zone B. This is interpreted to indicate an increase in mobilized Ca and lake pH due to the increase of deciduous hardwood taxa (Dijkstra and Smits, 2002). The relative fraction of organic carbon increases from 13.5 ka BP through the early Holocene (∼ 10 ka BP), during the transition between Zones C1 and C2 coincident with the rise of Pinus pollen, The organic carbon fraction declines again at 9 ka BP, as carbonates increase >20%.

Al/Zr ratios, which have been used as a proxy for eolian-derived sedimentary inputs (Huag et al., 2003; Roy et al., 2006, 2009), are low but variable during the Pleistocene, decreasing slightly in variability after 14.8 ka, coincident with the onset of Bølling-Allerød warming in Greenland. A period of high (>10,000 cps) peaks during pollen Zone C (from 12.5 to 10.5 ka BP) indicates increased eolian activity. This inference of increased eolian activity between 12.5 ka BP and 10.5 ka BP is consistent with recent evidence of dune mobilization in northwest Ohio (Campbell et al., 2011) during this interval, which Campbell et al. suggest is caused by colder and dryer conditions during the Younger Dryas. Peaks in the V/Cr ratio also correspond with this interval, suggesting that the lake was more oxygenated during this time, perhaps due to enhanced water column mixing resulting from cooler and/or windier conditions (Brown et al., 2000). Pollen Zone C is characterized by peaks in Picea and Pinus pollen, as well as an interval of relatively high background CHAR; fire and/or drier conditions may have contributed to dune mobilization.

Rb/Sr ratios are variable but high during the late-glacial portion of the record, reaching peak values around 17 ka BP and 14.5 ka BP, and generally declining into the Holocene. High Rb/Sr ratios are associated with weak weathering energy (i.e. cold, dry) (Jin et al., 2005; Roy et al., 2009), and so this record suggests increased weathering intensity associated with rising temperatures. The most striking feature of the Rb/Sr record is the interval of sustained low values from 13.9 ka to 13.1 ka BP, coeval with Zone B in the pollen record. During this interval, Ca and Sr values are also high, and

Mg/Ca ratios are low, suggesting humid conditions and/or an input of litter-derived Ca and Sr. Most of the peaks in Sr (16.6 ka BP, 15.5 ka BP, 13.9 ka BP, 11.8 ka BP, 9.5 ka BP, and 8.7 ka BP) are associated with charcoal peaks, which indicates post-fire inputs of from litter layers.

4. Discussion

4.1. Silver Lake & Ohio vegetation and climate history

Our study updates Ogden's (1966) classic fossil pollen record with a sub-centennial vegetation reconstruction, a new AMS radiocarbon chronology that should be minimally affected by hard water contamination, a well-preserved late-glacial sedimentary sequence, and several new paleoecological and paleolimnological proxies, including macroscopic charcoal, elemental concentrations from XRF and ICP-AES, and *Sporormiella*. We sampled a thicker sediment sequence than Ogden's original core (13.8 m recovered in our core versus 8.9 m collected by Ogden) but both his cores and ours reached basal till and a trash layer. In other words, while both records apparently capture the same sequence, our new cores have a higher sediment accumulation rate and thus higher potential temporal resolution. For example, the pollen-assemblage composition is similar between Zone A of this paper and Ogden's Zone 1, but Zone A here comprises 320 cm of sediments versus <200 cm in Ogden's original record. Our basal radiocarbon dates place the initiation of Silver Lake at 18.3 ka BP, several millennia older than Ogden's extrapolated estimate of 11 ka BP–14 ka BP, which was based on a radiocarbon date in Pollen Zone B, well above the top of the till sediments. This older estimate is consistent with a recent survey of basal radiocarbon dates from Ohio lakes and bogs, which suggests deglaciation of central Ohio by 18 ka BP (Glover et al., 2011; see also Shane, 1987).

Overall, our record confirms the previously established late-glacial vegetation history for Ohio (Shane, 1987; Shane and Anderson, 1993), but with an adjusted chronology. Pollen data from Zone A indicate a Picea-dominated woodland that lacked the Betula and Alnus components of modern boreal forests. This interpretation differs from Shane's (1987) classification of the Ohio Till Plain sites as “open tundra,” and the key question is whether the high abundances of Picea pollen indicate locally dense stands of Picea trees or long-distance transport of Picea pollen from forests elsewhere. The closest modern analogs for these fossil samples indicated by the dissimilarity analysis are in boreal forests of Ontario and Newfoundland, which supports our interpretation that the local vegetation around Silver Lake was a boreal woodland or parkland. The low rates of background charcoal accumulation at Silver Lake during this time period indicate a low fuel load and also support a more parkland or open-canopy forest structure.

Our updated chronology places the no-analog interval (Zones B and C) from 13.9 ka BP to 10.9 ka BP, approximately 500 years earlier than reported by Shane (1987; Shane and Anderson, 1993) and more than two millennia older than Ogden (1966), apparently ending with the formation of a Quercus forest or savanna with the onset of the Holocene. Earlier maps of vegetation dissimilarity by Williams et al. (2001; Williams and Jackson, 2007) from the North American Pollen Database indicate that no-analog communities persisted from 17 ka BP to 11 ka BP in this region, but the pollen records from Silver, Appleman, and Crystal Lakes (Fig. 7) suggest that the peak period of no-analog conditions was much more temporally constrained in the upper Midwest, beginning between 14.5 ka BP and 14.0 ka BP and ending between 12.3 ka BP and 11 ka BP (Gill et al., 2009; Gonzales and Grimm, 2009).

At Silver Lake, the no-analog interval was not compositionally homogeneous, but extended across pollen Zones B and C, indicated by SCD scores >0.3 from (13.9 ka BP to 10.7 ka BP). Assemblages from Zone B 13.9 ka BP to 10.7 ka BP had the highest SCD scores (>0.4), and were dominated by Fraxinus and Ostrya-type pollen, with a lower abundance of Picea and an absence of Pinus pollen. Zone C (13.1–10.7 ka BP), showed a second, though smaller, peak in Picea, as well peaks in as Abies and Pinus. Deciduous taxa, including Fraxinus and Ostrya, were still present in Zones C1 and C2, though at lower percentages than Zone B. These variations can be explained as responses to warmer conditions coincident with the Bølling-Allerød in Greenland, followed by cooler climates during the Younger Dryas. If so, this suggests that the phenomenon of the no-analog communities may be linked in part to millennial-scale climate oscillations. However, the rise in hardwood taxa and the formation of the no-analog communities at Silver Lake is dated to 13.9 ka BP, well after the start of the Bølling-Allerød event at

Greenland at 14.64 ka BP +/− 187 yrs (Rasmussen et al., 2006). The pollen and loss-on-ignition records at Crystal Lake, IL, the best-dated late-glacial lake record in the upper Midwest, also lag the Bølling-Allerød initiation in Greenland by 300–400 years (Gonzales and Grimm, 2009), as do the pollen and oxygen isotope records at White Lake, NJ (Yu, 2007). Thus, there is increasing evidence for an inter-regional asynchrony on the order of several centuries between the upper Midwest and the North Atlantic. This is perhaps unsurprising, as the upper Midwest is atmospherically upstream from Greenland, and thus may be more sensitive to local variations in the southern margin of the Laurentide Ice Sheet, which may itself have lagged changes in the North Atlantic by several centuries (Gonzales and Grimm, 2009).

Grimm and Jacobson (2004) suggested that the lack of post-fire successional taxa such as Betula papyrifera and P. banksiana indicated a lack of fire during the late-glacial no-analog communities. However, an increase in background CHAR and the highest-magnitude peak in the record (CHAR >14) coincide with the increase in SCD values and the *Sporormiella* decline at 13.9 ka BP. Thus, the charcoal data at both Silver and Appleman Lakes strongly link an enhanced fire regime to the development of the no-analog communities. The low abundances of Betula and Pinus in the no-analog communities remain unexplained. During the peak no-analog interval, Betula is located primarily along the coast in the Northeast, before briefly moving into Ohio around 12 ka BP (Williams et al., 2001). The synoptic scale of Betula distributions indicates that climate, rather than fire activity, is a likely factor in explaining the lack of Betula in the upper Great Lakes region at this time. Background CHAR increased at 12 ka BP, coinciding with the peak in Pinus. The fire regime at Silver Lake thus appears to be related both to an increase in fuel loads (due either to climate change, herbivory release, or both) and to community composition during the establishment of Pinus forests from 12 ka BP to 10.9 ka BP.

Several explanations are possible for the abrupt rises in Ca and Sr at 13.9 ka BP, coincident with the beginning of pollen Zone B. First, this increase may be due to increased groundwater flow transporting bicarbonate and carbonate ions into the lake basin (Gonzales and Grimm, 2009). Increased lake productivity and authigenic production of inorganic carbonates, perhaps caused by warming temperatures during Zone B, may also have contributed to this signal. Alternately, the increase in broadleaved deciduous taxa may have facilitated the mobilization of calcium in soils (Pennington, 1984; Willis et al., 1997); deciduous forests produce calcium-rich litter that increases the pH of soils, as opposed to the more acidic litter produced by conifers (Russell, 1961; Wild, 1993). This explanation is supported by the observation that Ca and Sr concentrations are higher from 13.9 ka BP to 13.2 ka BP, then drop when Pinus pollen abundances rise, but does not explain why Ca and Sr concentrations remain low when Quercus abundances rise during the early Holocene.

The second half of pollen Zone B (13.5 ka BP–12.0 ka BP) is also characterized by low fire frequencies and background CHAR (Fig. 5B), corresponding to a sustained period of slightly lower abundances of arboreal pollen (Fig. 5C) relative to Zones A, C and D. Increased aeolian activity and vegetation response to cooler, drier conditions during the Younger Dryas have been observed at several sites in northwest Ohio (Campbell et al., 2011); increased aridity and landscape openness at Silver Lake may have reduced fire activity through a decrease in available fuel loads. Background charcoal increased (>3 CHAR) during the interval of maximum Pinus pollen abundances (12.1 ka BP–10.9 ka BP). P. banksiana is particularly common in modern boreal forests that experience regular stand-replacing fires (Fowells, 1965; Gauthier et al., 1996). Peaks in Alnus (12.3 ka BP–11.5 ka BP) and Betula pollen (11.4 ka BP) coincided with increased Pinus and fire activity; while these taxa are also indicators of colder conditions, it is more likely that they represent post-fire establishment during the increased fire activity during Zone C. Zone C thus appears to represent a return to boreal parkland conditions, but with Pinus now a major element (unlike Zone A). However, dissimilarity values remain high during this period because the high abundances of Picea and Pinus coincide with the continued moderate to low abundances of broad-leaf deciduous taxa (including Ulmus, Acer, Corylus, Fraxinus, and Ostrya).

4.2. Evidence for megafaunal influences on late-glacial vegetation dynamics

Gill et al. (2009) hypothesized a causal linkage between megafaunal extinctions, changes in fire regimes, and the establishment of novel plant communities; this study further tests that hypothesis. The absolute timing and relative position of the *Sporormiella* decline replicates previous findings at Appleman Lake (Fig. 7) (Gill et al., 2009), strengthening the inferred linkage between megafaunal population declines and the formation of no-analog vegetation. The Silver Lake sequence yielded a more robust age-model than was possible for Appleman, and confirms both the relative sequence of events as well as the absolute timing of the changes (i.e. 13.9 ka BP +/− 400 years). Furthermore, the Silver Lake record demonstrates that the *Sporormiella* decline occurred in the absence of lithological change, and hence cannot be ascribed as an artifact of depositional environment.

At both Silver and Appleman Lakes, *Sporormiella* abundances were highest in late-glacial sediments, though relative abundances were variable, before declining to below 2% of the upland pollen sum at 13.9 ka BP. We interpret the <2% decline in *Sporormiella* as the local functional extinction of megaherbivores, rather than the final extinction (Gill et al., 2009), as it predates the youngest-dated fossils for the region (Faith and Surovell, 2009; Saunders et al., 2010; Woodman and Athfield, 2009). The *Sporormiella* declines continued until 13.3 ka BP, but the relationship between *Sporormiella* abundances and megafaunal activity is insufficiently understood to interpret this as a progressive decline in megafaunal abundance or activity. At Silver Lake (as at Appleman Lake), the *Sporormiella* decline was immediately followed by an increase in minimum SCD values to >0.3, indicating no-analog vegetation developed immediately following the local megafaunal declines (Fig. 7). At Silver Lake, the *Sporormiella* decline at 13.9 ka BP (Fig. 4) precedes the appearance of no-analog pollen assemblages by two samples (4 cm) in the core, which is <20 years.

One difference between Appleman and Silver Lakes is that fire activity began slightly earlier at Silver with the first large peak at 15.5 ka BP, prior to the *Sporormiella* decline. However, as at Appleman, the *Sporormiella* decline was immediately followed by an increase in background CHAR, and the highest-magnitude peak of the record. A single peak in charcoal with a magnitude several times higher than preceding peaks has been suggested as a potential indicator of human arrival on islands (Burney et al., 1994; Burney and Burney, 2003), but it is not yet known whether and to what extent North American Paleoindian activity is reflected in late-glacial charcoal records (but see Marlon et al., 2009).

At both Appleman and Silver Lakes (Fig. 7), the absolute timing and relative sequence of landscape change (*Sporormiella* decline → increased vegetation dissimilarity and enhanced fire activity) is consistent with the hypothesis that Pleistocene megaherbivores played a role in mediating the effects of climate on vegetation. The sharp increase in deciduous pollen types and arboreal pollen percentages suggest that the loss of megafaunal browsers and grazers resulted in a release of palatable hardwoods. Additionally, the decline in megaherbivores may have contributed to an increase in fire activity due to the buildup of fuel loads. The increase in both Ca and Sr immediately following the *Sporormiella* decline may represent a pulse in these elements into the lake following their accumulation in plant litter, suggesting that the decline in megaherbivores may have had cascading effects on nutrient cycles and soil pH. Recently, Faith (2011) suggested that changes in nutrient cycling reduced forage quality, contributing to the late-Quaternary megafaunal extinctions. Our results indicate that the loss of megaherbivores may have instead have resulted in cascading effects on nutrient availability in terrestrial and freshwater ecosystems.

4.3. A hierarchy of controls on late-Quaternary vegetation dynamics and megafaunal extinctions

We propose a hierarchy of controls on vegetation dynamics at Quaternary timescales (Fig. 8). In this model, a plant's fundamental niche is determined by climate and the other abiotic factors that control its geographic range, but its relative abundance on a given landscape is then influenced by megaherbivory and other biotic interactions. Owen-Smith (1987) hypothesized that some species of Pleistocene megaherbivores, particularly mammoths and mastodons, may have acted as ecological keystones, and that the extinction of these taxa would have resulted in widespread ecological change. In modern systems, megaherbivores have been shown to alleviate plant competitive exclusion (Dyer et al., 1993; Edenius et al., 1993), maintain vegetation openness (Weigl and Knowles, 1995; Olofsson et al., 2004), alter nutrient cycle dynamics (Hobbes et al., 1991; Kielland and Bryant, 1998; Ritchie et al., 1998), facilitate seed dispersal (Howe and Smallwood, 1982), reduce single-species dominance through generalist grazing (Parker et al., 2006), and alter community composition through selective browsing (Anderson and Katz, 1993). Additionally, megaherbivores influence fire regimes via the removal of flammable biomass, and mediate tree-grass coexistence in savanna systems (Fuhlendorf and Smeins, 1997; Sankaran et al., 2005; Waldram et al., 2007; Holdo et al., 2009).

We therefore suggest that understanding the cause and patterns of the megafaunal extinctions is essential to understanding late-Quaternary vegetation change. Viable hypotheses for the extinctions are typically classified as either climatic or anthropogenic (Koch and Barnosky, 2006). At Appleman and Silver Lakes, the timing of the *Sporormiella* decline predates vegetation change, and vegetation primary productivity would be expected to improve as climates warmed (Allen et al., 2010), so the pollen data are difficult to reconcile with a diet-driven cause of the megafaunal extinctions. Alternately, humans, (perhaps arriving as early as 15.5 ka BP (Waters et al., 2011) may have driven down megafaunal populations and/or altered fire regimes, leading to vegetation change. *Sporormiella* records in North America cannot yet rule in or rule out anthropogenic mechanisms for the megafaunal extinctions. Further work is needed at additional sites to determine the spatial extent of sites recording the *Sporormiella* decline, and to test whether the *Sporormiella* decline is synchronous more broadly or shows a time-transgressive pattern. Recently, Lorenzen et al. (2011), using a combination of ancient DNA and species distribution models, concluded that for many megafaunal taxa, both human and climatic factors are necessary to explain the extinctions; we suggest that further multi-proxy studies integrating models, fossils, and ancient DNA with *Sporormiella* will help to further refine our understanding of the late-Quaternary extinctions.

A second critical need is a better understanding of the *Sporormiella* proxy itself. A growing number of studies are incorporating *Sporormiella* as a proxy for megaherbivore presence in lake sediment analyses for a range of regions and intervals, including late-glacial North America (Davis, 1987; Robinson et al., 2005; van Geel et al., 2008; Gill et al., 2009), late-Holocene Madagascar (Burney et al., 2003), Mozambique (Ekblom and Gillson, 2010), alpine France (Cugny et al., 2010), and Holocene islands (Wood et al., 2011). However, much remains unknown about spore taphonomy, taxonomic affinities, and the influence of climate and other environmental factors on the production, dispersal, and preservation of coprophilous fungi (Feranec et al., 2011). For example, Raper and Bush (2009) found that *Sporormiella* abundances may be more concentrated in lake margin sediments, while Parker & Williams (in press) found that within-lake variations in spore percentages were influenced not only by the presence of grazers, but also by basin morphology. As yet, no study has tested whether spore percentages or concentrations can be quantitatively linked to megafaunal biomass. Additionally, while *Sporormiella* spores exhibit a unique morphology that allows for identification at the genus level, it remains unclear whether spores can be identified to species, which could in turn be linked to taxonomic preferences for particular host herbivores, both extinct and extant.

5. Conclusions

A new multi-proxy paleorecord from Silver Lake, OH, replicates both the absolute timing and the relative sequence of events observed at Appleman Lake, IN: the decline in spore abundances of the coprophilous fungus *Sporormiella* (13.9 ka BP; during the Allerød warm period in Greenland and before the Younger Dryas) was followed by 1) increased abundances of deciduous hardwood taxa, 2) the development of novel plant communities, and 3) increased fire activity, including the highest-magnitude charcoal peaks of both records. Climatic influences on the no-analog plant communities are also likely; the duration of the no-analog communities at Silver Lake (13.9–11.8 ka BP) corresponds to periods of peak seasonality of insolation and the modeled peak climatic dissimilarity for this region (Williams et al., 2001; Williams and Jackson, 2007). Growing evidence from this and other new, well-dated paleorecords suggests that the no-analog communities were more temporally constrained in the Great Lakes region and formed several millennia later (ca 14 ka BP) than reported in previous sub-continental syntheses (Williams et al., 2001; Williams and Jackson, 2007). Further constraining the timing of the no-analog communities across a broad geographic region with new and updated pollen chronologies will help to identify the causes of these communities and their response to environmental change. It is also important to note that the late-glacial no-analog communities were not static, uniform assemblages, but were dynamic in terms of their composition, structure, and function through time.

The continued study of *Sporormiella* as a proxy for megaherbivores provides a promising way forward in understanding the ecological role of megaherbivores in late-glacial landscapes, but there remains a critical need for further understanding of the dispersal and taphonomy of *Sporormiella*, its host preferences, and its quantitative relationship to megaherbivore biomass. The data from Silver Lake supports Owen-Smith's keystone herbivore hypothesis, and indicate that ecosystem change, including changes in community composition, structure, and function (e.g., fire activity and nutrient cycling), may have been a consequence rather than a cause of the end-Pleistocene decline in megafaunal populations. However, the loss of Pleistocene megaherbivores coincided with climate change, and thus the late-glacial no-analog communities likely resulted from a combination of both biotic and abiotic factors. We therefore favor a hierarchical model of the drivers of Quaternary vegetation change that incorporates herbivory and other biotic interactions as well as the direct influences of climate change on vegetation composition and structure. As in the late Pleistocene, modern ecosystems are also experiencing species extinctions and climate change, so there is an opportunity to use both the present and the past to jointly inform our understanding of community dynamics during times of global change.

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Tables

Table 1

Ogden 1966				**This Paper**		
Zone	Climate Interpretations	Vegetation	Calibrated Age Interval	Zone	Phenomena	Age
1	cold to coil, moist	*Picea-Abies* maximum	Est. 14ka to 11ka	A	High *Picea*, *Sporormiella*	18.3 ka to 13.9 ka
2	dry, warmer	*Pinus* max, *Quercus*, no-analog	?? to 9.8ka	B	High *Fraxinus*, *Ostrya*, no-analog	13.9 ka to 13.1 ka
				C	High *Pinus*, *Abies*, 2nd *Picea* peak	13.1 ka to 10.9 ka
3a	warm, wetter	deciduous forest, *Fagus* max (6 ka)	9.8ka to ~4ka	D	High *Quercus*, *Ulmus*, *Carya*,	10.9 ka to7.5ka
3b	warm, drier	*Quercus-Carya* max, *Fagus* min	4ka to 1.3ka		*Not recorded*	
3c	cooler, moister	modern	1.3ka to 260			
3d	as present	sharp rise in *Ambrosia*	260 to present			

Table 1 – Comparisons in the timing of vegetation events between Ogden (1966) and this paper.

Table 2

Lab #	Depth (cm)	^{14}C Age	1-σ	Cal. Age Range	Material
OS-79440	601.5	7530	95	8330-8540	Twig
OS-79804	741.5	1220	25	1146-1256	Plant macrofossil
OS-79267	771.5	10000	55	11480-11740	Plant macrofossil
OS-79434	811.5	11250	95	13150-13340	Bud scale
OS-79293	877.5	12150	60	13100-14180	Twig
OS-79433	897.5	11500	80	13350-13560	Twig
OS-79291	927.5	13350	70	16470-16840	Conifer needle
OS-79810	1087.5	14150	100	17220-17580	Conifer needle
OS-65298	1129	14850	70	18120-18520	Wood
OS-65293	1136.5	14750	50	17940-18460	Wood
OS-65299	1138	14750	60	17940-18470	Wood
OS-65267	1183	14850	65	18120-18520	Wood
OS-65857	1184	14950	200	18100-18580	Wood

Table 2 – 95% calibrated age ranges, and the 50% median probability ages were identified using the CLAM program and the IntCal09 calibration curve (Blaauw, 2010)

Figure 1: Map of Silver Lake

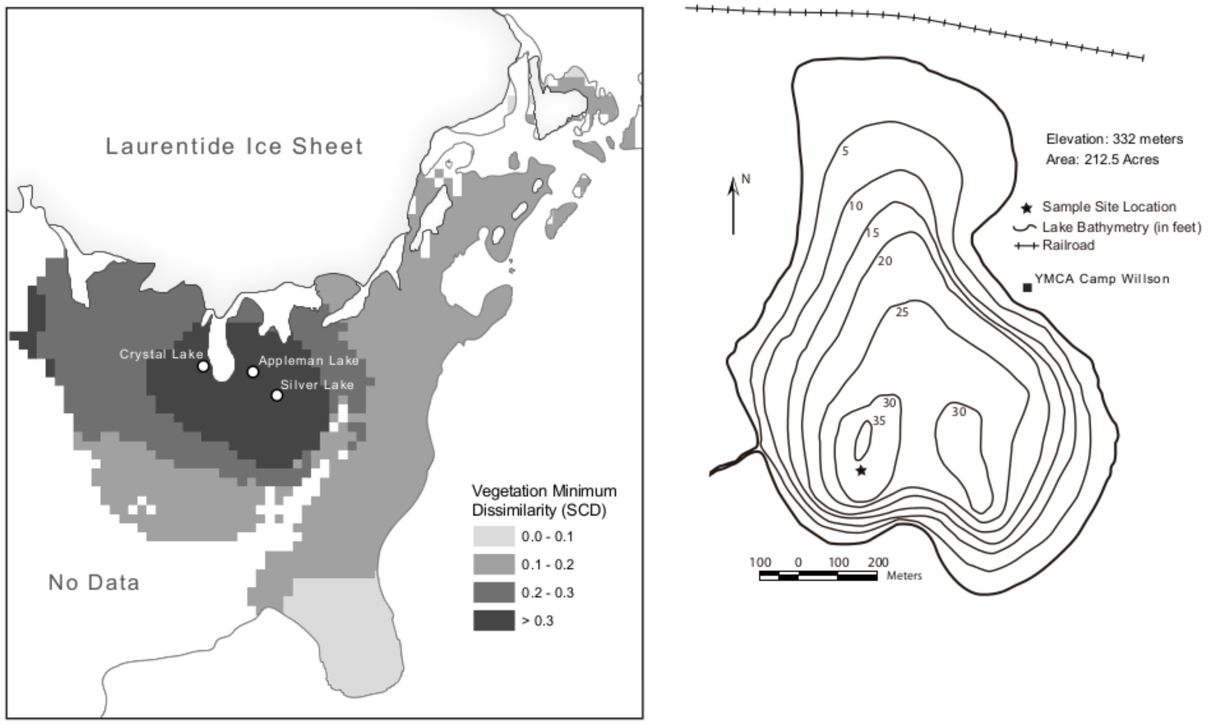


Figure 2: Silver Lake age model

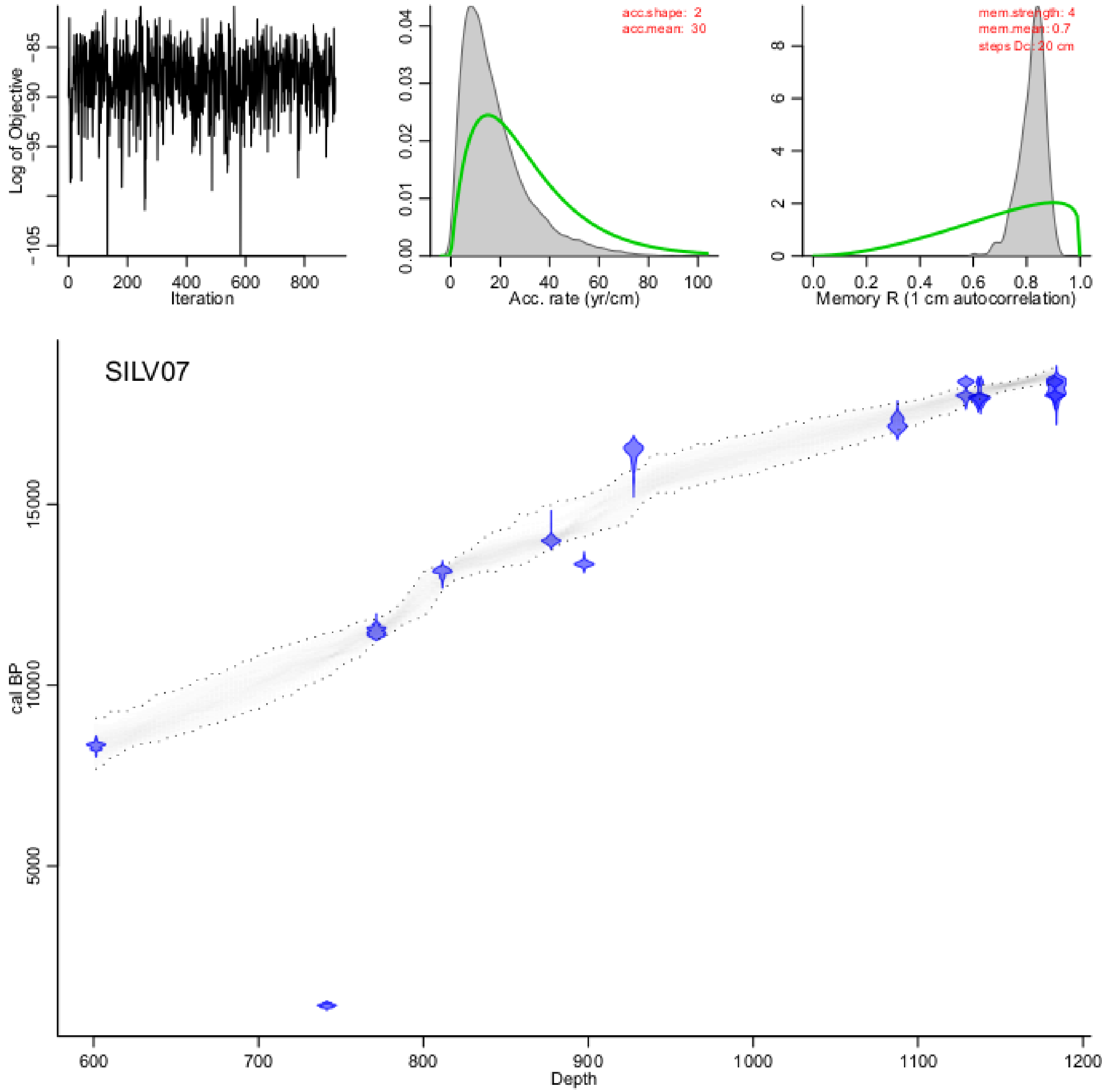


Figure 3: Silver Lake pollen diagram

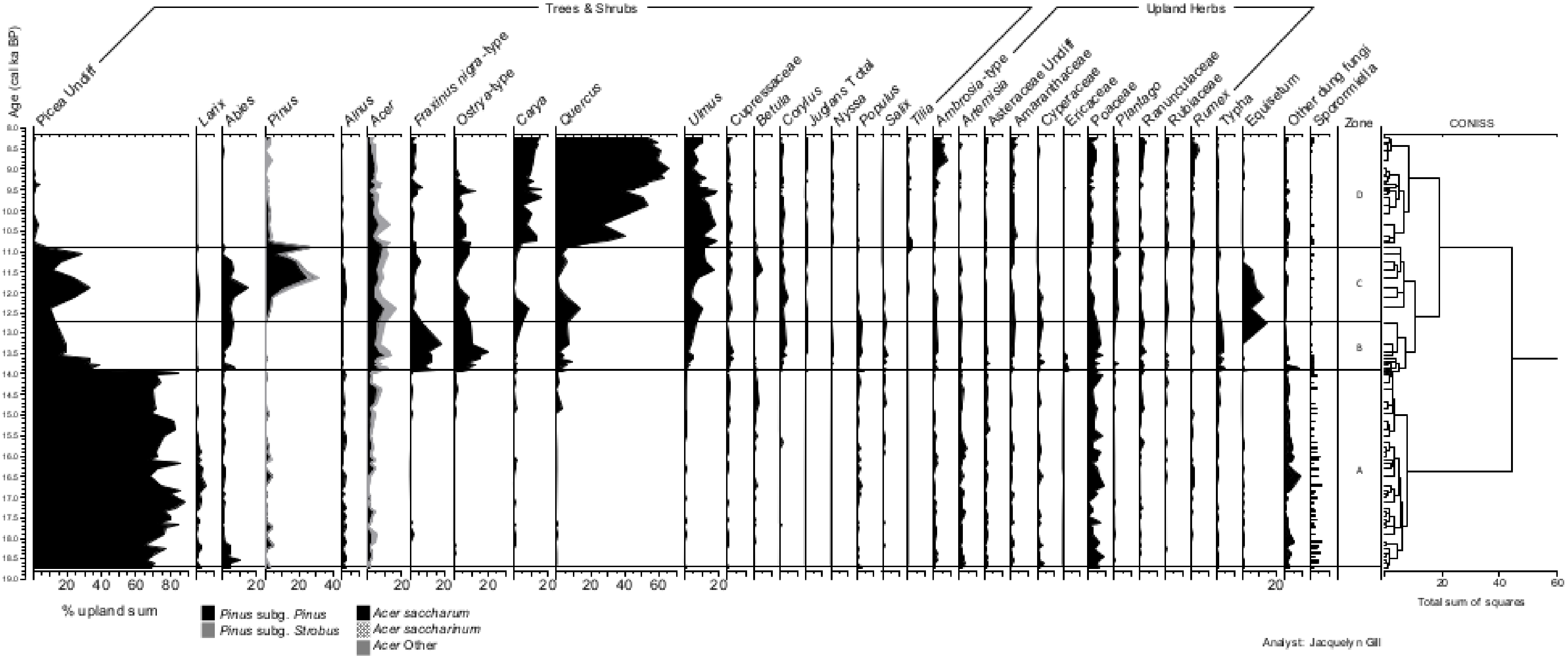


Figure 4: Bayesian change-point analysis

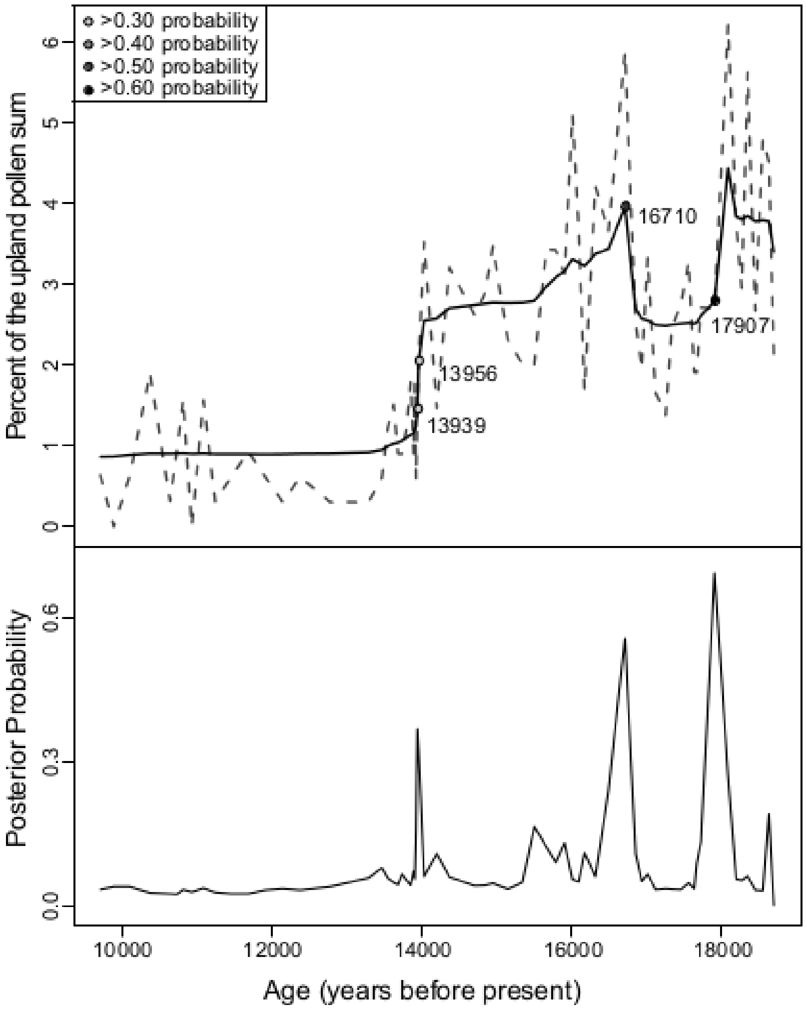
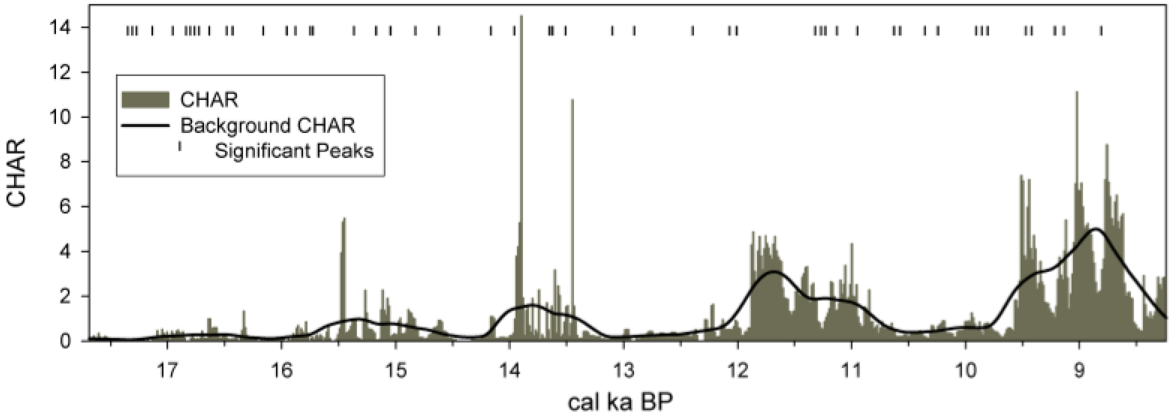
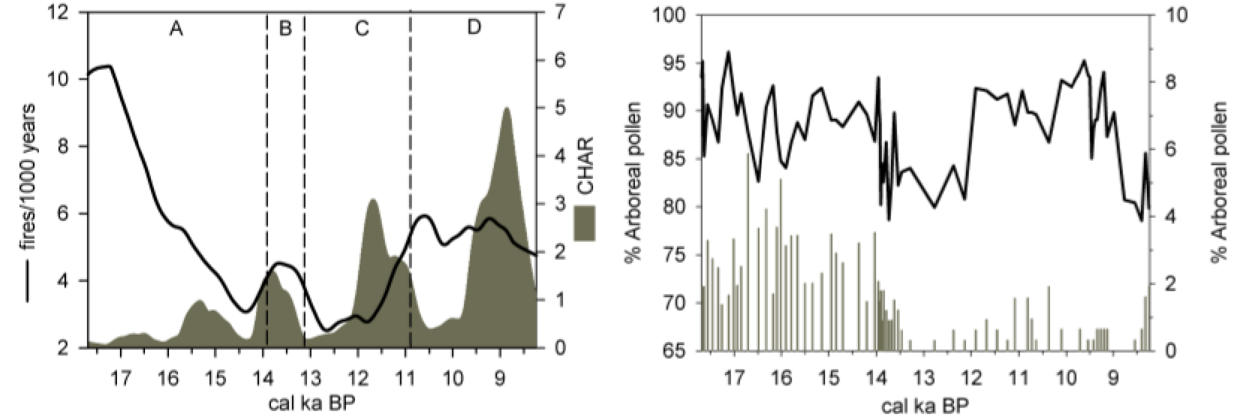


Figure 5: Silver Lake charcoal analysis

A) Charcoal Influx, background, & peaks



B) Fire Frequency, Background CHAR & Pollen Zones C) Arboreal Pollen & *Sporormiella*



D) Select charcoal morphotypes

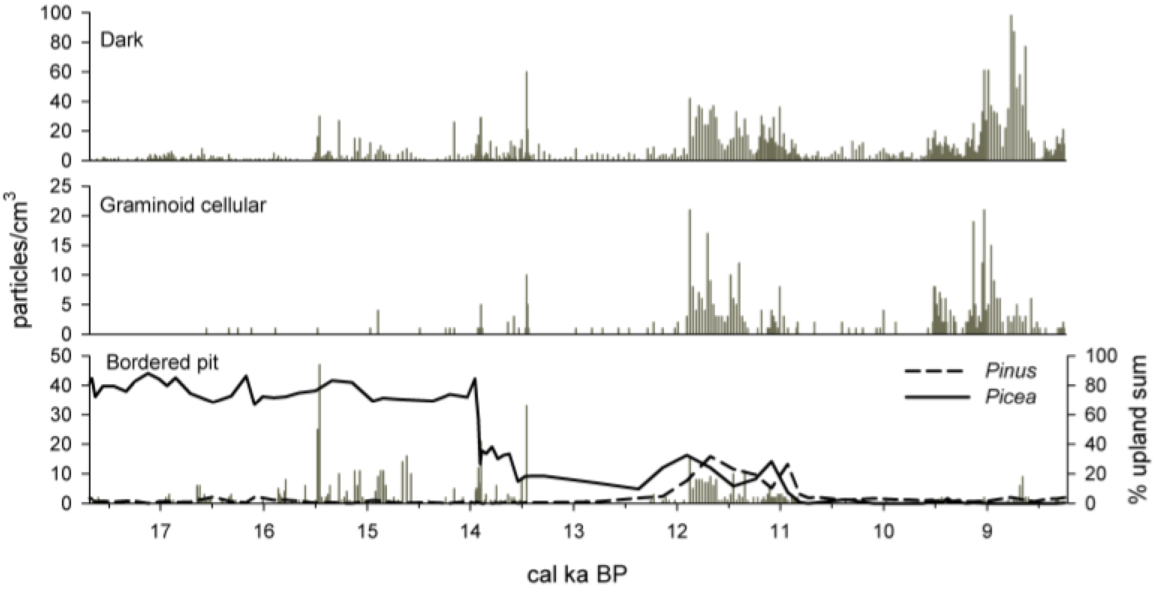


Figure 6: Physical and geochemical data

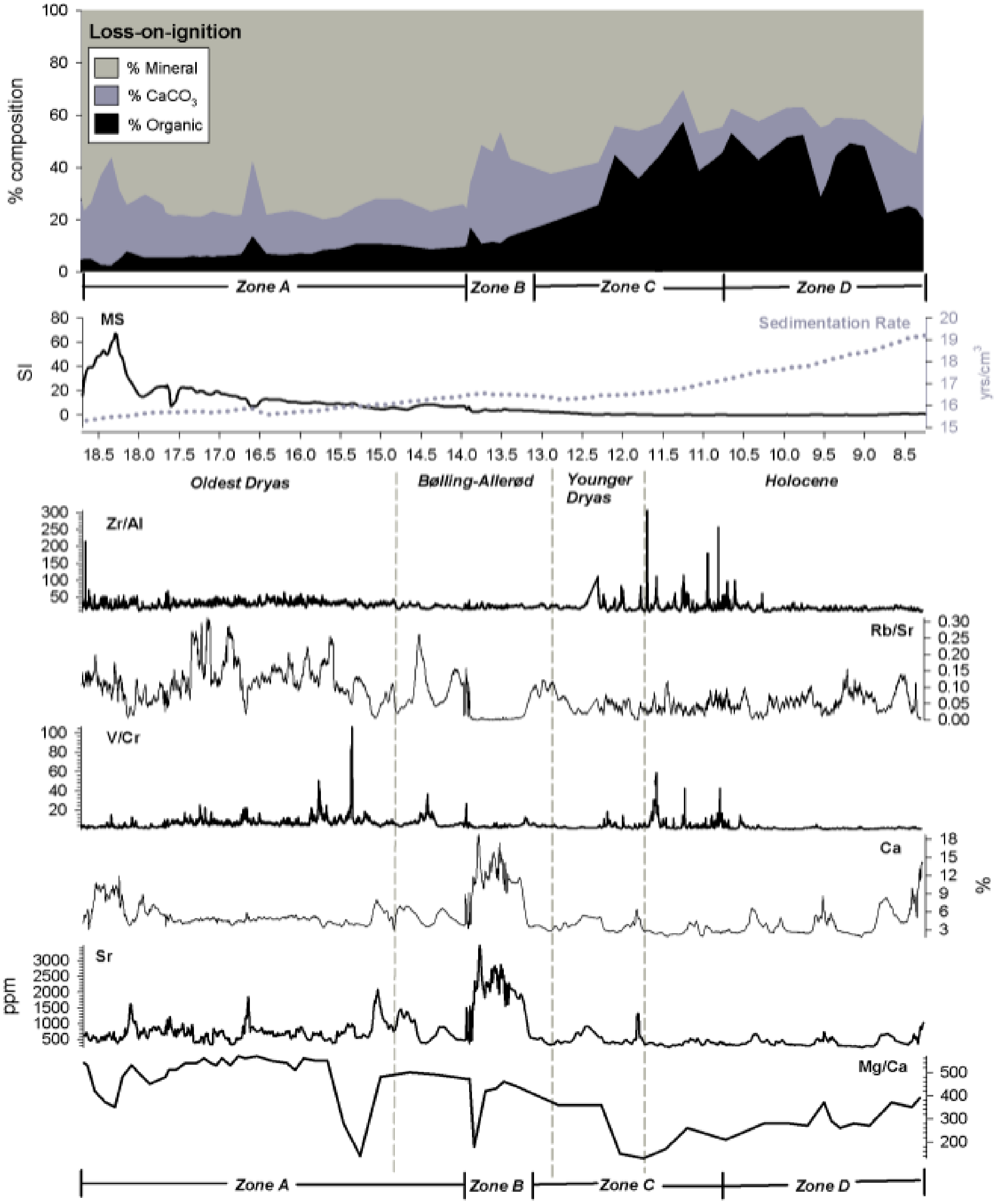


Figure 7: Silver, Appleman, and Crystal Lakes

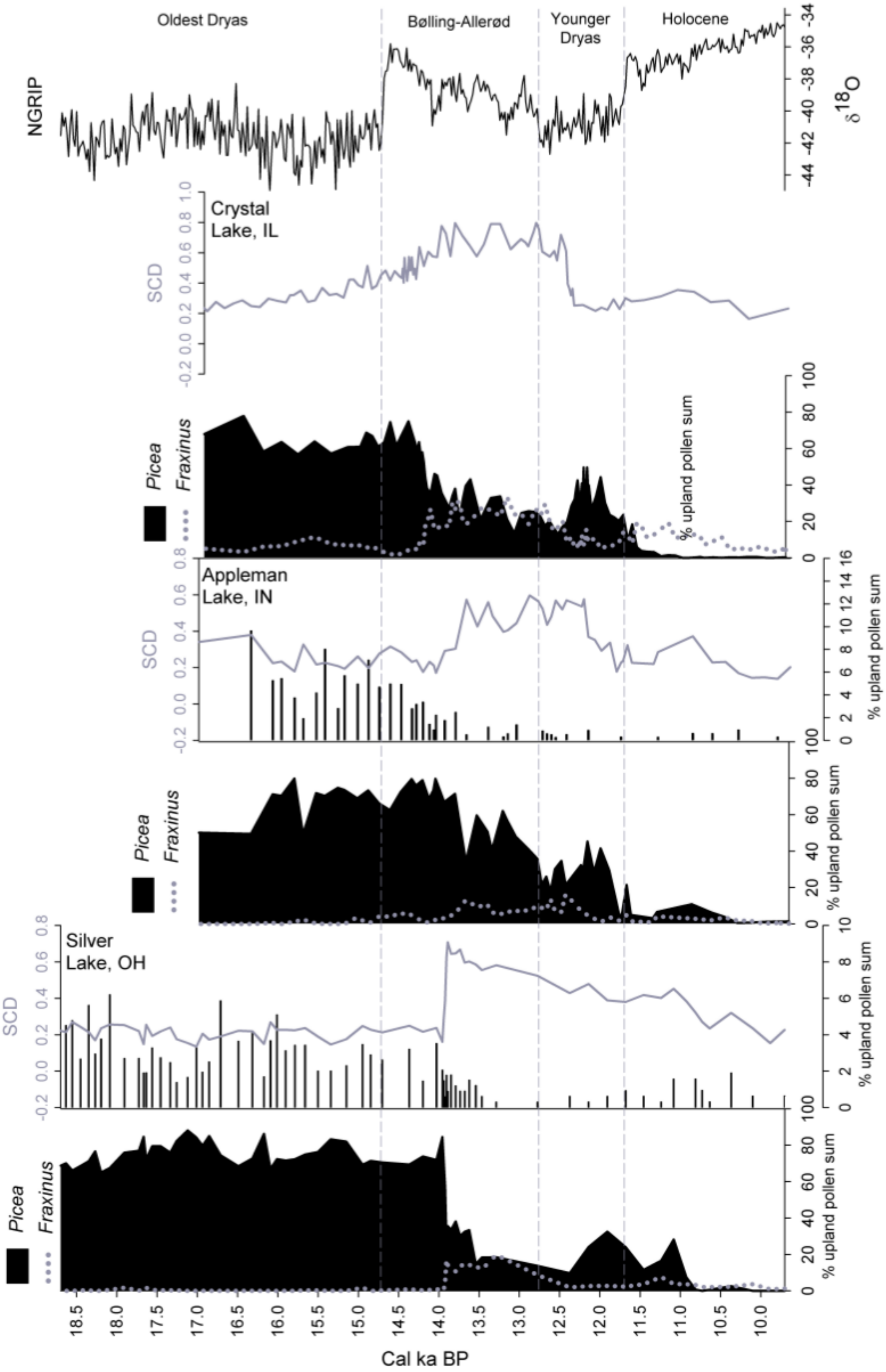


Figure 8: Conceptual diagram of drivers of Quaternary vegetation dynamics

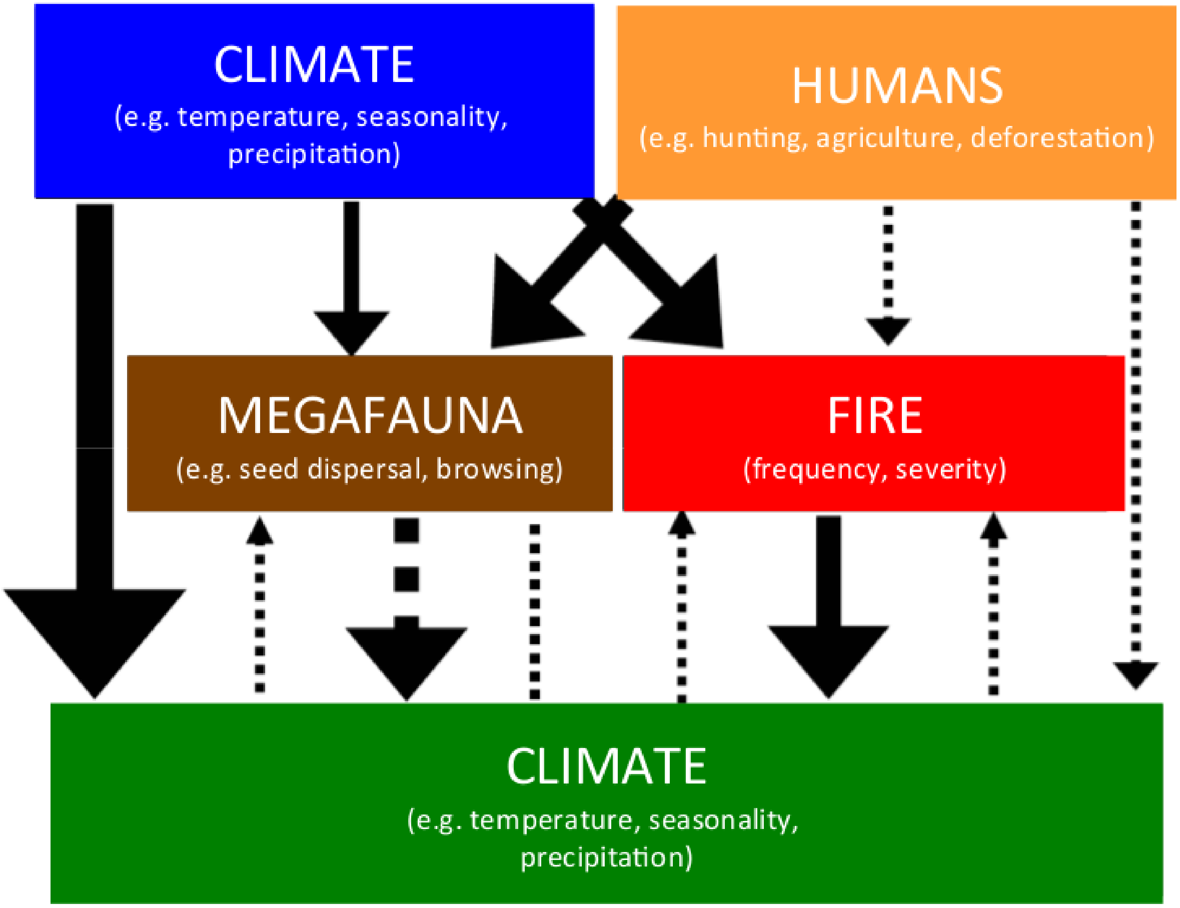


Figure Legends

Figure 1: Map of Silver Lake. Left: Map of minimum vegetation dissimilarity from present, mapped as squared chord distance values for 14 ka BP. Right: Bathymetric map of Silver Lake with 5 ft. contour intervals, digitized from Ogden (1966).

Figure 2: Age model. Bayesian age model output from Bacon (Blaauw and Christen, 2011), based on the probability density function for each calibrated radiocarbon age (a). Age model probability is represented by a grayscale cloud, bounded by dotted-line error ranges. Inset figures show the prior (lines) and posterior densities (area fills) for the mean accumulation rate (a; sedimentation rate) and memory (b; autocorrelation strength at 1 cm intervals), the two prior estimates in the age model. Bacon assumes linear accumulation, and so the apparent outlier radiocarbon date at 741.5 cm increases model uncertainty in this portion of the record but not the maximum likelihood estimate for the model.

Figure 3: Pollen diagram of abundant taxa. Abundances are expressed as a percent of the upland pollen sum; *Sporormiella* was not included in that sum. Pollen zones were calculated using constrained incremental sum of squares (CONISS) analysis in Tilia v. 1.7.14 (Grimm, 2011).

Figure 4: Bayesian change point analysis. Top: Bayesian change point analysis (Erdman and Emerson, 2007) of the *Sporormiella* time series (dashed gray line), showing the posterior means (black line) and probabilities of a change at each point (circles). Bottom: Posterior probability estimates of a significant change in the *Sporormiella* time series.

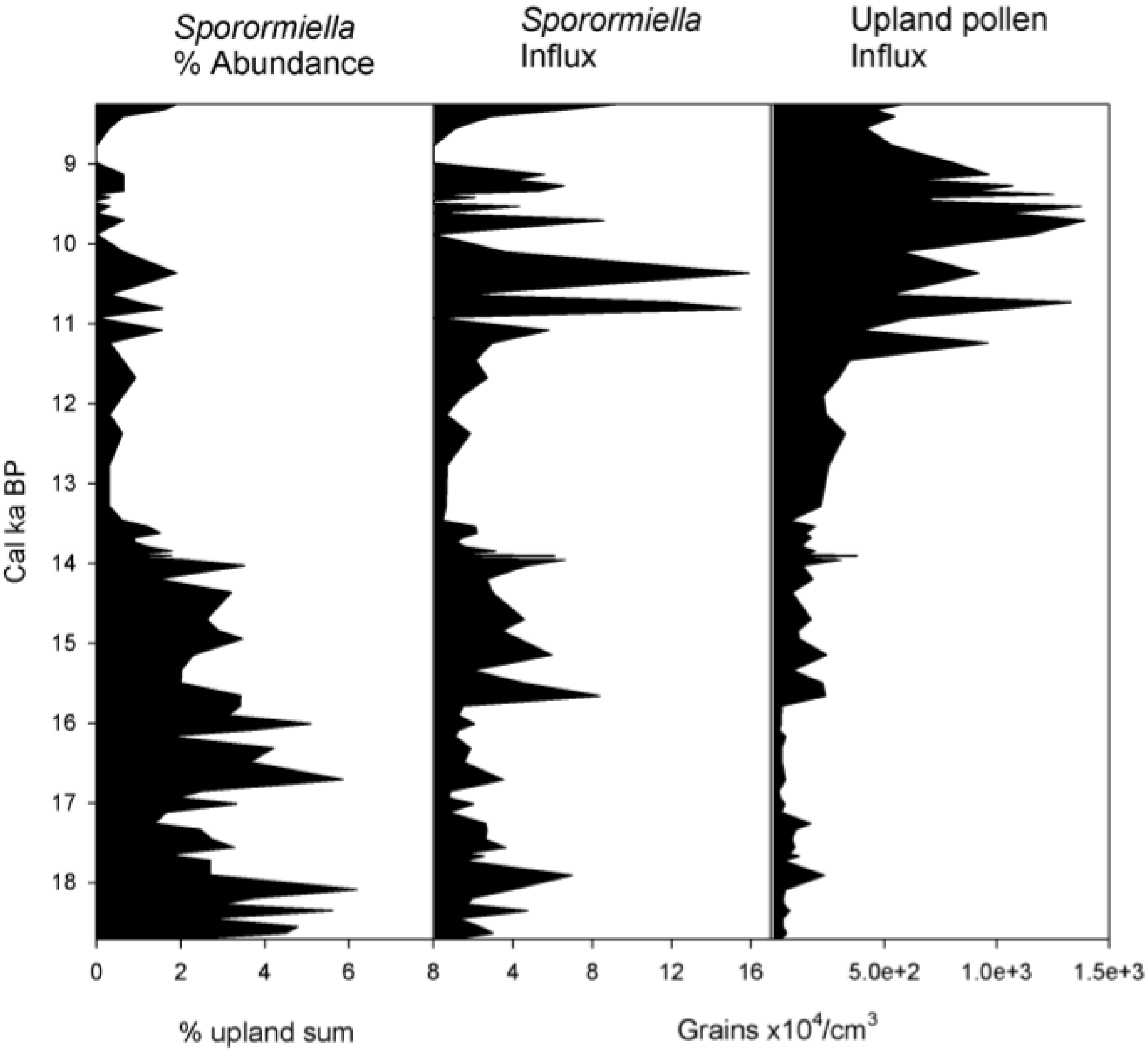
Figure 5: Charcoal data. A) Charcoal influx, resampled to the median temporal resolution (gray bars), and background CHAR (black line; particles/cm2/year) from Silver Lake. Background CHAR was calculated in CharAnalysis with a LOWESS smoother, which applies a locally weighted scatter plot smoother using least squares polynomial fitting; we set the moving window to 700 years. Vertical dashes at the top indicate significant fire events, based on a local threshold identified using a Gaussian mixture model in CharAnalysis. B) Fire frequency (black line; fires/1000 years) and background CHAR (gray area fill), with pollen zones identified with CONISS. C) *Sporormiella* (vertical bars) and % arboreal pollen. D) A subset of charcoal morphotypes, including dark (woody material), graminoid cellular (grasses), and bordered pits (conifer wood). Data are plotted as raw charcoal concentrations (particles/cm3).

Figure 6: Summary of physical and geochemical data. Loss-on-ignition analysis shows the relative fractions of organic carbon, carbonates, and minerals, calculated as a proportion of weight loss from successive burns at 100 ˚C (dry weight), 550 ˚C (to remove organic carbon), and 1000˚C (to remove carbonates, leaving the mineral fraction). Magnetic susceptibility (black line) and sedimentation rate (gray dotted line) show opposite trends; increased sedimentation during the early Holocene apparently resulted from increased organic input. Zr/Al, Rb/Sr, and V/Cr ratios were obtained using high-resolution scanning XRF analysis; Ca and Sr were calibrated from XRF intensities using ICP-AES elemental analysis. Mg/Ca ratios were obtained from ICP-AES results at 10 cm resolution. Climatic events are overlaid on these time series (dashed gray line) based on the NGRIP oxygen isotope record (Rasmussen et al., 2006).

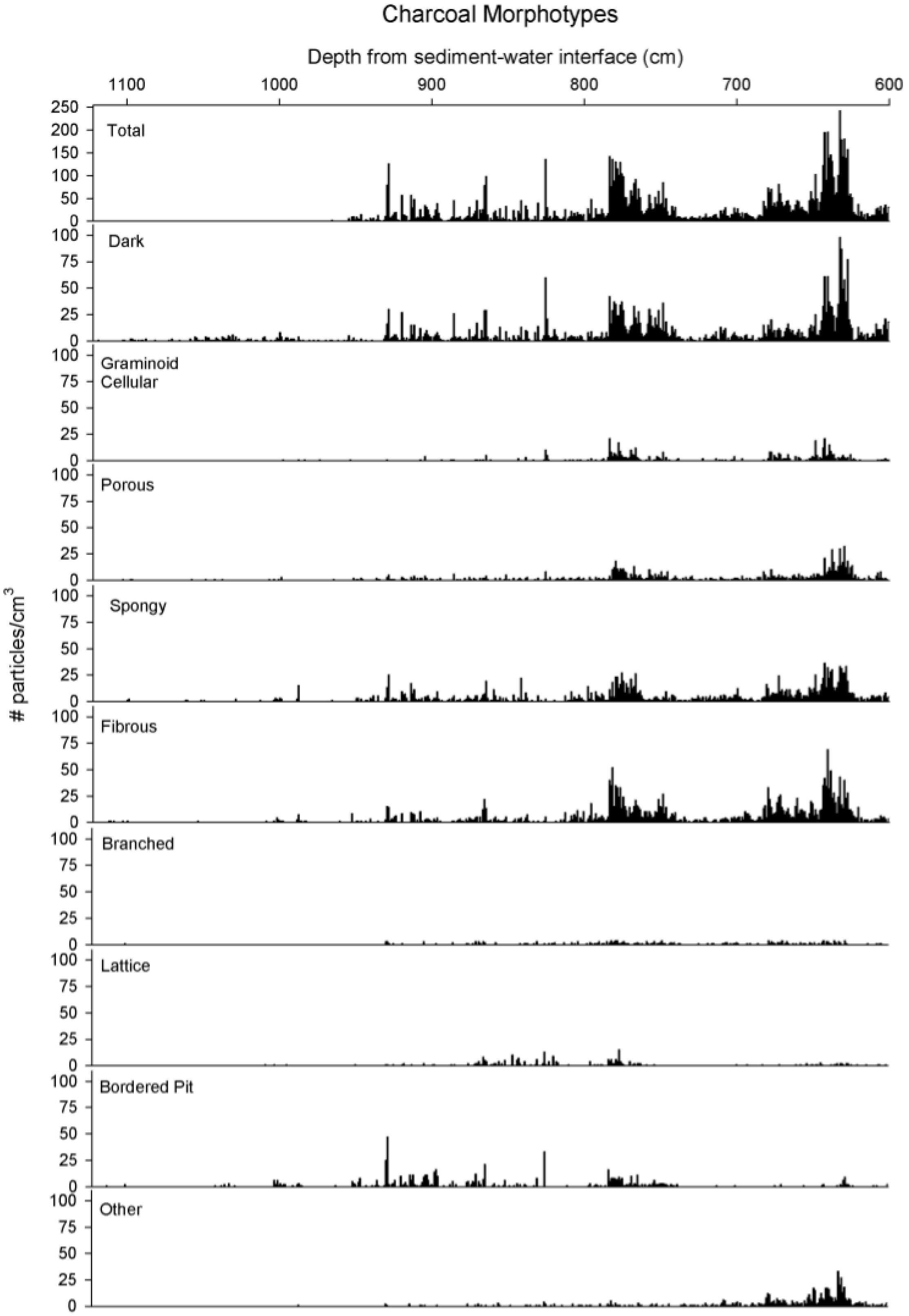
Figure 7: Comparison of Silver, Appleman, and Crystal Lakes. A summary of Picea (black area fill), Fraxinus (gray dotted line), *Sporormiella* (black bars), and minimum vegetation dissimilarity represented as square-chord distance scores (gray line) for Silver Lake (this paper), Appleman Lake (Gill et al., 2009), and Crystal Lake (Gonzales and Grimm, 2009), compared with the NGRIP oxygen isotope record (Rasmussen et al., 2006). Major transitions in the NGRIP record are indicated with the dashed gray line.

Figure 8: Controls on Quaternary vegetation dynamics. A conceptual diagram representing proposed top-down drivers of Quaternary vegetation dynamics mediated by biotic interactions. Arrow thickness represents the hypothesized relative importance of each coupling; dashed arrows indicate relationships that are particularly poorly understood or under-explored.

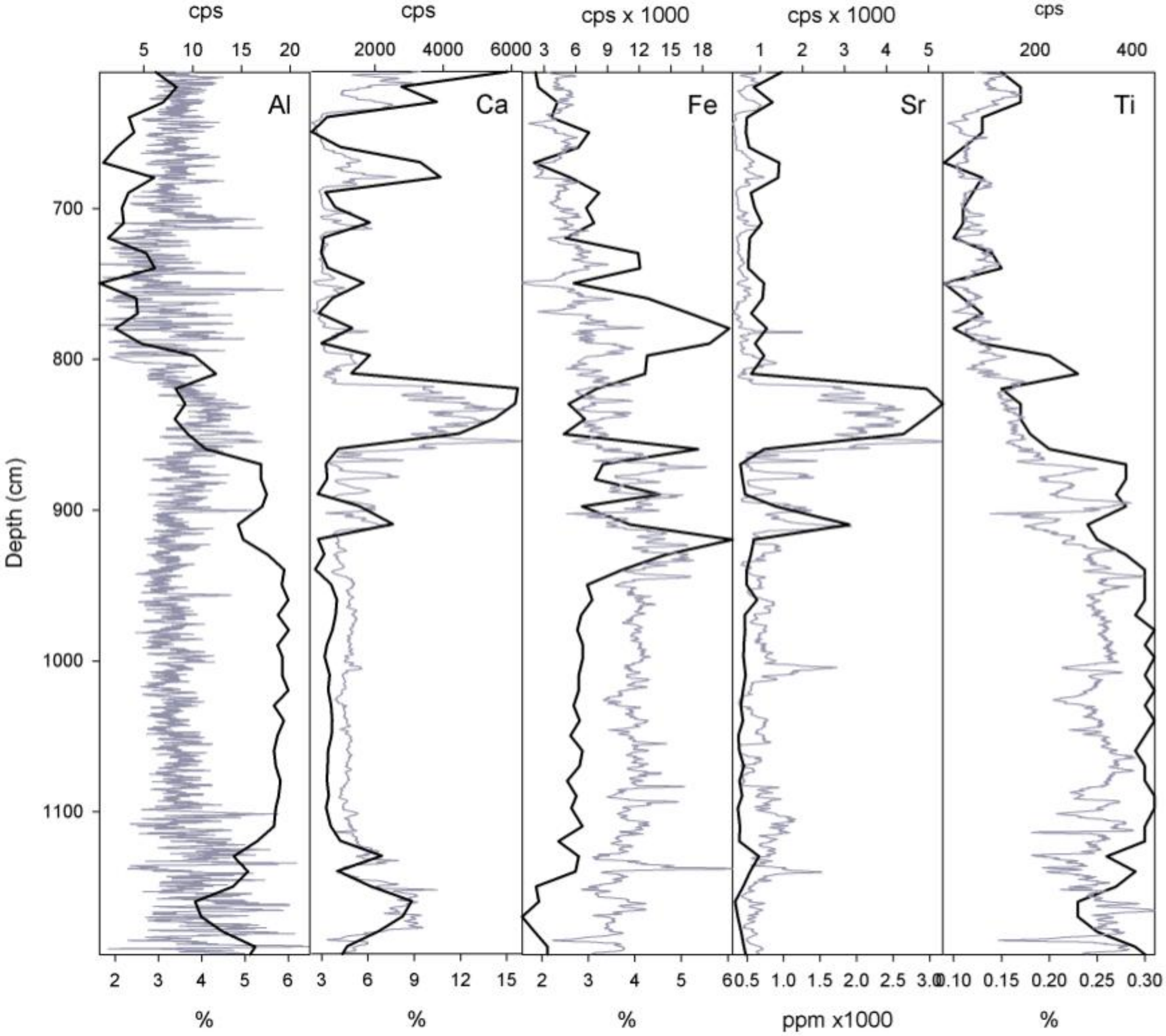
Supplemental Figure 1: *Sporormiella* and Upland pollen influx



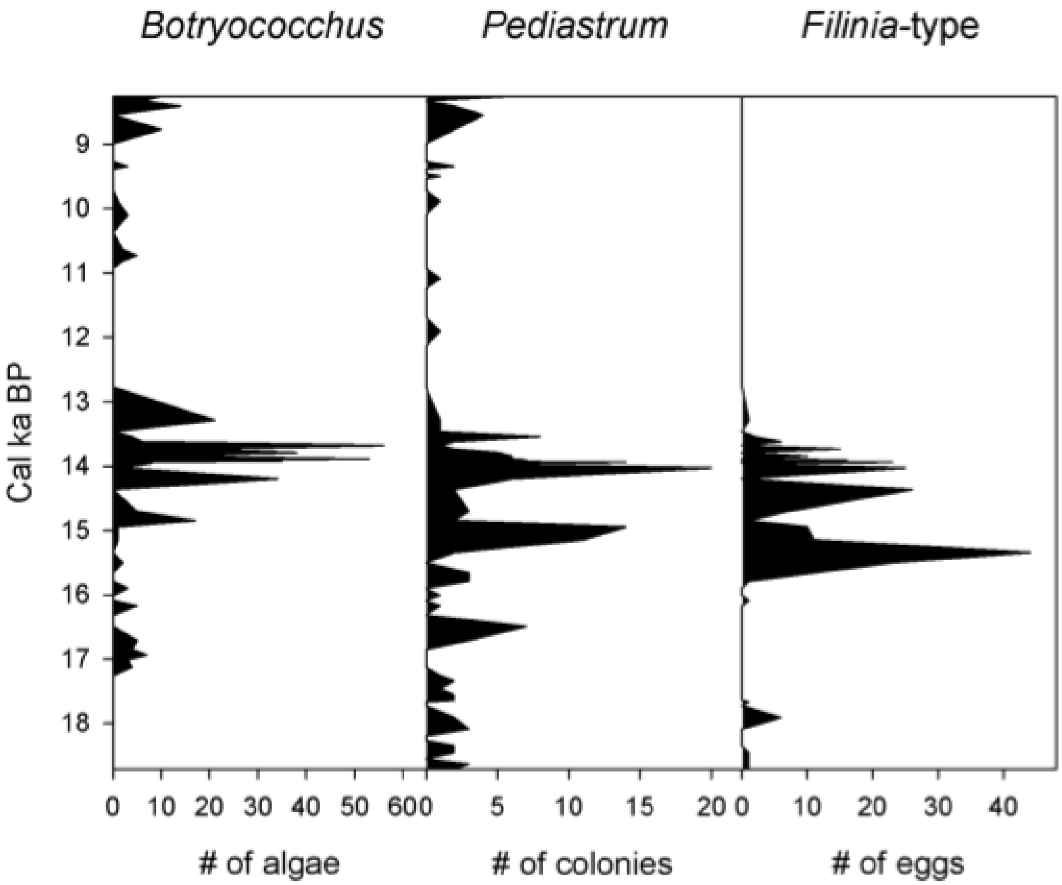
Supplemental Figure 2: Charcoal morphotypes



Supplemental Figure 3: XRF Conversions



Supplemental Figure 4: Non-pollen palynomorphs



Supplemental Figure Legends

Figure S1: Upland Pollen and *Sporormiella* influx. *Sporormiella* abundances are represented as a percent of the upland pollen sum, and are compared with *Sporormiella* influx (spores × 104/cm2/year) and the upland pollen influx (grains × 104/cm2/year). The decline in *Sporormiella* is not an artifact of changes in accumulation rates of other taxa.

Figure S2: Charcoal morphotypes. Time series of concentrations (particles/cm3) of all macroscopic charcoal morphotypes, including dark (woody material), graminoid cellular (grass), porous, spongy, fibrous, branched (deciduous leaf veins), lattice, bordered pit (conifer wood), and “other” (which includes unidentifiable types or rare types that lack a pre-established morphotype).

Figure S3: XRF-ICP-AES conversions. Comparisons of elemental data from XRF (gray, counts per second) and ICP-AES (black, % w/w or ppm) analyses. Depths are from the sediment–water interface of core C.

Figure S4: Select non-pollen palynomorphs. Non-pollen palynomorphs, including the algae *Botryococcus* and *Pediastrum* (colonies), and eggs of the rotifer *Filinia longiseta*.

CHAPTER 3

PLAINS BISON (*BISON BISON)* GRAZING INTENSITY AT KONZA PREDICTS THE ABUNDANCE OF THE DUNG FUNGUS *SPORORMIELLA* IN SURFACE POLLEN TRAPS

Abstract

Studies of the role of keystone megaherbivores in past vegetation dynamics are of growing interest in paleoecology, fueled in part by the use of fossil spores from *Sporormiella* and other coprophilous fungi as biomarkers for megafaunal biomass in historic and prehistoric sediment records. Previously, the quantitative linkage between spore abundances and megaherbivore biomass and/or grazing intensity was assumed, but unknown. The Konza Prairie Long-Term Ecological Research Station is home to a herd of native megaherbivores (*Bison bison bison*) inhabiting the largest remnant tallgrass prairie in the United States, and thus provides the ideal setting to test the effects of megaherbivores on grassland plant communities and their signature in the palynological record. Using a previously existing network of twenty-eight modified Tauber traps located inside and outside the bison enclosure, I collected pollen and spores during the 2009 and 2010 flowering seasons. Bison grazing intensity (kg/m^2/year) was calculated within concentric circles with increasing radii around each trap (25 m to 500 m), using annual data on total herd biomass and locations of radio-collared bison matriarchs to track herd position. *Sporormiella* showed a significantly positive qualitative and quantitative response to bison at Konza. Both relative and absolute abundances of *Sporormiella* were significantly higher in traps within the enclosure than in traps outside of the enclosure, with an optimal discrimination threshold for *Sporormiella* relative abundances of 2.8%. Relative and absolute abundances of *Sporormiella* also correlated positively to the fraction of a trap's source area that was inside the bison enclosure and to bison grazing intensity. The relationship between *Sporormiella* spore abundances and grazing area was strongest at short radii (25 to 100 m), supporting prior interpretations that *Sporormiella* spores usually do not disperse far

from their source. Thus, *Sporormiella* should be viewed as a local-scale indicator of megaherbivore presence. This work also establishes that, despite many potential mesoherbivore (<100 kg) mammalian and bird hosts for *Sporormiella* at Konza, high abundances of *Sporormiella* spores are mainly sensitive to the presence and abundance of the bison megaherbivores (>100 kg). Additionally, traps in grazed areas had significantly higher percentages of *Ambrosia* and lower percentages of Poaceae pollen than traps from ungrazed areas, consistent with well-documented effects of bison grazing on vegetation. This suggests that the pollen record has the potential to detect top-down trophic effects on grassland community composition. These results suggest that joint *Sporormiella* and pollen analyses from lake sediments may help understand the drivers of Holocene grassland dynamics in the Great Plains, including the possible role of bison in mediating grass-forb interactions during the variable moisture regimes of the last eleven thousand years.

Introduction

Large mammalian herbivores can be keystone species that exert strong influences on the composition, structure, and function of terrestrial ecosystems. Effects include the alleviation of plant competitive exclusion (Dyer et al. 1993, Edenius et al. 1993), maintenance of vegetation openness (Weigl and Knowles 1995, Olofsson et al. 2004, Hester et al. 2006), the facilitation of vegetation mosaics (Olff et al. 1999), promotion of tree-grass coexistence in the savanna biome (Sankaran et al. 2005, Wiegand et al. 2006, Goheen et al. 2007), alteration of the spatiotemporal dynamics of landscape nutrients (Hobbes et al. 1991, Kielland and Bryant 1998, Ritchie et al. 1998, Chapman et al. 2006), plant dispersal (Howe and Smallwood 1982, Janzen and Martin 1982, Dudley 2000, Shiponeni and Milton 2006, Blake et al. 2012), altering species richness and evenness (Anderson and Katz 1993, Olff and Ritchie 1998, Bakker et al. 2006, Parker et al. 2006), and triggering ecological tipping points (May 1977). In the conceptual framework developed by Mills et al. (1993) and building on the original terminology by Paine (Paine 1966, Paine 1969) megaherbivores are potentially both “keystone modifiers,” and “keystone predators,” because they exert direct and indirect effects on the biotic and abiotic environment to influence other trophic levels.

Our understanding of megaherbivory as an ecological process is mostly based on contemporary experimental manipulations (Hester et al. 2000, Asner et al. 2009) or the post-hoc assessment of the effects of local extirpations or management practices (Constible et al. 2005, Ter Beest 2006, Yelenik and Levine 2010). In recent decades there has been a growing interest in understanding the ecological effects of the global wave of megaherbivore extinctions during the end-Pleistocene and Holocene (Johnson 2009), despite the challenge that the signature of herbivory and other species interactions usually is more indirect in paleorecords. Owen-Smith (1987) first hypothesized that the loss of keystone megaherbivores, including mammoths (*Mammuthus*) and mastodons (*Mammut*) contributed to the extirpation of 35 genera of megafauna at the end of the Pleistocene in North America (Koch and Barnosky 2006, Faith and Surovell 2009) via cascading effects on vegetation structure and habitat availability. Key questions are emerging in paleo-herbivory research, many of which have direct conservation and management implications: Were the early Holocene forests of Europe more open than at present, and did the extinction of megaherbivores alter forest composition due to changing light availability as canopies closed following herbivory release (Bradshaw and Mitchell 1999, Vera 2000, Mitchell 2004, Vera et al. 2006)? Did declines in megaherbivore populations contribute to the formation of no-analog plant communities and changes in fire regime in eastern North America during the last deglaciation (Gill et al. 2009, 2012)? Did the megafaunal extinction directly or indirectly influence the composition of the atmosphere, either due to the reduction of biogenic methane (Smith et al. 2010) or trophic cascades to terrestrial carbon budgets (Doughty et al. 2010, Smith et al. 2010)? What were the causes and ecological context of the megafaunal extinctions in Australia (which, unlike in North America, did not take place during a glacial-interglacial transition), and what were the relative importance of humans, fire, and vegetation (Miller et al. 2005, Rule et al. 2012)? What are the long-term dynamics of the influence of grazers on tree-grass coexistence in the savanna (Ekblom and Gillson 2010)? Was top-down megaherbivory by bison a factor in the centennial-scale quasi-periodic cycles in grassland composition in the Great Plains (Craine and McLauchlan

2004) or were these vegetation dynamics a direct response of plant species to drought variability (Clark et al. 2002, Grimm et al. 2011)?

The increasing use of spores from coprophilous fungi such as *Sporormiella*, preserved in in sedimentary archives (Davis 1987, Davis and Shafer 2006, van Geel 2002), have begun to shed light on the ecological legacy of the loss of megaherbivores throughout the late Quaternary, including changes in plant community composition and fire regimes in New York (Robinson et al. 2005, Widga et al. 2010) and Madagascar (Burney et al. 2003), as well as the formation of novel ecosystems in the Great Lakes region of North America (Gill et al. 2009, Gill et al. 2012) and shifts in biomes in Australia (Rule et al. 2012). A *Sporormiella* spore must pass through a herbivore's digestive tract in order to complete its cycle; the fungus then sporulates on dung after passage through the gut. Newly released spores are then passively dispersed to the surrounding vegetation, where they are consumed by herbivores (Richardson 2001, Nyberg and Persson 2002) or, in some cases, washed or blown into sedimentary basins. The *Sporormiella* proxy is complementary to the fossil bone record because the latter offers direct but discontinuous evidence of megafaunal presence, while *Sporormiella* spores are best preserved in lake and mire sediments, and so are often temporally continuous, can be counted for estimates of relative and absolute abundance, and are found in the same depositional environments as fossil pollen and other paleoecological and paleoclimatic proxies. *Sporormiella* has many hosts (Ahmed and Cain 1972), but its signal in late Quaternary records appears to be strongly linked to megafaunal population abundances. In North America, *Sporormiella* spores are abundant in mammoth coprolites and late-Pleistocene sediments (>11,700 BP) in North America (Davis 1987, Robinson et al. 2005, Gill et al. 2009, Gill et al. 2012), and are rare (usually

<2% of the upland pollen sum) in Holocene (<11,700 BP) lake and bog records, though spores apparently decline in the Great Lakes region of North America earlier (>13,700 BP) than in the American west (<12,700 BP) (Faith 2011). At several sites, *Sporormiella* abundances remain low through the Holocene until the historic introduction of cattle, horses, and other domesticated herbivores (Robinson et al. 2005, Davis and Shafer 2006).

However there remains a critical need to better understand the factors governing the production, transportation, deposition, taphonomy, and preservation of *Sporormiella* and other coprophilous fungal spores (Feranec et al. 2011), as is standard when working with paleoecological proxies (Jackson 2012). Previous studies have shown a positive relationship between the abundance of *Sporormiella* in recently deposited lake and mire sediments and the historic presence of large grazers (Graf and Chmura 2006, Raper and Bush 2009, Parker and Williams 2011). However these analyses did not quantify the source area of spores, and were limited by a lack of detailed data on recent and historic megaherbivore densities. Hence, these studies have successfully linked *Sporormiella* to the presence of megaherbivores, but the quantitative relationship between *Sporormiella* abundances and megaherbivore biomass and/or grazing intensity is less well known.

The Konza Prairie Long-Term Ecological Research Station (39.08° N, 96.58° W, mean elevation 397 m) located in the Flint Hills of Kansas, USA (Fig. 1), represents a unique opportunity to test the relationship between *Sporormiella* and megaherbivory. Konza is home to a well-studied herd of free-roaming Plains bison (*Bison bison bison*) in an enclosure divided into experimental watersheds with different combinations of fire, grazing, and browsing treatments, which have been ongoing since 1981. Annual records of bison biomass are available from yearly fall roundups, when individuals are vaccinated, tagged, weighed, and/or culled to maintain a sustainable herd size. Bison position and landscape usage within the enclosure is monitored via GPS telemetry of radio-collared bison matriarchs. Bison are one of only ten out of forty-five genera of megaherbivores to survive the late Quaternary extinctions in North America (Koch and Barnosky 2006, Faith and Surovell 2009), and are considered a keystone species of the tallgrass prairie for their well-documented influences on grassland structure, composition, and function (Knapp et al. 1999). Bison diets are typically composed of >98% grass (Coppedge et al. 1998) and at Konza, bison routinely avoid most forb plant species. *Ambrosia psilostachya* and *Vernonia baldwinii*, both perennials, are the most common forbs on grazed patches at Konza (Fahnestock and Knapp 1994, Hartnett et al. 1996). Grazing increases available light for lower-statured forbs by decreasing above-ground leaf area of grasses and thus allowing for greater utilization of water and nutrients by shallower-rooted forbs (Fahnestock and Knapp 1994). Habitat selection by bison is strongly structured by fire, due to a strong preference for spring-burned patches (Vinton et al. 1993, Fuhlendorf and Engle 2004). In a study of bison and fire effects on Great Plains diversity, bison spent as much as 75% of their grazing effort in burned patches, resulting in shifting mosaics of patches with high forb diversity and increased bare ground relative to the surrounding prairie matrix (Fuhlendorf and Engle 2004). The effects of bison and cattle grazing differ, including in their preference for warm season, C_4 grass species. At Konza, bison reduced *Schizachyrium scoparium* relative to cattle-grazed plots, while cattle plots had increased abundances of *Andropogon serardii*; both treatments saw overall increases in annual and perennial forbs and cool season graminoids, but the increase was greater in bison treatments (Towne et al. 2005).

Bison also influence vegetation composition through the creation of wallows, which are shallow depressions in the soil caused when bison roll or lie in mud to protect themselves from heat and insect bites (Fig. 2 b). These patchy disturbances in the prairie landscape can persist for a century or more, and often contain different species than the surrounding vegetation matrix (Collins and Uno 1983). Formed in the spring and summer, wallows typically hold more water during the rainy season than the surrounding undisturbed soils, and often provide habitat for wetland or mesic taxa (Collins and Uno 1983, Uno 1989). Compact soils in wallows provide disturbed habitat where *Ambrosia* and other forbs are particularly able to out-compete deep-rooted grasses for water. McMillan et al (2011) estimate there may have been >100 million wallows over the 70,000 ha of the prairie prior to European settlement, representing a fundamentally different disturbance regime than is currently present in the cattle-grazed or ungrazed portions of the modern prairie. The late Holocene near-extirpation of bison is expected to have significantly influenced the ecology of the modern Great Plains, and bison grazing, along with fire, has become an important component of prairie restoration efforts (Hartnett et al. 1996, Collins et al. 1998, Martin and Wilsey 2006, Fuhlendorf et al. 2008).

In this study, I combine GPS tracking-based estimates of bison presence, herd population, and herd biomass in order to calculate localized estimates of annual grazing intensity (bison kg/m^2/year) and compare these estimates with the abundance of *Sporormiella* and other pollen and spore types collected from a pre-existing network of 28 traps placed throughout Konza (Fig. 1, 2a). I use this data as the basis for the most detailed study yet of the relationship between the *Sporormiella* proxy and megaherbivory. My results show a significant effect of bison grazing intensity on both the relative and absolute abundances of *Sporormiella* at a very local (<50 m) source area. Additionally, I demonstrate that the well-established influence of bison grazing on grassland vegetation composition (Cid et al. 1991, Vinton et al. 1993, Fahnestock and Knapp 1994, Pfeiffer and Hartnett 1995, Hartnett et al. 1996, Towne et al. 2006) is captured by the pollen record, with higher abundances of *Ambrosia*-type pollen and lower abundances of Poaceae pollen in pollen traps placed in bison-grazed watersheds. This finding is consistent with hypotheses that centennial-scale oscillations in *Ambrosia* and Poaceae pollen abundances in the Great Plains (Clark et al. 2002) were driven by bison grazing dynamics (Craine and McLauchlan 2004). However, there is also strong evidence that these oscillations were paced by drought (Grimm et al. 2011), because *Ambrosia* is more abundant during the drier periods (Grimm 2001). Given the well-documented mechanisms by which plant communities in the tallgrass prairie are influenced by a combination of bison, fire and drought (Collins and Calabrese 2012), I attempt to reconcile these alternative hypotheses with a conceptual model of the relationships between bison, fire, drought variability, and vegetation, whereby drought affects the spatial heterogeneity of bison influences on Poaceae-*Ambrosia* interactions.

Methods

Site Description and Context

The Konza Prairie Biological Station (hereafter “Konza”) is a 3,487-ha National Science Foundation Long-Term Ecological Research station located in the Flint Hills region of Kansas (Fig. 1). Konza is situated in one of the last surviving uncultivated remnants of tallgrass prairie in the Great Plains, historically protected from agricultural use by the region’s high topographic relief. Konza is characterized by flat ridge-tops with shallow and/or rocky soils alternating with wide valleys with relatively deeper soils, separated by terraced slopes of Permian limestone; the mean relief is 120 m (Collins and Calabrese 2012). A herd of free-roaming bison is present throughout the year in a 1000-ha enclosure (Fig. 1), and is not provided with supplemental feed. Konza is divided into forty-six experimental watersheds with several replicated grazing and fire treatments, ten of which are located within the bison enclosure. Grazing cattle are seasonally present in some watersheds (separate from the bison enclosure); grazing treatments changed in 2010 to include more watersheds (Fig. 1). Bison are the dominant megaherbivore within the enclosure, although white-tailed and mule deer can jump over the enclosure fence. See Table 1 for a list of mammals recorded at Konza and their observational frequency (updated from McMillan et al. 1997).

The vegetation matrix at Konza is predominately C_4 perennials, including big bluestem (*Andropogon gerardii*), indiangrass (*Sorghastrum nutans*), little bluestem (*Schizachyrium scoparius*), and switchgrass (*Pancium virgatum*), along with more than 600 species of subdominant C_3 and C_4 graminoids, forbs, and woody plants (Freeman and Hulbert 1985). Gallery forests consisting of *Quercus* spp. and *Celtis* are common in the lowlands (Abrams 1986). Vegetation at Konza is highly structured by bison and fire treatments (Fig. 2b-c); both grazing and periodic fire are necessary to maximize diversity and community stability (Collins and Calabrese 2012). Shrubs encroach in the absence of both grazing and fire (Ratajczak et al. 2011). Topography is also an important control of plant community composition. Water stress occurs earlier and is more severe at upland sites, which have shallow and/or rocky soils overlying limestone and shale bedrock and so the response of vegetation to drought is highly variable within Konza (Collins and Calabrese 2012).

Pollen and Spore Data

As part of a broader study on the annual variability of pollen productivity (McLauchlan et al. in prep.), 28 modified Tauber pollen traps (Fig. 2a) made from PVC pipes were deployed in October 2008 (Tauber 1974, Hicks and Hyvarinen 1986) throughout the experimental watersheds at Konza, both inside and outside the bison enclosure (Fig. 1). Trap deployment locations were determined by a randomizing GIS algorithm balancing accessibility, level soil surface (so as not to bias the dispersal of pollen and spores into the trap), equal coverage of grazed and ungrazed locations, and even distribution throughout the watersheds. No trap was allowed to be within 500 m ground-distance of another trap. Traps were deployed in October 2008, at the end of the flowering season; deployment and collection coincided with the annual bison roundup. Trap contents were collected in October 2009 and 2010. Many of the 2009 traps were found to contain large amounts of fungal growth, dung beetles that had fallen into the traps, or both. The 2010 traps were modified to include a finer mesh (to prevent beetle entry but not restrict air flow and pollen transport) and 2 g of the fungicide thymol was added to prevent growth of fungus within the trap (this fungicide did not affect the preservation of fungal spores transported to the trap). Due to the high volume of contaminants in the 2009 traps, only 11 traps had contents suitable for pollen and spore analysis. All 28 of the 2010 traps were collected and analyzed. Grazing treatments changed in 2010 to include more watersheds, and so three of the 2010 traps (710, 763, and 764) were located inside seasonally grazed cattle watersheds for which stocking densities and grazing intensities were unavailable (Fig. 1). These were designated as ‘cattle’ samples and were excluded from most analyses, except where explicitly stated otherwise.

Trap contents were collected in the field by rinsing each trap with deionized (DI) water into a clean plastic gallon jug. The amount of water in the traps varied widely, due to the influence of surrounding vegetation on evaporation rates. Some traps, particularly those in ungrazed areas (e.g. Fig. 2c), were >50% full of rainwater, while those located in bison-grazed ‘lawns’ were often dry. All collected material was rinsed through a carbon-based filter with glacial acetic acid to preserve the contents and prevent the growth of mold or fungi. Samples were processed using standard methods for pollen analysis, modified to include a method for dissolving vacuum filter samples (Faegri and Iverson 1989). Each filter was soaked in 15 ml each of glacial acetic acid and acetic anhydride for five minutes in a 250 ml beaker. A mixture of 45 ml acetic anhydride, 15 ml of glacial acetic acid, and 7 ml of concentrated sulfuric acid was then added to each sample to dissolve the filters. Samples were condensed and rinsed four times with DI water in 50 ml centrifuge tubes, after which they were treated with HCl, hot HF (20 minutes) to remove silicates, post-HF HCl (to remove the colloid byproducts of HF digestion), hot KOH to disaggregate any clumps of organic matter, two ethanol rinses to replace water, and finally tertiary butyl alcohol, which was evaporated and replaced with 1,995 cs silicone oil. In order to calculate pollen and spore concentrations (reported as number of grains/trap, because trap liquid volume varied and volumes were not preserved), a known quantity of reference material was added to each sample (Stockmarr 1971). For the 2009 batch, three tablets of exotic *Lycopodium* spores (batch #483316; one tablet = 18,583 spores +/- 764) were added to each sample before processing; for these samples, the initial HCl rinse was done at the beginning of pollen processing in order to dissolve the carbonate matrix of the tablets. For the 2010 samples, I switched to polystyrene microspheres (2ml 5.0×10^4 spheres/ml +/- 8%; Ogden III 1986). Samples were counted on microscope slides at 400x magnification with a Zeiss Axio Imager. At least 400 pollen grains and spores were counted for each sample.

Bison Location and Grazing Intensity

The bison location data, which was the basis for the localized estimates of megaherbivore biomass and grazing intensity around each trap, consisted of GPS radio-collars reporting bison position. From October 2008 to October 2009, position data were collected every 30 minutes for some matriarchs and every 1 hour for others, and from October 2009 to October 2010 some collars were added with a 2-hour reporting frequency. For this analysis, I obtained the total number of GPS hits within concentric rings around each trap (at 25 m, 50 m, 100 m, 200 m, 300 m, 400 m, and 500 m). All collar data were normalized to the 2-hour frequency data by multiplying the number of hits on the 30-minute collars by ¼, and the hourly collar data by ½. Bison are matriarchal, and so the position of bison matriarchs is a good indicator of overall herd position. Six bison matriarchs were collared in 2008-2009 out of a total herd of 387 bison (adults and juveniles), and eleven matriarchs were collared in 2009-2010 out of a herd size of 349 bison (Table 2). From this information and annual data on herd size and total herd mass (Table 2), I calculated grazing intensity near each trap as follows:

$$I_i = N_{Cij}/\text{year} * N_H/N_C * M_H/N_H * 1/A_{ij}$$

where I_i is grazing intensity (kg/m/yr^{-1}) at trap i, N_{Cij} is the number of collared bison in the herd at trap i (i.e., the number of GPS hits reported at a trap over the course of a year within radius j), N_H is the number of bison in the herd, M_H is the mass of the herd in kg, and A is the total circular source area of trap i at radius j. See Table 2 for the values of N_C, N_H, and M_H for 2009 and 2010. This formulation assumes that the number of bison and herd biomass is fully and evenly distributed among the collared matriarchs, such that each GPS 'hit' for a collared matriarch is assumed to reflect a fixed proportion of the overall herd biomass. This formation also assumes that pollen and spore dispersal is anisotropic. Because traps are collecting pollen and spores from both inside and outside the bison enclosure, estimates of A used full circle area, thereby including source regions both inside and outside the enclosure.

Because of the limited size of the dataset, I pooled all trap data for 2008-2009 (hereafter referred to by collection year, "2009") and 2009-2010 ("2010") for all analyses, except for the three traps in the cattle-grazed watersheds from 2010. Note that some traps located outside the bison enclosure included ring area within the enclosure, and vice-versa. This pooling assumes that *Sporormiella* abundances in the traps were not significantly affected by interannual variations in environmental factors such as aridity. Moreover, by using annual data for herd biomass, I do not account for seasonal variability in average bison weight, herd size (due to the addition of calves or the culling of adults mid-season), or bison land use preference. Violations of these assumptions are a source of unexplained variance in the statistical models linking *Sporormiella* abundances to grazing intensity.

Statistical Analyses

For these analyses, the response variable is *Sporormiella* abundance, represented as either absolute concentrations (# of spores/trap) or relative abundance (% or natural-log-%, as indicated). I report results for several different predictor variables, representing alternate measures of megafaunal presence and grazing intensity, and statistical analyses, including 1) a Kruskal-Wallis test for a significant relationship between treatment type (i.e. whether a trap was in a bison, ungrazed, or cattle watershed) and *Sporormiella* abundance, 2) ordinary least-squares regression (OLS), in which the predictor variable was the area of the circle inside the bison enclosure (with separate analyses for each radius), and 3) OLS in which the predictor variable was grazing intensity, as calculated above. I also tested OLS regression models that included elevation as a predictor variable, as well as a model where elevation was the sole predictor, in order to determine whether the effect of landscape position on spore transport was able to explain any of the observed patterns. OLS R^2, Spearman's rank correlation *rho*, and ANOVA R values are reported as measures of goodness of fit. Tests were performed for each circle distance, in order to better assess the source area of *Sporormiella*. For ordinary least-squares linear regression, percentage data was converted to natural log-percentages, so that the distribution would approximate the normal distribution required for OLS. Logarithmic and square-root transformations of percentage data are common in the analyses of compositional data (including pollen analyses) to down-weight the signal from over-represented pollen types (Aitchison 2003). Response variables were tested for spatial autocorrelation using a Moran's I test (Moran 1950), both on the original data and on the residuals after OLS regression. Receiver-operating characteristic (ROC) analysis was conducted on the treatment data (i.e. whether traps were in grazed vs. ungrazed areas) to detect an optimal *Sporormiella* % threshold for the prediction of the presence of bison, selected to maximize the area under the curve (AUC). All analyses were done using R (R Development Team 2011), except for the ROC analysis, which was done using Sigmaplot 12.2 (Systat Software, 2011).

Results

Sporormiella abundances significantly differed between the bison and ungrazed treatments, being significantly higher within the bison enclosure for both (untransformed) relative abundances (Kruskal-Wallis $\chi 2 = 23.27$, df = 2, p= <0.001) and absolute concentrations (Kruskal-Wallis $\chi 2 = 24.87$, df = 2, p = <0.001) (Fig. 3). The average percent abundance of *Sporormiella* in bison-grazed locations was 6%, versus 1.2% in the ungrazed locations and 0.7% for the cattle-grazed traps. ROC analysis indicated that 2.8% *Sporormiella* was the optimal threshold for discriminating between traps in ungrazed versus bison-grazed locations (Fig. 4), based on a maximization of the area under the ROC curve (AUC 96.78%, p = <0.0001). This threshold equally balanced test sensitivity (88.89%) and specificity (94.74%), because neither Type I or Type II errors were prioritized in this analysis (Wahl 2004). The three traps located inside cattle-grazed pastures appear to have had variable spore abundances (Fig. 2), although the sample set is too small for formal analysis and implications are difficult to assess given that data on cattle stocking densities were not available. These traps were excluded from further tests.

Linear regressions of *Sporormiella* abundances predicted by the total grazed area within each circle around the traps resulted in p <0.01 at all circle radii, and variance explained ranged from 0.192 to 0.263 (*Sporormiella* concentrations) and from 0.342 to 0.456 (log *Sporormiella* %)

(Fig. 5; Table 3). The strongest relationship between grazed area and *Sporormiella* abundances occurred at the smallest circle radius tested, 25 m, for both concentration ($R^2 = 0.26$, F = 12.12, p = <0.001) and log percent abundance ($R^2 = 0.46$, F = 28.94, p = <0.001) (Fig. 5, Table 3). The Spearman rank correlation between grazed area and *Sporormiella* abundance is also significant, both for log percentages (rho = 0.81, p = <0.001) and concentration (rho = 0.73, p = <0.001). For both percent and abundance data, the Spearman rank correlation coefficient also declines with increasing distance from the trap (Fig. 5).

There is also a significant positive relationship between bison grazing intensity (kg/m^2/year) and spore abundance (Fig. 6, Table 4), but the spatial scaling of that pattern differs between percent and concentration data. Grazing intensity has the strongest relationship to spore concentrations at 25 m (Fig. 4a, b), the closest ring distance from the trap ($R^2 = 0.54$, F = 40.83, p = <0.001), which is the same pattern observed when grazed area is the predictor variable (Fig. 5). When log *Sporormiella* percentages are the response variable, however, there was no clear relationship between source radius and the strength of the relationship (Fig. 6 c, d), with the strongest relationship observed at 400 m ($R^2 = 0.38$, F = 20.63, p = <0.001). Elevation was not a significant predictor of spore abundances in a multiple regression model including grazing intensity at 25 m (for grazing intensity, $\beta = 63.043$, p = <0.0001, while for elevation, $\beta = -3.233$, p = 0.907) or in an OLS model of elevation as a predictor alone ($R^2 = 0.03$, p = 0.311). Because pollen percentages are affected by the pollen accumulation rates of other taxa while absolute concentrations are not, I hypothesize that the different relationships observed for the percentage and concentration data are because 1) the percentage *Sporormiella* data is confounded by the influence of grazing pressure on grassland composition and hence the pollen accumulation rates of other taxa, and/or 2) percentage data may be more heavily influenced by vegetation differences due to topographic heterogeneity.

The residuals of the regression models of spore percent abundances and concentrations as predictors of grazing intensity showed low and non-significant spatial autocorrelation at all circle radii. Because the OLS models showed the strongest predictive power at 25 m, Moran's I statistic is reported for that radius only. For the residuals of the concentration model, Moran's I = 0.089 (expected = -0.028, p = 0.08), and for the residuals of the percent abundance model, Moran's I = 0.024 (expected = 0.028, p = 0.256). Raw spore concentration (Moran's I = 0.156 versus the expected -0.028, p = 0.017) and percent abundances (Moran's I = 0.193 versus the expected -0.028, p = <0.001) also showed low spatial autocorrelation.

In modern systems, bison selectively reduce grasses, which increases the relative abundance of forbs (particularly *Ambrosia* spp.) via the reduction of competition for water and light (Fahnestock and Knapp 1994). Given this, I tested whether there was a significant impact of grazing on the pollen abundances of these two taxa. Species of Poaceae and *Ambrosia* are not distinguishable in the pollen record; *Ambrosia* abundances therefore include both annual and perennial species, the latter of which includes *Ambrosia psilostachya*, which is an abundant forb at Konza prairie in the presence of grazing (Fahnestock and Knapp 1994). Abundances of *Ambrosia* pollen were significantly higher in traps located in grazed than ungrazed watersheds, both for concentration (Kruskal-Wallis χ^2 = 8.29, p = 0.004) and untransformed percentage data (Kruskal-Wallis χ^2= 9.42, df = 1, p = 0.002). Conversely, Poaceae percent abundances were significantly lower in grazed than in ungrazed sites (Kruskal-Wallis χ^2 = 5.18, df = 1, p = 0.023), but concentrations were not significantly different (Kruskal-Wallis χ^2 = 0.73, df = 1, p = 0.39).

Discussion

Understanding the Sporormiella Proxy

This study reinforces prior findings that the abundance of *Sporormiella* spores in depositional environments is heavily influenced by the presence and number of large mammalian grazers and browsers (Graf and Chmura 2006, Raper and Bush 2009, Parker and Williams 2011). Moreover, the detailed data available at Konza on bison biomass and landscape utilization allows this study to move beyond the presence/absence correspondences reported in prior papers and demonstrate both a positive correlation between megaherbivore grazing intensity and *Sporormiella* abundances and a palynological signal of the effect of grazing on grassland composition.

The clear differences in *Sporormiella* abundances between traps inside and outside the bison enclosure (Fig. 3) suggest that the rates of *Sporormiella* deposition are strongly influenced by the presence and density of megaherbivores such as bison. The megaherbivore signal appears to override any *Sporormiella* signal associated with the activity of meso- and/or transient herbivores. Other common mammalian herbivores at Konza include white-tailed-deer (*Odocoileus virginianus*), eight species of rodents, and the eastern cottontail (*Sylvilagus floridanus*) (McMillan et al. 1997; Table 1). Deer have been observed jumping the bison enclosure fence, and should thus be considered to be present throughout the preserve. Given that Konza is not a single herbivore system (though it perhaps may be considered a single keystone-herbivore system), the robustness of *Sporormiella* as a predictor of bison presence alleviates concerns that late Quaternary *Sporormiella* fluctuations were driven by fluctuations in the population of smaller mammalian herbivores, such as lagomorphs (Feranec et al. 2011).

Rather, meso- and microfauna appear to set a background level of *Sporormiella* rates of deposition, beyond which a megafaunal signal can be detected. The threshold value of 2.8% indicated by the ROC analysis of the trap data is consistent with the 2% threshold proposed by Davis (1987) for establishing megafaunal extirpations from *Sporormiella* in late Quaternary sediments. *Sporormiella* spore percentages in the traps were lower than the abundances in the bison dung processed from Konza (16%) for this study, as well as mammoth dung (16%) reported by Davis (1987). At many North American sites, *Sporormiella* is found at values >2% during the late Pleistocene (18.7 ka to 13.8 ka BP), is absent or present in trace amounts during the Holocene, and then increases >2% again with the local introduction of domestic megaherbivores (Davis 1987, Robinson et al. 2005, Gill et al. 2009, Faith 2011, Gill et al. 2012). These results suggest that Holocene North American megaherbivore biomass was lower than the Pleistocene, and that those megaherbivore species that survived the end-Pleistocene extinctions did not replace the biomass of the extinct taxa (Barnosky 2008).

The existence of an association between *Sporormiella* abundances and megaherbivory is robust to the choice of response variable (both absolute concentrations and relative abundances of *Sporormiella*) and to the choice of predictor variable (grazed vs. ungrazed treatments, area grazed around traps, and grazing intensity), and does not appear to be an artifact of elevation or spatial autocorrelation. However, the form and strength of this relationship varies depending on whether relative (percentage) or absolute (concentration) abundances are used. The fact that concentration data shows the strongest response to bison grazing area suggests an effect of grazing on vegetation structure that may be influencing pollen accumulation rates for some taxa and hence partially confounding the relative abundance data.

Our work confirms prior reports that *Sporormiella* has a short dispersal distance (Raper and Bush 2009, Parker and Williams 2011). The presumed primary modes of transport in general are short-distance wind transport, slope wash and saltation; spores that enter Tauber traps are likely to be via wind, not water (Tauber 1974). These data suggest that the relevant source radius (Sugita 1994, Sugita et al. 2010) of *Sporormiella* is on the order of 25 m or less, which indicates that they are a very local indicator of the presence of megaherbivores in paleorecords.

Differences in the depositional processes of lakes and pollen traps affect which of these inferences may be extrapolated to lakes, and which may not. Pollen is released from the top of the canopy, after which it is transported some distance (the “source area”) and falls onto a surface (Prentice 1985, 1988). In lakes, pollen is mixed within the basin over seasons or even years before finally being incorporated into the sediment record (“pollen loading”) (Sugita 1993). Within lakes, the pollen source area includes both local and regional vegetation; as lake size increases, source area increases, because of the increased relative contribution of regional pollen (Sugita 1993, Davis 2000). Conversely, Tauber traps are non-volumetric sedimentary samplers with small (typically 5 cm) openings, and may be more susceptible to variations in wind speeds and surface turbulence and therefore pollen grain size and fall speed, which varies among taxa (Levetin et al. 2000). Because trap openings are very small relative to lakes, the source area of pollen is much more local for traps than for lakes (Tauber 1974, Hicks and Hyvarinen 1986, Sugita 1994). One standard assumption in the use of Tauber traps is that trap aerodynamics are designed to minimize collection biases among traps (Tauber 1974, Hicks and Hyvarinen 1986, Levetin et al. 2000). In this study, this assumption may be violated because bison grazing strongly affects vegetation structure (Fig. 2), with lower-stature grassland communities in the grazed areas, which could have some effect on the transport and deposition of pollen and spores to the trap.

At Konza, the observed differences between percent and concentration trends may be a phenomenon specific to the Tauber traps, which tend to collect both pollen and *Sporormiella* locally, as opposed to lakes, which have a mixture of local and regional pollen sources but presumably a local *Sporormiella* source area. It is also important to note that modes of pollen and spore transport differ between lakes and traps; most pollen in lake and trap records is be primarily wind-dispersed, while spores will be primarily dispersed by low-level wind in Tauber traps, and slopewash in lakes and mires. Therefore, while the quantitative link between increased *Sporormiella* abundances and bison grazing intensity reported here strengthens the use of the *Sporormiella* spores in pollen analysis, these results should not be extrapolated to the explicit conversion of *Sporormiella* abundances to bison grazing intensity or biomass around lakes.

An additional caveat is that the Konza study is based on bison herd sizes and behavior inside a managed enclosure, which may differ from bison populations and behavior in past ecosystems. While the bison abundances are carefully controlled at Konza to maintain sustainable herd sizes without supplemental feeding (Konza Prairie Research Program), the conditions bison experience at Konza differ from the paleorecord in that 1) bison at Konza are restricted in their ability to migrate seasonally or from year to year, and 2) bison were historically more abundant in short-grass prairie than in tall-grass prairie (Hill et al. 2006). One important test in resolving this question would be the replication of this study in short-grass prairie locations with lightly managed populations of bison, such as Yellowstone National Park or Teddy Roosevelt National Park.

Implications for Megaherbivory and Climatic Drivers of Holocene Vegetation Dynamics

These results suggest that *Sporormiella*, when combined with fossil pollen and other paleoenvironmental proxies, may aid recent inquiries into the significance of megaherbivory as a top-down regulator of vegetation dynamics during the Quaternary (Owen-Smith 1987, Gill et al. 2009, Johnson 2009, Gill et al. 2012) and the role of bison in the Holocene Great Plains in particular (Craine and McLauchlan 2004, Grimm et al. 2011). As one of the few survivors of the late Pleistocene megafaunal extinction event in North America (Koch and Barnosky 2006), Plains bison provide a rare opportunity to continuously study the interactions among vegetation, megaherbivores, and climate dynamics since the last deglaciation. At the end of the Pleistocene, bison were widespread across North America and occupied a range of habitat types. Both the range of bison and average body size were reduced during the mid-Holocene (from 8-6 ka BP to 2 ka BP), coeval with the expansion of C_4 grasses during warmer and drier climates (Hill et al. 2008). Like their modern counterparts, Mid-Holocene bison were matriarchal, and primarily grazers, with similar diets (Widga 2006). The diets of these mid-Holocene bison were similar to those found in the modern tallgrass prairie, and apparently little movement either seasonally (<50 km) or interannually (<500 km) over 4-5-year periods (Widga et al. 2010). Constrained ranges and the absence of evidence for large-scale seasonal migration suggests that resource availability was regular and predictable, even during the drier conditions that persisted during the mid-Holocene (Widga 2006). Given that the land-use patterns and dietary preferences appear to have been similar to modern bison, landscape use by Holocene and bison may have structured local grassland composition in similar ways (Fahnestock and Knapp 1994, Knapp et al. 1999, Collins and Calabrese 2012).

Several well-dated, high-resolution Great Plains lake sediment records record 100 to 160 year oscillations of drought variability during the early to middle Holocene (9.8 ka BP to 2.8 ka BP) (Clark et al. 2002, Nelson et al. 2004, Grimm et al. 2011). Dry periods are indicated by peaks in lake sediment quartz (produced by dust and enhanced erosion), while moister conditions are indicated by peaks in aragonite, caused by increased groundwater flow and solute delivery to the basin. Pollen records from these sites show increases in charcoal during moist conditions—fire is fuel-limited in the tallgrass prairie, and so charcoal production tends to be reduced during periods of drought (Camill et al. 2003, Nelson et al. 2006, Umbanhowar et al. 2006). These oscillations in moisture availability are recorded in the pollen record by high Poaceae abundances during wet intervals and high *Ambrosia* abundances during dry intervals. This pattern has been called the "*Ambrosia* paradox" (Grimm 2001) because shallow-rooted *Ambrosia* and other forbs are less able to compete with grasses for moisture and so would be expected to decline during dry periods. *Ambrosia* is a genus with twenty-four native species in North America, including both annuals and perennials and a wide range of growth forms including shrubs, but these types are generally not distinguishable in the pollen record. Fluctuations in the abundance of *Ambrosia* pollen has been linked to moisture availability (Grimm 2001), with higher abundances potentially indicating increases in bare ground during dry intervals (potentially caused by lower lake levels; Grimm et al 2011). *Ambrosia* pollen productivity may also reflect climatic conditions, because pollen productivity in ragweed is positively correlated with spring precipitation (though dispersal tends to be ineffective when relative humidity is >70%) (Payne 1963, Everitt et al. 2007, McLauchlan 2011).Grimm et al. (2011) hypothesized that increased moisture variability during drier intervals may have favored the expansion of *Ambrosia* by creating more disturbed habitat. Craine & McLauchlan (2004), however, proposed an alternative hypothesis that the observed *Ambrosia*-Poaceae cycles were instead driven by population dynamics in bison, in which periods of high bison grazing intensity suppressed Poaceae, favored *Ambrosia*, and reduced available fuels for fire. During the late Holocene (<4.5 ka BP), grass pollen and charcoal abundances increased at Kettle Lake, while *Ambrosia* abundances remained low in spite of the continued widespread distribution of bison on the northern Great Plains during this time (Grimm et al. 2011).

Although this study of recently deposited *Sporormiella* does not directly bear on these Holocene dynamics, the results here are consistent with the hypothesis that megaherbivory by bison may have contributed to the observed Holocene grass-*Ambrosia* cycles, because they indicates that the well-documented effects of bison megaherbivory on grassland composition (i.e., *Ambrosia psilostachya* increases on bison-grazed landscapes) can be transmitted to the palynological record (Fig. 5). However, the question remains: how can strong evidence that drought variations were closely linked to past grassland and fire dynamics be reconciled with the equally strong evidence that in contemporary systems bison grazing alone is a critical determinant of grassland community and function?

One possibility that combines elements of the Grimm et al. and Craine and McLauchlan hypotheses is that climate variability is regulating both bison populations and behavior and grassland composition during the Holocene, but bison act as a key mediator of the effect of climate on vegetation during dryer conditions. In this hypothesis, drought acts to alter the spatial heterogeneity of the effect of bison on grassland composition, while bison serve as a mechanism to enhance the relative abundance of *Ambrosia* during dry conditions, both by 1) reducing below-ground competition for water through selective removal of grasses, and 2) the production of wallows, which provide optimal *Ambrosia* habitat during intervals of water stress.

Periods of water stress are common in the prairie, and can enhance the effects of herbivory on vegetation (McNaughton 1983, Frank and McNaughton 1992). Grazing, wallowing and burning facilitate landscape heterogeneity by creating patches at different levels of disturbance (Collins and Calabrese 2012). Hence, drought may have altered the spatial scale of grassland patch dynamics, bringing bison—and therefore the patchy landscapes associated with bison activity—closer to potable lakes. During dry periods in the Holocene, lake levels across the Great Plains were reduced, and many lakes dried up when aridity was most severe (Digerfeldt et al. 1993, Valero-Garcés and Kelts 1995, Haskell et al. 1996, Laird et al. 1996). Periodic deposits of struvite, a phosphorous-rich mineral that is often associated with guano deposits, in sediments at Kettle Lake suggest that this lake acted as a refuge for migratory waterfowl, presumably because other shallower lakes were dry or severely lowered (Donovan and Grimm 2007).

A conceptual model outlines several testable hypotheses for the long-term relationships between bison (represented by *Sporormiella*), fire (charcoal), and vegetation (pollen) under different moisture conditions (Fig. 6). 1) In a landscape characterized by high bison population densities and high moisture availability (Fig. 6a), vegetation would be structured by high levels of grazing induced by high levels of forage availability, moderate fire activity (due to fuel reduction by grazing and the establishment of shifting patch mosaics), moderate abundances of *Ambrosia* and other forbs (facilitated by bison grazing, but suppressed because they usually cannot out-compete grasses for moisture and light except in disturbed areas), and possibly an increase in wetland and/or mesic taxa due to the persistence of wallows and ephemeral pools. 2) In a landscape characterized by high moisture availability but low bison population densities (Fig. 6b) more biomass would be available to burn, and so charcoal accumulation rates should increase significantly, while forbs should be even less abundant in the absence of structural mediation by grazers. The absence of wallows would reduce standing pools of water and disturbed patches, reducing heterogeneity, which should be reflected in a decrease in wetland and hydric/mesic plants in the pollen record. 3) During periods of drought, landscapes with high bison population densities should favor the expansion of forbs on bison-disturbed, compact wallows where they can out-compete for water with the deeper-rooted grasses (Fig. 6c). Fire activity should be greatly reduced compared to the high-moisture scenarios, due to the lack of available fuels. Reduced vegetation cover should be indicated by lower pollen accumulation rates. Depending on the seasonality of available moisture, a low bison-reduced moisture landscape may still support forb expansion, due to the presence of wallows and other soil disturbances. 4) Conversely, arid landscapes with low bison population abundances may have weakened disturbance regimes – both because of the low abundances of bison and because of low fuel loads for fire – and so may have reduced rates of soil disturbance, and therefore the least abundance of forbs, low charcoal, and reduced pollen influx due to low productivity (Fig. 6d). Note, however, that interannual drought variability may be an important disturbance mechanism facilitating *Ambrosia* expansion during arid times (Grimm et al., 2011).

This conceptual framework draws on elements Grimm et al. (2011) – who focus primarily on oscillations between high and low levels of moisture availability (6a,b vs. 6c,d) and heightened interannual variability to explain the observed oscillations, and on Craine & McLauchlan (2004)'s hypothesis that top-down controls by bison could explain the observed *Ambrosia*-Poaceae dynamics (though they do not explicitly rule out moisture as an influence). Of course, Holocene bison dynamics are presumably also driven in part by climate, both direct via moisture availability and indirectly via moisture controls on net primary productivity of vegetation.

These alternate hypotheses (climate control, megaherbivory control, and joint control) can be tested by multi-proxy analyses of Holocene lake sediments, focusing on *Sporormiella*, pollen, charcoal and paleolimnological indicators of drought. The above relationships should be manifested bothby within-lake variations in these proxies through time, and in between-lake variations across lakes that exhibited different moisture balances during the Holocene. If herds are tied to lakes that maintain fresh water during the driest portions of the mid-Holocene, then the *Sporormiella*, *Ambrosia*, fossil charcoal, and drought signals should vary across sites with different freshwater conditions (indicated by changes in lake salinity). Because the hydrology of Great Plains kettle lakes are strongly influenced by groundwater, lake position relative to the water table should have a strong effect on a given lake's moisture balance throughout the Holocene (Almendinger 1993). Two practical challenges to this approach will include 1) dating uncertainty that complicates comparisons of inter-lake variations, and 2) the possible sensitivity of *Sporormiella* to shoreline position (see: Raper and Bush 2009). A new generation of high-resolution pollen records in the Great Plains is providing new long-term records of Holocene climate variability in relation to drought; the addition of *Sporormiella*, which has historically been overlooked in the majority of pollen analyses, will allow for the explicit test of the importance of keystone megafaunal over millennial timescales.

Conclusions

Our results 1) demonstrate the first quantitative link between *Sporormiella* abundances and megaherbivore biomass, for both percentage and concentration data, 2) support a local (<100 m) relevant source area for *Sporormiella*, 3) show that high *Sporormiella* abundances can be linked to the sustained presence of megaherbivores, and that this signal is detectable above a background level contributed by mesofauna, 4) support (or slightly raises) the previously reported 2% threshold as a cutoff for megafaunal presence, and 5) establish that some of the well-documented effects of bison herbivory on vegetation can be seen in the pollen record.

This work supports the continued use of the *Sporormiella* proxy to test the relationship between megaherbivores and vegetation, an emerging discipline of paleoecology. A growing number of studies, including this one, suggest that biotic interactions like herbivory can leave a measurable signature in the paleorecord. Process-based models of the drivers of Quaternary vegetation dynamics should be expanded include megaherbivores, as well as interactions between megafauna and climate. The Holocene Great Plains were one of the few habitats in

North America to sustain large populations of megaherbivores following the end-Pleistocene extinctions, and therefore represent a unique opportunity to test hypotheses about the interactions between climate variability and keystone herbivores on vegetation dynamics at centennial to millennial timescales.

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Table 1 – Fauna at Konza Prairie (McMillan et al. 1997)

Order	Species	Status
Didelphimorphia	Virginia opossum (*Didelphis virginiana*)	Common
Insectivora	Elliot's short-tailed shrew (*Blarina hylophaga*)	Common
	Least shrew (*Cryptotis parva*)	Present
	Eastern mole (*Scalopus aquaticus*)	Present
Chiroptera	Big brown bat (*Eptesicus fuscus*)	Present
	Hoary bat (*Lasiurus cinereus*)	Present
Primates	Human (*Homo sapiens*)	Present
Carnivora	Coyote (*Canis latrans*)	Common
	Domestic dog (*Canis lupus*)	Present
	Red fox (*Vulpes vulpes*)	Present
	Domestic cat (*Felis silvestris*)	Present
	Bobcat (*Lynx rufus*)	Common
	Striped skunk (*Mephitis mephitis*)	Common
	Long-tailed weasel (*Mustela frenata*)	Present
	Least weasel (*Mustela nivalis*)	Present
	Mink (*Mustela vison*)	Present
	American badger (*Taxidea taxus*)	Common
	Raccoon (*Procyon lotor*)	Common
Artiodactyla	Mule deer (*Odocoileus hemionus*)	Occasional
	White-tailed deer (*Odocoileus virginianus*)	Common
	American bison (*Bison bison*)	Captive
	Cattle (*Bos taurus*)	Captive
Rodentia	Woodchuck (*Marmota monax*)	Occasional
	Thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*)	Common
	Fox squirrel (*Sciurus niger*)	Common
	American beaver (*Castor canadensis*)	Occasional
	Plains pocket gopher (*Geomys bursarius*)	Common
	Hispid pocket mouse *(Chaetodipus hispidus*)	Uncommon
	Meadow jumping mouse (*Zapus hudsonius*)	Present
	House mouse (introduced; *Mus musculus*)	Rare
	Prairie vole (*Microtus ochrogaster*)	Common
	Woodland vole (*Microtus pinetorum*)	Rare
	Southern bog lemming (*Synaptomys cooperi*)	Local

	Eastern woodrat (*Neotoma floridana*)	Common
	Deer mouse (*Peromyscus maniculatus*)	Common
	White-footed mouse (*Peromyscus leucopus*)	Common
	Western harvest mouse (*Reithrodontomys megalotis*)	Common
	Plains harvest mouse (*Reithrodontomys montanus*)	Rare
	Hispid cotton rat (*Sigmodon hispidus*)	Local
Lagomorpha	Eastern cottontail (*Sylvilagus floridanus*)	Common

Table 2 – Annual Bison Data

Year	# Collars (N_C)	Herd Size (N_H)	Herd Mass (M_H)	Average kg/Bison
2009	6	387	135,746 kg	350.77 kg
2010	11	349	118,209 kg	338.71 kg

Table 3 – *Sporormiella* source area

***Sporormiella* concentration**

Circle Radius (m)	R^2	Anova F	p-value	Spearman's Rho	p-value
25	0.263	12.124	0.001	0.727	<0.001
50	0.246	11.105	0.002	0.715	<0.001
100	0.210	9.064	0.005	0.693	<0.001
200	0.192	8.101	0.007	0.715	<0.001
300	0.198	8.415	0.006	0.711	<0.001
400	0.207	8.852	0.005	0.706	<0.001
500	0.215	9.286	0.004	0.704	<0.001

***Log Sporormiella* %**

Circle Radius (m)	R^2	Anova F	p-value	Spearman's Rho	p-value
25	0.460	28.295	<0.001	0.810	<0.001
50	0.452	28.016	<0.001	0.761	<0.001
100	0.397	22.377	<0.001	0.734	<0.001
200	0.358	18.993	<0.001	0.736	<0.001
300	0.360	19.200	<0.001	0.739	<0.001
400	0.360	19.151	<0.001	0.726	<0.001
500	0.343	17.724	<0.001	0.696	<0.001

Table 3 – *Sporormiella* and grazing intensity

Sporormiella concentration

Circle Radius (m)	R^2	Anova F	p-value	Spearman's Rho	p-value
25	0.546	40.835	<0.001	0.805	<0.001
50	0.454	28.276	<0.001	0.761	<0.001
100	0.414	24.063	<0.001	0.811	<0.001
200	0.247	11.160	0.002	0.666	<0.001
300	0.266	12.291	0.001	0.687	<0.001
400	0.238	10.597	0.003	0.695	<0.001
500	0.205	8.485	0.006	0.668	<0.001

log *Sporormiella* %

Circle Radius (m)	R^2	Anova F	p-value	Spearman's Rho	p-value
25	0.257	11.782	0.002	0.768	<0.001
50	0.287	13.465	<0.001	0.704	<0.001
100	0.377	20.588	<0.001	0.788	<0.001
200	0.354	18.612	<0.001	0.788	<0.001
300	0.362	19.262	<0.001	0.694	<0.001
400	0.378	20.635	<0.001	0.717	<0.001
500	0.338	16.874	<0.001	0.677	<0.001

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Figure 1: Map of Konza Prairie LTER

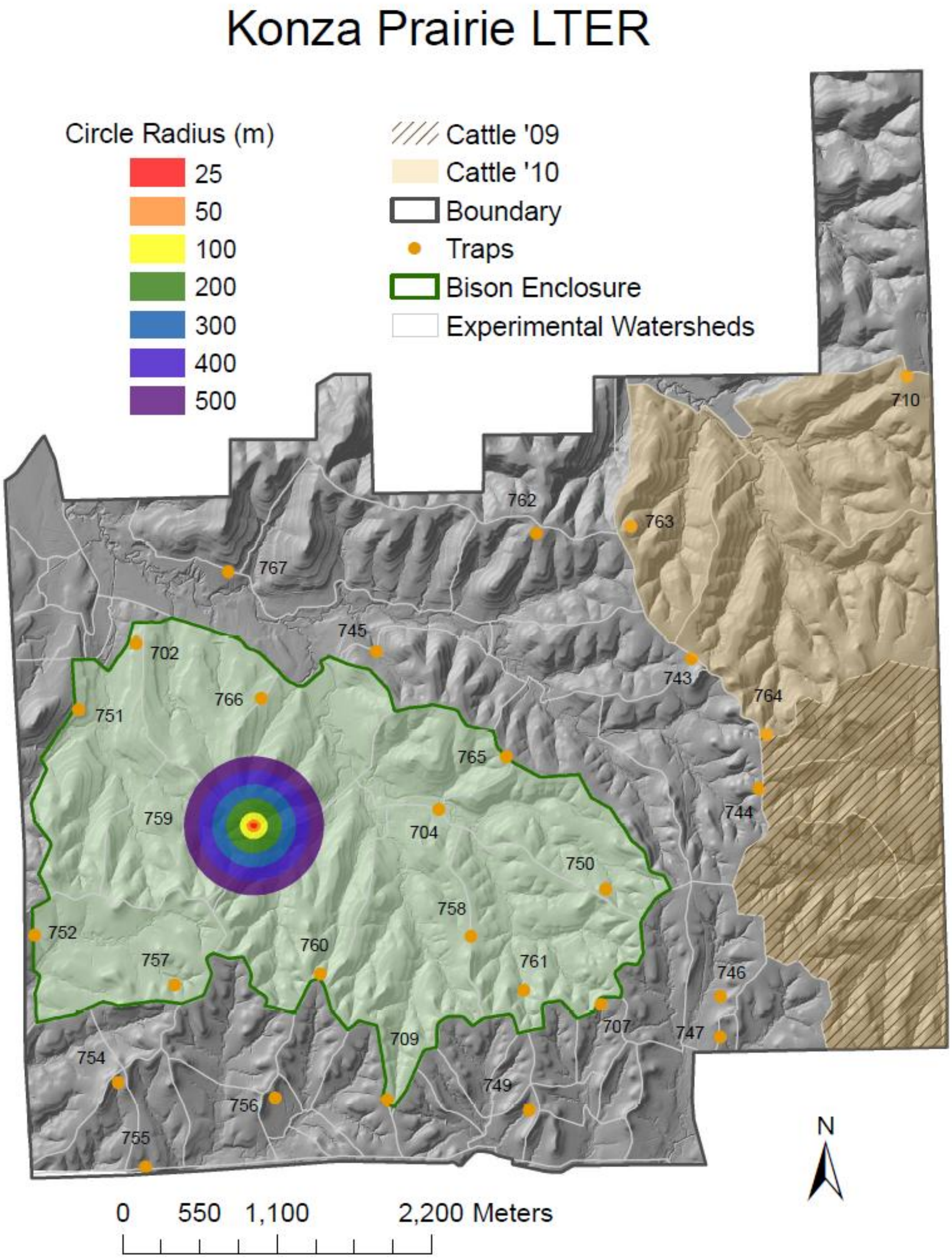


Figure 2: Konza Prairie LTER

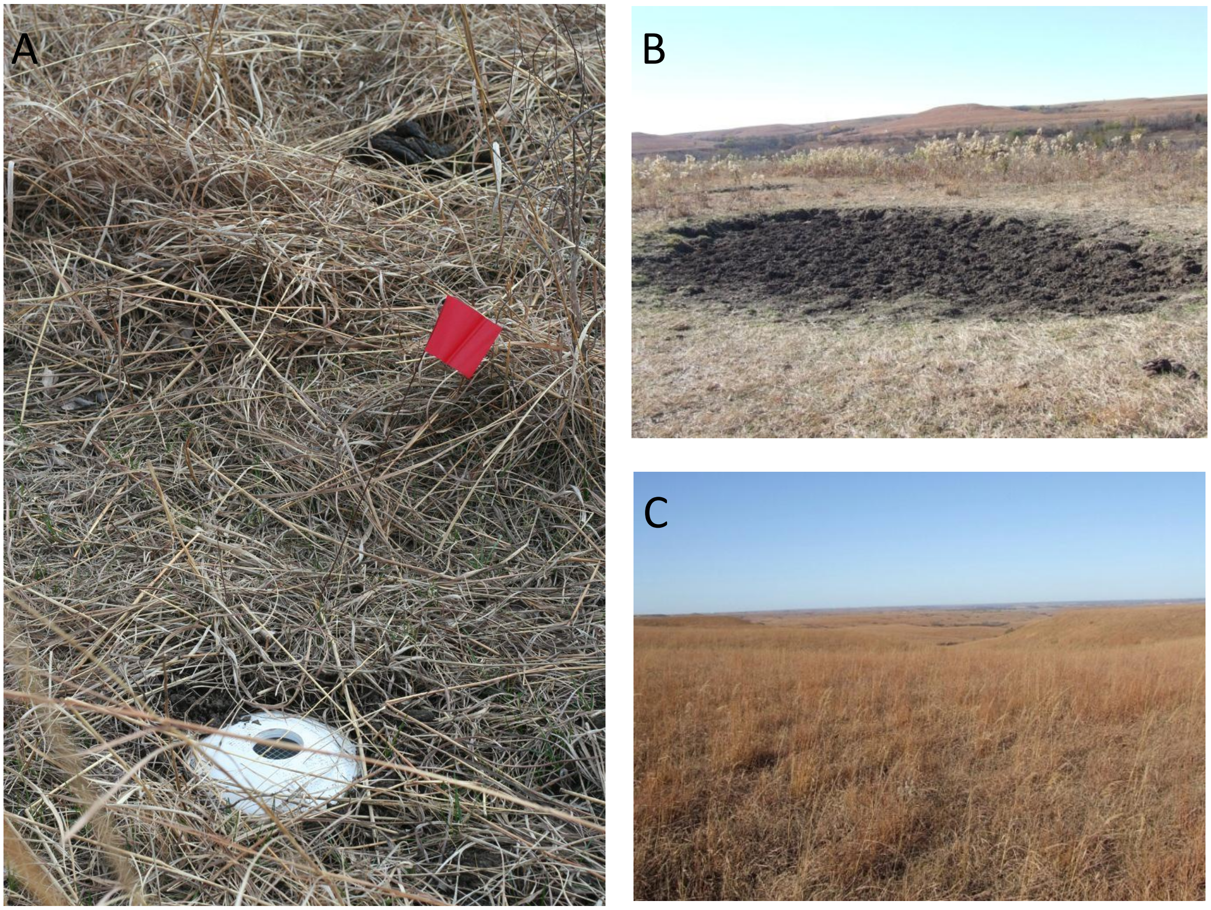


Figure 3: *Sporormiella* abundance by treatment

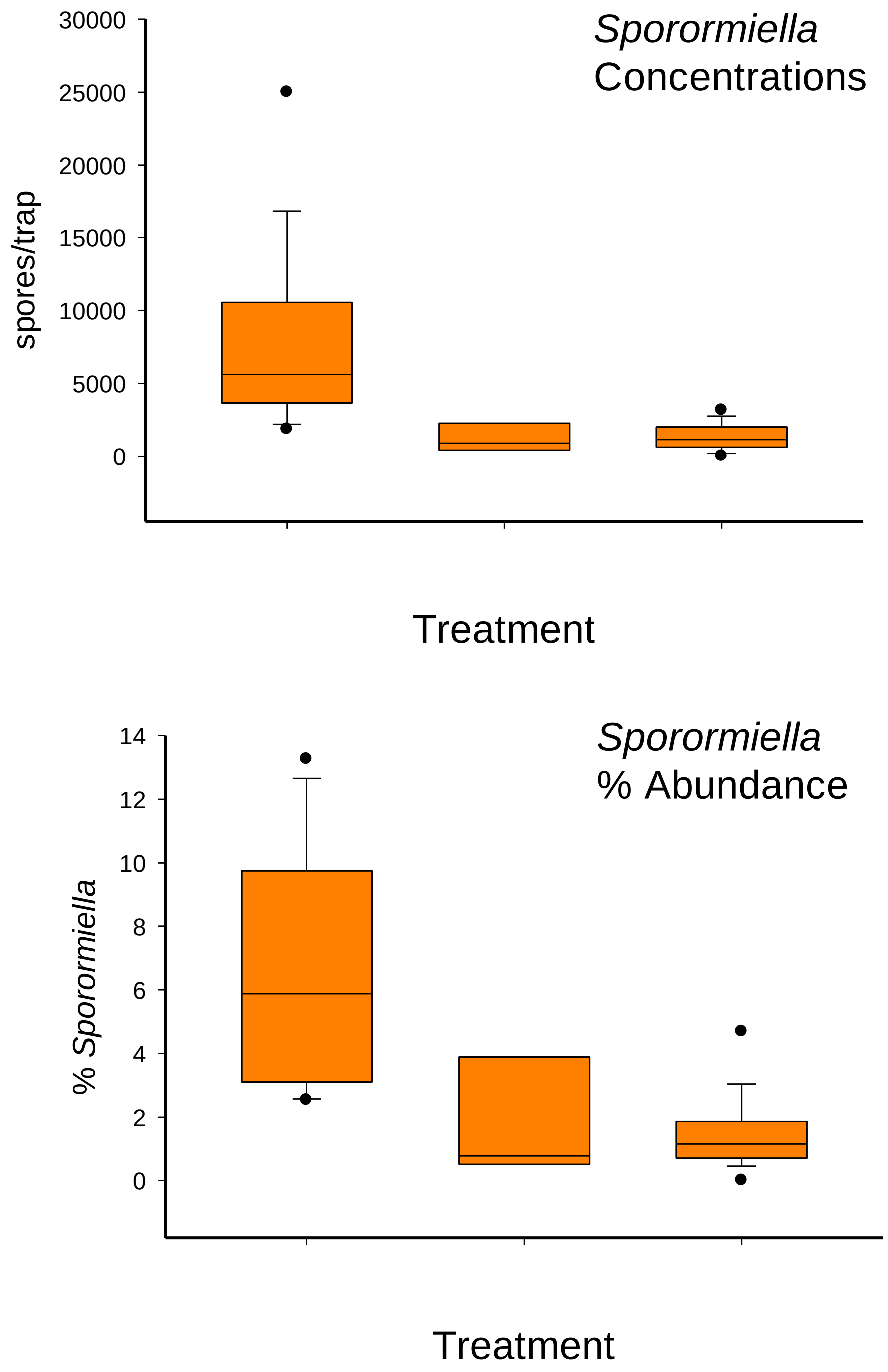


Figure 4: Receiver-operating characteristic analysis

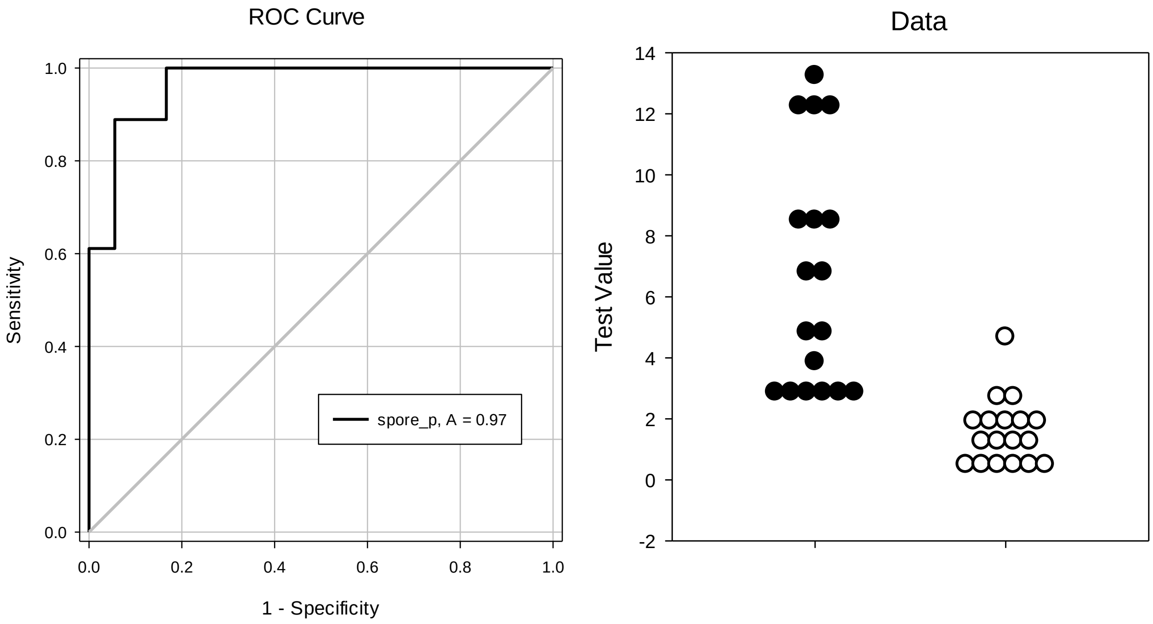
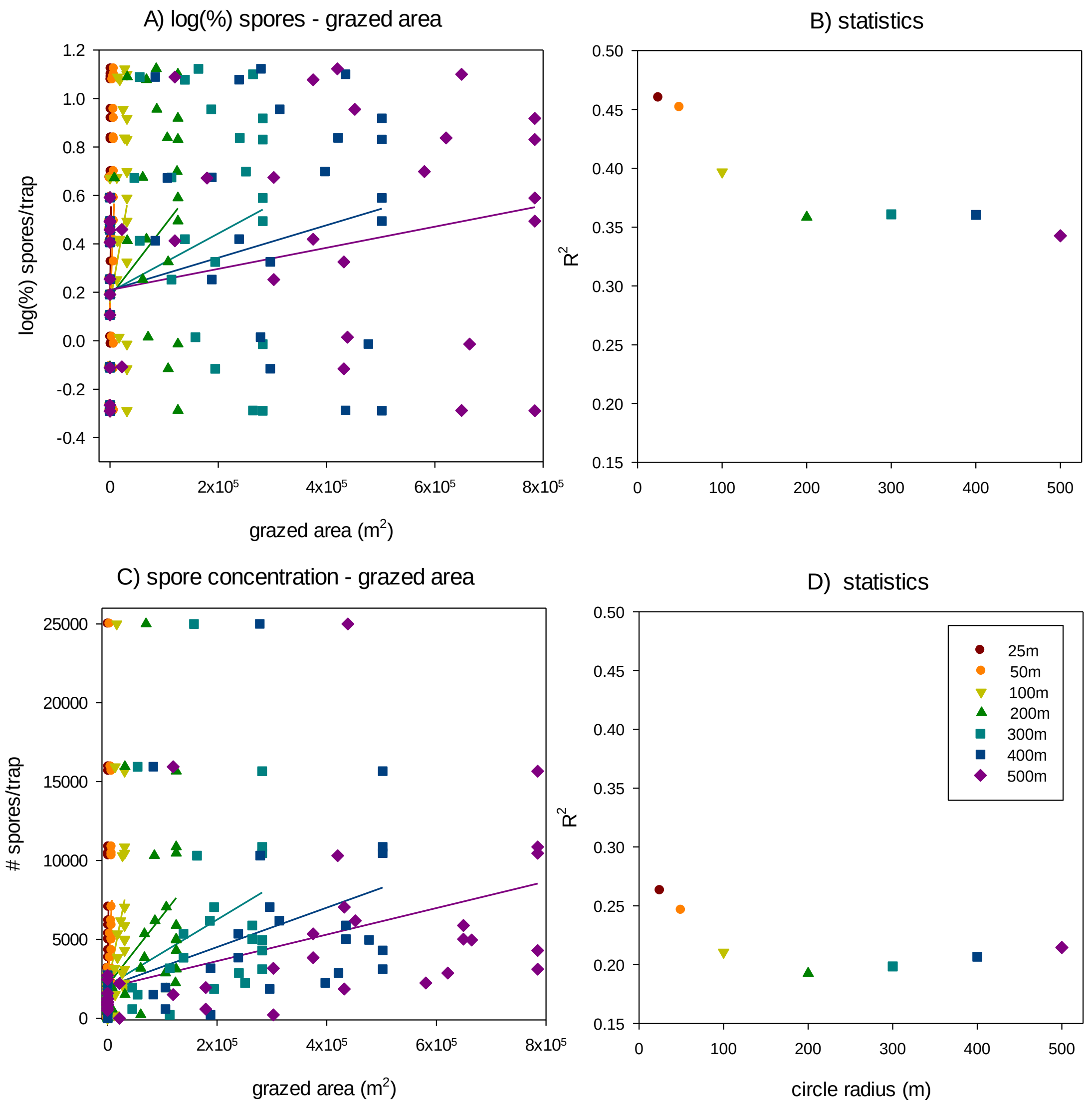


Figure 5: *Sporormiella* source area



● **OLS R²**

○ **rho**

Figure 6: *Sporormiella* and grazing intensity

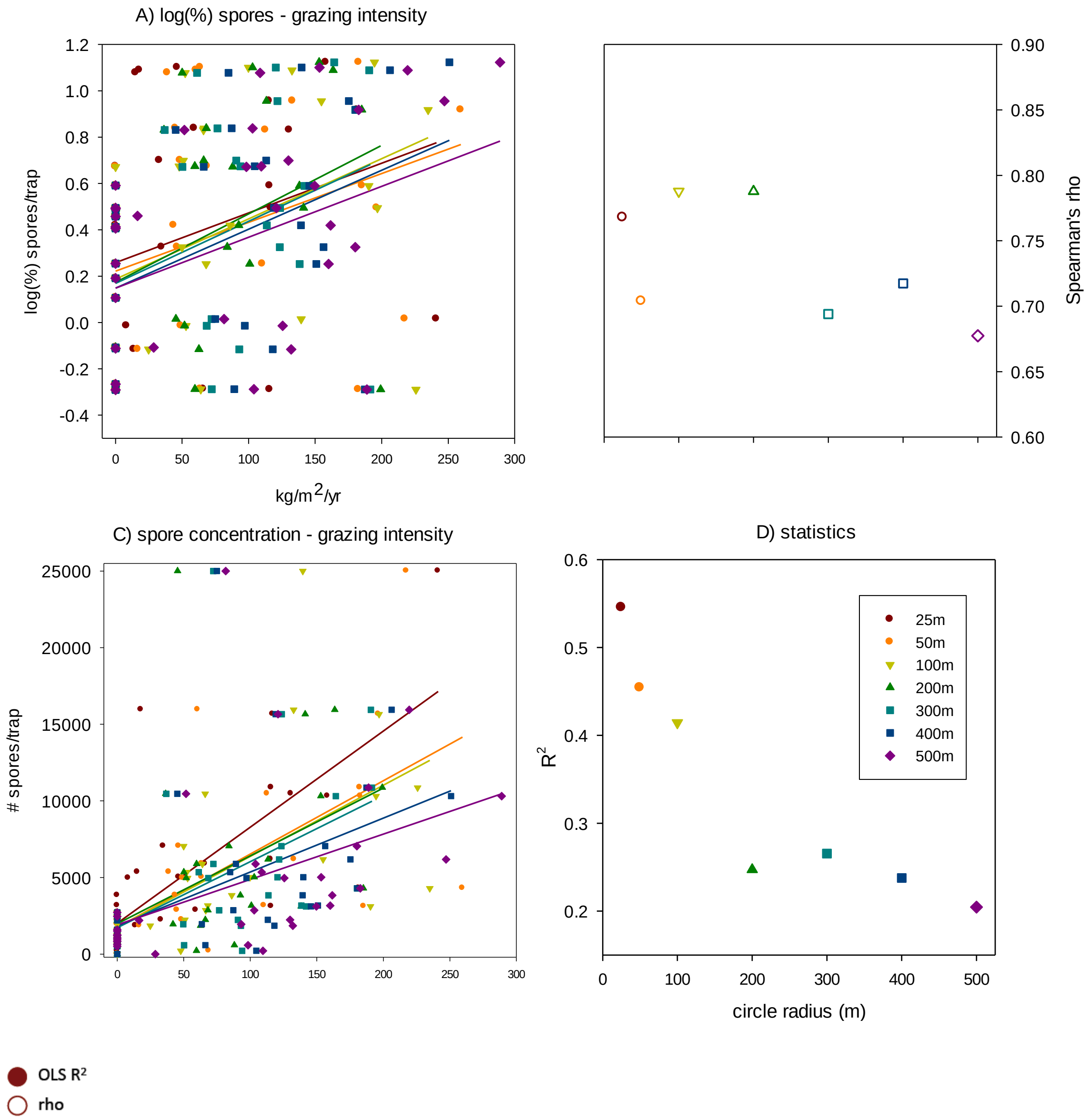


Figure 7: Poaceae abundance by treatment

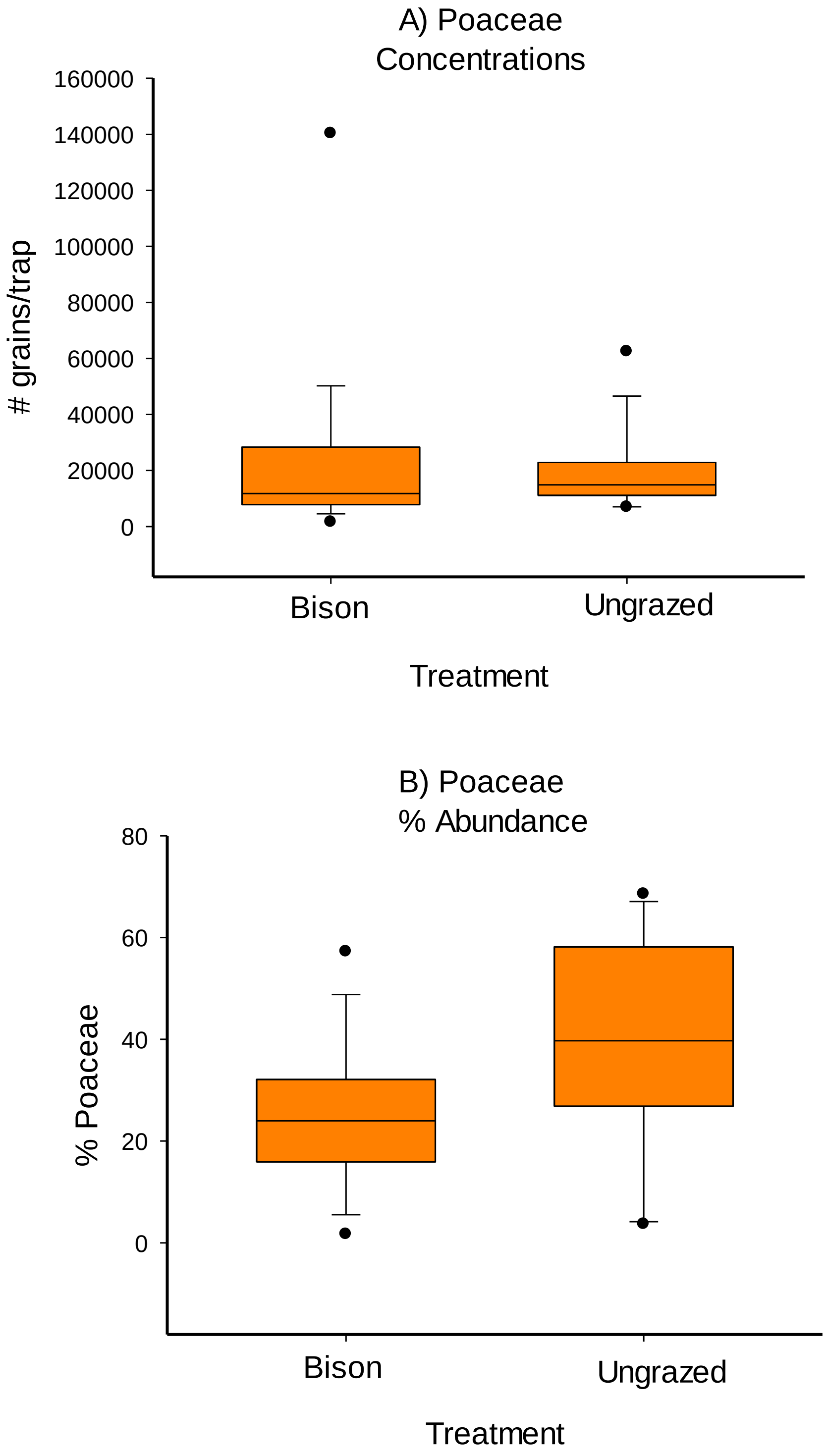
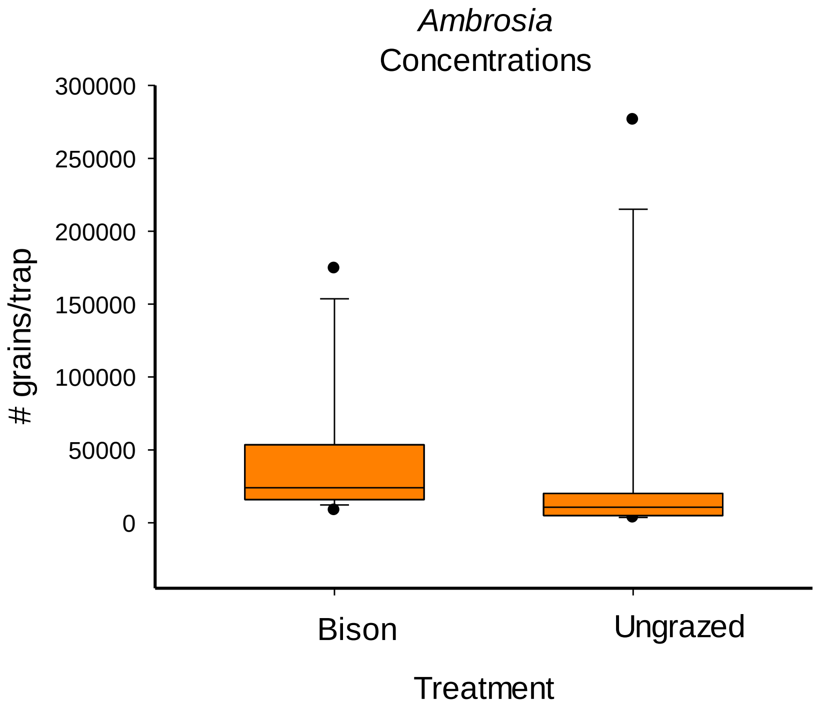


Figure 8: *Ambrosia* abundances by treatment



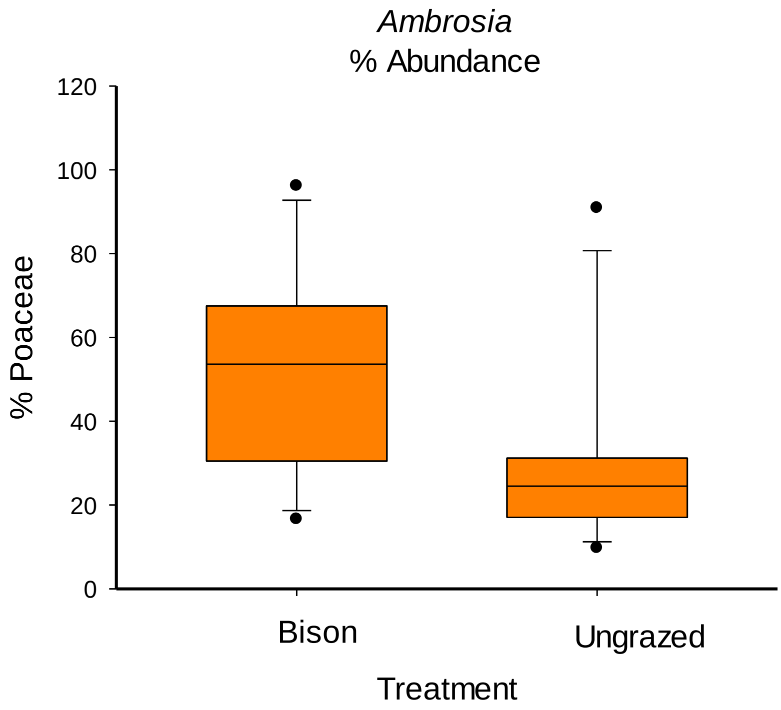
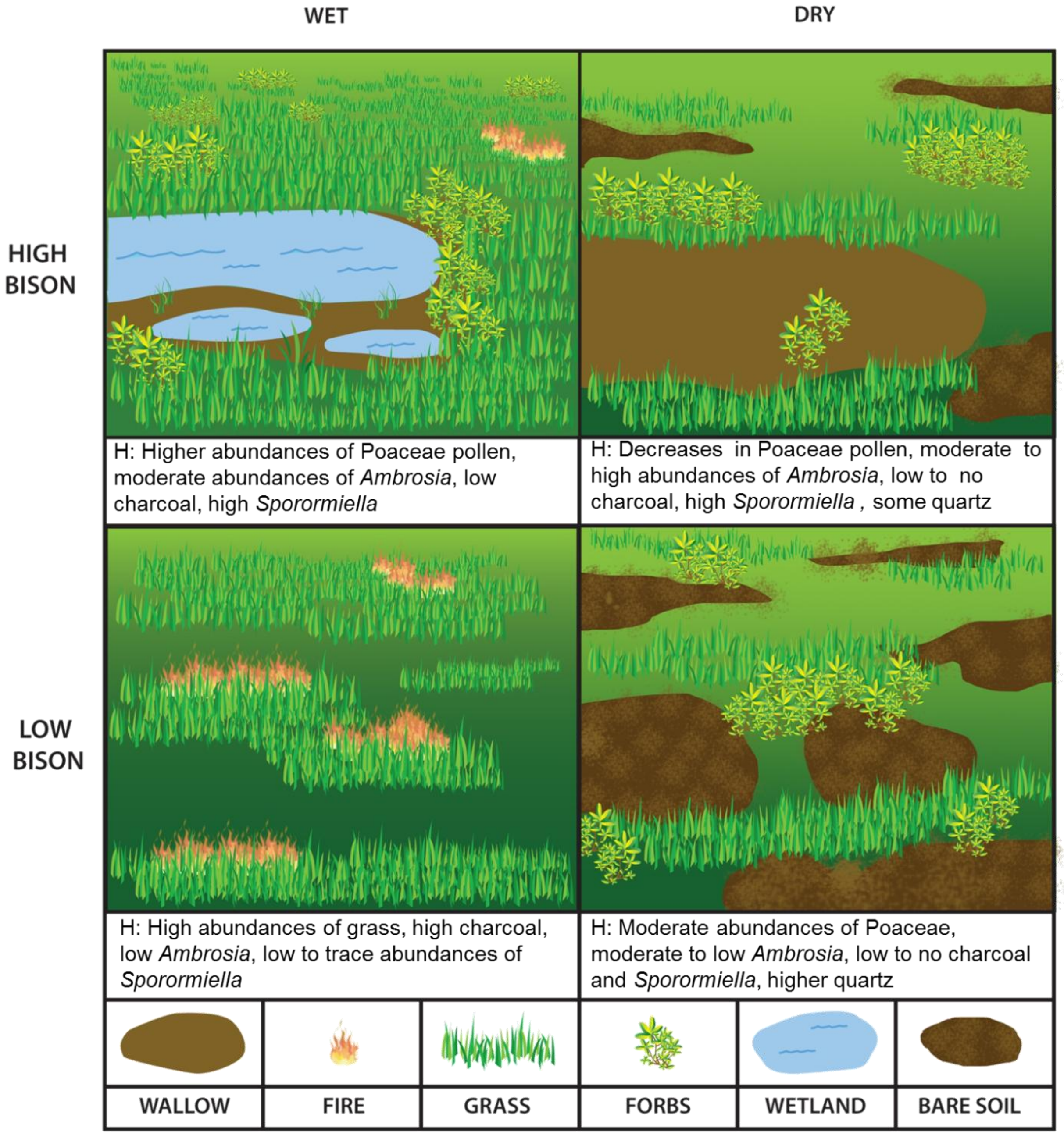


Figure 9: Conceptual diagram of bison-aridity-grass-*Ambrosia* dynamics



H: Higher abundances of Poaceae pollen, moderate abundances of *Ambrosia*, low charcoal, high *Sporormiella*

H: Decreases in Poaceae pollen, moderate to high abundances of *Ambrosia*, low to no charcoal, high *Sporormiella* , some quartz

H: High abundances of grass, high charcoal, low *Ambrosia*, low to trace abundances of *Sporormiella*

H: Moderate abundances of Poaceae, moderate to low *Ambrosia*, low to no charcoal and *Sporormiella*, higher quartz

Figure Legends

Figure 1: Map of the Konza Prairie Long-Term Ecological Research area. The bison enclosure is indicated by the green line and shading. Cattle area (orange) doubled between 2009 (brown hatches) and 2010. Numbered trap locations are indicated with orange dots. For traps near watershed divides, the position of the number indicates in which watershed the trap is located. Ring distances are color-coded to indicate increasing distances, using trap 759 as an example; this color scheme is also used to indicate ring distances in Figs. 4-5.

Figure 2: Photographs of Konza Prairie, including (a) a modified Tauber pollen trap with dung nearby, (b) a bison wallow on a grazing lawn, and (c) an ungrazed area outside the bison enclosure. Photo A was taken by Kendra McLauchlan; B and C were taken by Jacquelyn Gill.

Figure 3: Box plots of *Sporormiella* abundances by treatment. Relative (percent) abundance (a) and absolute concentrations (b) of *Sporormiella* from traps in bison, cattle, and ungrazed treatments. Mean *Sporormiella* values are significantly higher in bison-grazed than in the three cattle-grazed or twelve ungrazed plots. The extreme upper and lower whiskers represent the upper and lower range of *Sporormiella* values, respectively. The open circles represent outliers, which are calculated as less than Q1 - 1.5*IQR, or greater than Q3 + 1.5*IQR, where Q1 is the lower quartile and Q3 is the upper quartile, and IQR = Q3- Q1.

Figure 4: Receiver-operating characteristic analysis for determining an optimal threshold for *Sporormiella* abundance as a predictor of bison grazing. Area under the ROC curve is 0.97 (a).The optimal threshold of 2.8% maximized the area under curve, and equally weights sensitivity and specificity. (b) Data used in the ROC analysis, which include bison-grazed (black circles) and ungrazed (open white circles) but not cattle-grazed plots. The ungrazed sample with the highest *Sporormiella* value (>4%) is from Trap 743, which is located just outside a cattle-grazed watershed.

Figure 5: Regression analysis of *Sporormiella* abundances and grazed area at increasing circle distances from each trap. Each circle distance is indicated by a unique color and shape, with increasing distances represented by the progression of colors through the primary color spectrum. Both natural-log(%) abundance (5a) and concentrations (5c) of *Sporormiella* show a positive significant relationship with grazed area, but this relationship is strongest at the circle radii closest to the trap (5b and 5d, respectively). Relative abundance shows a stronger relationship to grazing area than concentration data.

Figure 6: Regression analysis of *Sporormiella* abundance and grazing intensity (kg/m^2/year) at increasing circle distances from each trap. Each circle distance is indicated by a unique color and shape, with increasing distances represented by the progression of colors through the primary color spectrum. Both natural-log(%) abundance (6a) and concentrations (6c) of *Sporormiella* show a positive significant relationship with grazed area. For relative abundance data, this relationship is not significantly different across circle radii, while concentration data

does show the strongest significant relationship between *Sporormiella* and grazing intensity closest to the traps (25 m).

Figure 7: Box plots of *Ambrosia* (a) and Poaceae (b) relative abundances (percent) by treatment. Mean *Ambrosia* values are significantly higher in bison-grazed than in ungrazed traps, while Poaceae abundances are higher in ungrazed traps. Figure format with respect to use of whiskers and open circles follows usage in Fig. 3. .

Figure 8: Box plots of *Ambrosia* (7a) and Poaceae (7b) absolute abundances (concentration) by treatment. Mean *Ambrosia* values are significantly higher in bison-grazed than in the ungrazed traps, while Poaceae abundances are lower, but not significantly so. Figure format with respect to use of whiskers and open circles follows usage in Fig. 3..

Figure 9: Conceptual diagram of *Ambrosia*-Poaceae-bison dynamics during the variable moisture regimes of the Holocene. Poaceae-*Ambrosia* competition should be mediated by bison in both wet and dry environments, due both to selective grazing and soil disturbances such as wallows.

CHAPTER 4

LATE-GLACIAL NO-ANALOG PLANT ASSOCIATIONS IN THE UPPER MIDWEST: LINKING PATTERN AND PROCESS

Abstract

The Pleistocene-Holocene transition in North America (17 ka BP to 8 ka BP) was a time of widespread ecological and climatic change. Humans arrived and 35 genera of megaherbivores went extinct during a time of rising temperatures and sea levels, melting ice sheets, and individualistic shifts in species' ranges. The widespread formation of novel plant associations during this interval is presumed to be the result of novel environmental conditions, but the relative importance of various proposed causal mechanisms remains unclear. I conducted a detailed review of late-glacial vegetation dynamics and no-analog plant associations in the Great Lakes region of the Midwestern United States, focusing on the time period from 17 ka and 8 ka BP. This synthesis is based upon seven well-dated and high-resolution pollen records, including new sites and re-cored classic sites. This improved timing suggests that the formation and disappearance of the no-analog associations in the Great Lakes is linked in part to millennial-scale climate variability in the Northern Hemisphere. I first use standard measures of palynological dissimilarity to describe the formation and disappearance of the no-analog plant associations, showing that they were more narrowly constrained in this region (14.5 ka BP to 11.8 ka BP) than reported in previous sub-continental-scale syntheses (17 ka BP to 11 ka BP). I describe the trajectory of communities in ecological space through time using nonmetric multidimensional scaling (NMDS), and then show how these no-analog communities emerged from individualistic taxon-level dynamics by providing detailed reviews of vegetation history at the level of individual pollen types. I then apply this information, in conjunction with the information about abiotic and biotic drivers of vegetation change, to understand global and regional drivers of late-glacial vegetation dynamics in the Great Lakes

and in particular the no-analog communities. My results show a distinct northwest-southeast time-transgressive pattern, as well as interregional phenomena within the no-analog interval. I argue that local site factors and periglacial conditions influenced the response of vegetation to extrinsic abrupt forcing, including megafaunal extinction and climate change, to produce particular novel plant associations that were unique to the Great Lakes region of the Midwest.

Introduction

The Pleistocene-Holocene transition in North America (17 ka BP to 8 ka BP; all ages are reported as calendar years before 1950) was a time of widespread and rapid ecological change, as plant species responded individualistically to changes in orbitally paced climates, retreating ice sheets, megaherbivore extinctions, and the arrival of humans (Figure 1). The progression from late-glacial to Holocene plant associations was primarily driven by the temperature rises and other climate changes accompanying the last deglaciation, which caused species to expand northwards from glacial refugia into newly deglaciated regions; species migrated individualistically and in dynamic equilibrium with climate at orbital timescales (Webb 1986, Williams et al. 2001) and with rapid responses to centennial- to millennial-scale climate variations (Williams et al. 2002). Within North America, the Upper Midwest has been a major focus for paleoecological research (Wright et al. 1963, McAndrews 1966, Wright 1968, Webb et al. 1983), because of its placement at the intersection of several major ecotones, the widespread availability of lakes suitable for paleoecological analysis, and the early demonstration from fossil pollen records of several major vegetation changes during and after the last deglaciation. Pollen records from this region (Wright et al. 1963, Ogden 1966, Shane 1987, Gonzales and Grimm 2009) consistently show a five-part sequence of major pollen zones that are broadly similar across sites, although sites differ in critical details with respect to both the timing of particular events and the behavior of individual taxa. 1) The first post-glacial pollen assemblages are dominated by *Picea*, *Larix* and *Abies*, with some deciduous types present in low abundance, and are presumed to indicate open parkland-like vegetation due to moderate-to high abundances of *Ambrosia*, *Artemisia* and Poaceae pollen. 2) As temperatures rose, *Picea* declined but remained present in lower abundances, while deciduous taxa (particularly *Fraxinus nigra*-type, *Ostrya/Carpinus*, and *Quercus*) expanded. 3) Many, but not all, pollen records show a temporary reversal with a second peak in *Picea* at some sites as well as peaks in *Alnus* and *Betula*, which is interpreted as a response to cooling during the Younger Dryas (Shane and Anderson 1993). 4) A brief interval of *Pinus* dominance spans the end of the Younger Dryas cold interval and the beginning of the Holocene (Shuman et al. 2002). 5) In response to Holocene warming, the decline of *Picea* and *Pinus* was associated with a rise in deciduous taxa, although *Pinus* remained abundant at the northernmost sites.

The second pollen zone in particular immediately attracted the attention of paleoecologists because these assemblages lack any close modern analogs, suggesting that they represent species associations unlike any found today (Winter 1962l, Wright et al. 1963, McAndrews 1966, Ogden III 1966). These associations were composed of unusual combinations of boreal (e.g. *Picea*, *Larix*) and temperate deciduous taxa (e.g. *Quercus*), lacked other taxa that are abundant in modern boreal forests (e.g. *Pinus*, *Betula*, *Alnus*), were marked by anomalously high abundances of certain deciduous pollen types, such as *Fraxinus*, and had a presumed parkland-like structure inferred from moderate abundances of herbaceous taxa such as *Artemisia* and *Ambrosia* (Grimm and Jacobson 2004, Jackson and Williams 2004). These no-analog communities extended from modern-day Minnesota into Ohio in the east, and as far south as Kentucky and Tennessee (Overpeck et al. 1985, Webb 1987, Overpeck et al. 1992, Williams et al. 2001). Within the no-analog region, vegetation dissimilarity from present was centered in the Upper Midwest from 17ka to 11ka BP, peaking at 15 ka BP and during an interval of high climatic dissimilarity from present (Williams et al. 2001, Williams and Jackson

2007). For this reason, hypotheses for the initiation and maintenance of late-glacial no-analog vegetation have focused on climatic drivers, which included more seasonal-than-present temperatures and insolation (Williams et al. 2001, Williams and Jackson 2007) and possibly wetter than present conditions (Gonzales and Grimm 2009). Recently, release from Pleistocene megafaunal herbivory following the late-Quaternary extinctions has been suggested as an additional potential driver (Gill et al. 2009, 2012). At Appleman Lake, IN and Silver Lake, OH, the formation of novel plant associations and an increase in fire activity immediately followed the local collapse of megaherbivore populations, recorded by the reduction of spores from the dung fungus *Sporormiella* in the paleorecord between 14.8 and 13.7 Gill et al. (2009, 2012). This suggests that the expansion of hardwood deciduous taxa, including *Fraxinus* and *Ostrya*, and increased fire activity at least in part caused by herbivory release and the buildup of landscape fuel loads, respectively.

Determining the drivers of the no-analog plant associations is complicated by the multiplicity of major concurrent climatic and ecological changes (Figure 1). The Pleistocene-Holocene transition marked the fundamental shift from a glacial regime characterized by colder and drier climates, ice-sheet influences and periglacial environments, reduced CO_2 concentrations, and the presence of megaherbivores, to an interglacial world with elevated CO_2, warmer climates, an amplified hydrological cycle, and the replacement of megafaunal biomass by humans (Barnosky 2008). This warming was interrupted by millennial-scale climate oscillations characterized by abrupt (decadal-scale) shifts in atmospheric circulation (Shakun and Carlson 2010, Clark et al. 2012). At the NGRIP ice core in Greenland, the onset of the Bølling interstadial is dated to 14,692 b2k (before AD 2000), and Younger Dryas-Preboreal transition has been dated to 11,703 b2k (Rasmussen et al. 2006). Several sites now suggest that the timing of these atmospheric changes in east-central North America lag the NGRIP chronology: at Crystal Lake, IL, rapid shifts in vegetation show a lag of 300 to 400 years (Gonzales and Grimm 2009) – which they argue is a lag too long to be explained by vegetation inertia given the rapid vegetation responses to Younger Dryas variations at sites adjacent to the North Atlantic (Williams et al. 2002, Birks and Birks 2008, Peros et al. 2008). This lag is also seen in a multiproxy record from White Lake, NJ (Fig 1), in which both ∂^{18}O and pollen records correlate to major changes at Greenland but with a few hundred-year offset (Yu 2007). Gonzales and Grimm (2009) hypothesized that the mediating effects of the ice sheet on regional climates, combined with a lag in the response of the ice sheet itself, contributed to this offset. Throughout this paper, I use the oxygen isotopic record at White Lake as the basis for the regional timing of the Bølling-Allerød and Younger Dryas events and use the terms "Bølling-Allerød$_{WL}$" and "Younger Dryas$_{WL}$" when referring to these events.

The millennial-scale oscillations in temperature observed during the Pleistocene-Holocene transition were accompanied by other major environmental. Insolation was more seasonal than present (Fig. 1), which likely enhanced the effects of continentality on the seasonal temperature range experienced by vegetation. CO$_2$ levels were up to 160 ppm lower than pre-industrial levels (Fig 1), and increased with step-like changes as temperatures warmed. The margins of the Laurentide Ice Sheet (LIS) were dynamic during this interval, with the overall retreat of the ice sheet punctuated by the re-advancement of various lobes at different times (Dyke 2004). Fossil midge assemblages and mesoscale climate models indicate the presence of strong temperature gradients spanning up to 240 km south of the LIS (Levesque et al. 1997, Bromwich et al. 2005). This temperature gradient may have locally enhanced precipitation as cold air from the ice sheet came in contact with a warmer land surface (Bromwich et al. 2005). Meltwater from the nearby ice sheets would also have influenced local hydrology, particularly through raised water tables, glacial lakes, and surface meltwater, and vegetation would have experienced dynamic post-glacial landscapes dominated by periglacial features such as permafrost and hummocky topography created by stagnant ice (Clayton et al. 2001, 2008).

During the same period, 35 genera of megafauna were extirpated from North America as part of a global wave of faunal extinctions, an event unprecedented in previous glacial-interglacial transitions (Koch and Barnosky 2006, Faith and Surovell 2009). Only nine megafaunal genera (*Alces*, *Bison*, *Cervus*, *Rangifer*, *Odocoileus*, *Antilocapra*, *Ovibos*, *Ovis*, and *Oreamnos*) survived in North America, as members of a now highly reduced functional guild of browsers and grazers. Like their modern counterparts, Pleistocene megafauna are thought to have exerted a significant influence on ecosystem structure, function, and community composition, in some cases acting as habitat keystones (Owen-Smith 1987, Gill et al. 2009, Johnson 2009). In North America, the late-Quaternary extinctions are increasingly thought to be caused by human hunting of naïve prey, perhaps in synergistic combination with climate-induced population reductions (Barnosky et al. 2004, Koch and Barnosky 2006, Lorenzen et al. 2011). Human arrival predated both the end-Pleistocene extinctions as well as the onset of the no-analog interval, with optically-stimulated luminescence and ^{14}C dating indicating presence of humans in North America by 15.5 ka BP (Waters et al. 2011), as well as some evidence suggesting human presence in the Great Lakes region as early as 16.5 ka BP (Fig. 1; Overstreet and Kolb 2003, Johnson 2006, Waters and Stafford 2007)

Linking the timing of the these biotic and abiotic drivers to the vegetation changes in the Upper Midwest has been hampered by poor radiocarbon dating in many classic pollen records, including the use of pre-AMS and bulk sediment dates, and by coarse pollen sampling resolutions (Grimm and Jacobson 2004). Early pollen diagrams were typically analyzed at a lower resolution than present (>10 cm), and so were not able to resolve abrupt events and millennial-scale oscillations (Shuman et al. 2002). This has inspired a new generation of recounted and re-dated pollen records, with higher sampling resolution and improved temporal control, including the major revision of chronologies and the identification of regional "benchmark" pollen records to anchor chronologies (Blois et al. 2011). Paleoecologists now have the opportunity to reexamine the major vegetation transitions of the Pleistocene-Holocene transition more closely, and to reassess the timing and regional patterns of the formation of the late-glacial no-analog plant associations and the dynamics of their constituent taxa. High-resolution, well-dated records allow for the analysis of 1) whether key ecological events were regionally synchronous (and at what temporal scale) or time-transgressive, such as in the response of vegetation in New England to Younger Dryas cooling (Shuman et al. 2002), and 2) whether they were synchronous with or lagged major climatic and biotic events (Fig. 1).

Methods

Site Selection

In order to describe the spatiotemporal patterns of the onset and demise of late-glacial no-analog vegetation and other aspects of regional vegetation history in the upper midwest, I selected seven sites in a northwest-southeast transect of the Great Lakes region of the

Midwest, roughly following the former southern margin of the Laurentide Ice Sheet (Fig. 2, Table 1). These sites are: 1) Kirchner Marsh, MN, a newly recounted and redated pollen record (this paper) from a classic pollen record that had one of the first descriptions of the no-analog pollen zone (Winter 1962); 2) Devil's Lake, WI, another classic site with a new chronology based on AMS dates of terrestrial plant macrofossils (Maher Jr. 1982, Grimm et al. 2009); 3) Crystal Lake, IL, a particularly well-dated record with 35 radiocarbon AMS dates (Gonzales and Grimm 2009, Blois et al. 2011); 4) Chatsworth Bog, IL, a recently recounted and redated pollen record from a classic site (King 1981, Nelson et al. 2006),; 5) Spicer Lake, IN, a new site (this paper); 6) Appleman Lake, IN, a recently published record with a well-expressed *Sporormiella* decline (Gill et al. 2009, Blois et al. 2011); and 7) Silver Lake, OH, a recently recounted and redated pollen record from a classic site (Ogden III 1966, Gill et al. 2012). Field and analytical methods are described here for the two sites with previously unpublished data, Kirchner Marsh and Spicer Lake; see the citations in Table 1 for more information about the other sites.

At Spicer Lake, IN (41° 62.37' N, 85° 21.36W, 293 msl), two overlapping sediment cores were taken from within several meters of one another at the deepest point of the lake in July, 2006, using a modified Livingstone piston corer from an anchored floating platform. The sediment-water interface was retrieved using a Bolivian adapter and polycarbonate tubing; florist's foam was inserted above the sediments to remove water and preserve the sediment-water interface. I then cored with steel-barreled Livingstone piston corers, first with 7.62 cm diameters and then with 5.08 cm. Recovery for each drive was >95% (using a 100 cm barrel) except for the basal drive (38 cm) which reached stiff glacial clays. Drives were measured and described in the field, then wrapped with plastic wrap and aluminum foil and encased in split

PVC tubes. All analyses were performed on Core A, which was the longest (1057.5 cm) and richest in plant macrofossils, and so was most suitable for radiocarbon dating and high-resolution pollen and charcoal sampling.

Kirchner Marsh (44° 50.00' N, 93° 07.00 W, 293 msl), cored in July, 2008, is currently a *Typha*-dominated wetland, but originally was a kettle lake that paludified in the early Holocene (Winter 1962). I probed the sediments to survey the depth of sediments in the marsh and identify a coring location. At the deepest position, I retrieved two overlapping cores (A and B) from within a few meters of one another using a modified Livingstone piston corer with a 7.62 cm barrel. All depths at Kirchner are reported relative to the marsh surface. Recovery for all drives was >95% (using a 100 cm barrel) except for the basal drive (68.8 cm), which ended in a thick (50 cm) layer of wood and needles above clay and poorly sorted sand and gravel, inferred as to be a “trash layer” formed by melting and collapse of stagnant ice (Wright and Stefanova 2004) overlying till. All analyses were performed on Core A, which was longer and included more macrofossils.

All cores were taken to the Lacustrine Core Facility at the Limnological Research Center (LRC) at the University of Minnesota, where the cores were split longitudinally, imaged, and scanned for bulk density and magnetic susceptibility. Working halves of each core were brought back to the lab at the University of Wisconsin where they were sliced into 1 cm “cookies” for sampling. Both halves have been kept in cold storage (>0 °C). The archive halves were not sliced into cookies, but were marked every 10 cm to monitor expansion and contraction while in storage; these and all unused portions of the working cookies have been stored in the LAC/CORE repository at the LRC.

All seven sites are kettle lakes, formed by debris-covered stagnant ice blocks abandoned with the retreat of the LIS. All sediment cores except the one for Spicer Lake extend to basal till and gravel, and Silver Lake, Kirchner Marsh, and Appleman Lakes contain presumed trash layers (Wright and Stefanova 2004). Thus all sites (except possibly Spicer Lake) provide the longest possible record of vegetation change following basin formation. However, these records do not necessarily extend back to the exact time of ice sheet retreat; debris-covered blocks of stagnant ice can persist for centuries or even millennia, particularly if buttressed by permafrost (Clayton et al. 2001, Clayton et al. 2008). The timing of basin formation and onset of sediment accumulation varies among sites, with the southern sites tending to begin earlier than northern sites. The sediment records at Kirchner Marsh, Devil's Lake (Maher Jr. 1982, Grimm et al. 2009), and Spicer Lake begin at ca. 14.5 ka BP, while Crystal Lake has a basal date of 16.3 ka BP (Gonzales and Grimm 2009). The southernmost sites, Chatsworth (Nelson et al. 2004), Appleman (Gill et al. 2009), and Silver Lakes (Gill et al. 2012), have sediment records that extend prior to 17 ka BP, with the oldest basal date of 18.7 ka BP at Silver Lake, consistent with relatively early ice retreat in Ohio and Indiana (Glover et al. 2011) . All sites appear to have continuously accumulated sediments since their formation, but this synthesis focuses on vegetation history from 17 ka to 8 ka BP. The redating at Devil's Lake was limited to the late Pleistocene and earliest Holocene (>9 ka BP), as was the pollen and charcoal sampling accomplished to date at Kirchner Marsh, Spicer Lake, and Silver Lake.

Chronologies

The chronologies for Appleman Lake, Silver Lake, Devil's Lake, Chatsworth Bog, and Crystal Lake are all from previous publications (Table 1). For Appleman Lake and Silver Lake, I used the original site chronologies (Gill et al. 2009, 2012). For Devil's Lake, Chatsworth Bog, and Crystal Lake, I used the chronologies described in Blois et al. (2011) and archived in the Neotoma paleoecology database (www.neotomadb.org). Blois et al. (2011) calibrated radiocarbon dates using IntCal09 calibration curve (Reimer et al. 2009) and fitted age models as splines in *Clam*.

At Kirchner Marsh, twelve plant macrofossils were submitted for AMS radiocarbon dating and all dates were used to constrain the age model (Table 2). At Spicer Lake, sixteen samples were submitted for AMS radiocarbon dating: eight pieces of wood from terrestrial plants, six samples from charcoal picked from terrestrial plant materials, and two dates from fossil pollen extracts. Several charcoal samples from Spicer Lake were small (<5 micrograms of carbon) and yielded anomalously young dates compared to the other dated materials. The two pollen dates from Spicer Lake (see Gill et al. 2009 Supplemental Online Material for the pollen extraction methods) are several thousand years older than the wood dates from similar depths. I believe that the pollen dates are anomalously old due to contamination from algae (particularly *Pediastrum*), which can incorporate radiocarbon-depleted carbon from hard water (MacDonald et al. 1991). I also use the local biostratigraphic date of the *Picea* decline (11560 ka +/- 55 BP) to help constrain the age model at Spicer Lake, which is supported based on the site's close proximity to several of the benchmark sites identified by Blois et al. . This borrowing of strength means, however, that the age model used for Spicer is not fully independent of the age models at other sites.

All dates were calibrated and an age model was constructed (Fig. 3) using the Bayesian age model program *Bacon* in R (Blois et al. 2011), which calibrates dates according to the IntCal09 calibration curve (Blaauw and Christen 2011). To construct an age model, *Bacon* iteratively samples from the probability density function of each calibrated age to fit a number of splines, discarding fitted splines that violate the assumptions of stratigraphic ordering of dates and linear sedimentation (though age reversals and hiatuses may be identified by the user). Given these prior assumptions, Blaauw and Christen (2009) recommend that the user include all ages in a Bayesian age model, including anomalous dates, because the presence of outliers does not change the maximum likelihood spline fit but will influence the uncertainty around that estimate. This is the case for the charcoal-based dates, which were rejected by *Bacon* as inconsistent with the other available age constraints. However, at Spicer Lake, the pollen dates result in basal age estimates that are too old based on the regional vegetation record, and so were removed from the final age model based on the rationale described above. *Bacon* requires prior estimates of the mean sedimentation rate, or acc.mean. Users must also specify the section length of the piecewise-calculated splines, which determines the flexibility of the age model and its ability to accommodate changes in sedimentation rate. Based on the sedimentation rates from other late-glacial/early Holocene cores in the region (Gill et al. 2009, Blaauw and Christen 2011, Gill et al. 2012), I used a prior estimate of a mean accumulation rate of 30 cm/year for both cores, and used a section length of 28 cm for Spicer and 50 cm for Kirchner (indicated by the apparent fewer changes in sedimentation rate based visual examination of the lake sediment). *Bacon* estimated all other parameters, including the shape of the gamma distribution of the accumulation mean (acc.shape = 2) and the mean and strength of the memory parameter, which sets the relative influence of previous sections on each calculated section. For Spicer, acc.shape = 2, mem.strength = 4, and mem.mean = 0.7. For Kirchner, acc.shape = 2, mem.strength = 4, and mem.mean = 0.7. I did not extrapolate the age model beyond the available age controls, so data from undated portions of the core are not reported here. *Bacon* outputs a maximum likelihood age estimate at 1cm intervals from the population of individual splines; these were then interpolated to pollen and charcoal sample depths using the *Approx* function in R.

Pollen & Charcoal analyses

See the publications referenced in Table 1 for a description of the methods for laboratory analyses at Devil's Lake, Chatsworth Bog, Crystal Lake, Appleman Lake, and Silver Lake. Pollen samples for Kirchner Marsh and Spicer Lake were processed using a modified version of standard methods based on Faegri & Iverson (2009), as reported in Gill et al. (1989); charcoal samples were prepared based on a modified version of Whitlock and Larson (2012) as reported in Gill et al. (2001).

For this study, I describe vegetation history based on selected pollen types, with particular emphasis on taxa that shed light on the causes, nature, and ultimate demise of the late-glacial no-analog plant associations. Full pollen diagrams for Kirchner Marsh and Spicer Lake are available in the supplemental online material. Full pollen records from all sites are available in the original publications (Table 1) and at the Neotoma Database (www.neotomadb.org).

Numerical Analyses

The minimum vegetation dissimilarity from present was calculated for each sample for all sites using the *analog* (Gill et al. 2012) program in Matlab (Williams and Shuman 2008) and using the squared-chord distance (SCD) metric (MathWorks 2010). Squared-chord distance is a signal-to-noise metric, which balances under- and over-represented pollen types, and has been demonstrated to be more effective for paleoenvironmental inferences in modern-analog analysis than either unweighted or equal-weight metrics (Overpeck et al. 1985). I used a threshold of 0.3 to indicate no-analog samples, as is appropriate for continental-scale matches with the number of taxa (54) I used in the analysis (Gavin et al. 2003). Each fossil pollen sample was compared with a subset of 2259 samples from the North American Modern Pollen Database (Williams and Shuman 2008); to avoid false analogs due to low taxonomic resolution, I excluded from this analysis all modern samples containing western North American taxa (Thompson et al. 2000, Whitmore et al. 2005). Fifty-four upland plant taxa were used in the SCD analysis (Appendix 1). Because *Pinus* was not discriminated at the sub-genus level in all modern samples (although *P*. subg. *Pinus* and *P*. subg. *Strobus* were discriminated in all fossil pollen records except Devil's Lake), I used total *Pinus* in the analog analyses. For this analysis I used the average of the ten closest best analogs.

Charcoal analyses were performed using CharAnalysis v.1.1 for Matlab (Williams et al. 2006, Higuera et al. 2009, Higuera et al. 2010), in order to separate peak components from the background influx of charcoal. Charcoal data were converted to accumulation rates (CHAR) by multiplying concentrations (particles per cubic centimeter) by the estimated sedimentation rate for each 1 cm sample (the difference of the age of the top and bottom of each centimeter, as interpolated from the Bacon age model). CHAR values were interpolated to the coarsest sampling resolution for each core to account for uneven temporal sampling caused by core breaks and variations in sedimentation rates. Each CHAR time series was decomposed to identify peaks, which are interpreted to indicate one or more fire events in the watershed (Clark et al. 1996, Kelly et al. 2011). To calculate background CHAR, a LOWESS smoother was applied to each time series with a 700-year moving window. CharAnalysis identifies peaks using a locally-fitted Guassian mixture model; each peak is then tested for significant difference from the smallest non-peak in the preceding five samples using a modified two-sample Poisson test on the original, pre-smoothed concentration data (particles/cm3) (Whitlock and Millspaugh 1996).

Nonmetric multidimensional scaling (NMDS) analysis (Kruskal and Wish 1978, Higuera et al. 2009), was used to compare the late-glacial pollen assemblages to those in the North American Modern Pollen Dataset. NMDS non-linear ordination is well-suited to ecological data, that iteratively searches for the best positions of *n* entities on *k* predetermined axes. The resultant positioning minimizes the stress of the *k*-dimensional configuration (“stress” is the measure of departure from monotonicity in the relationship between the dissimilarity in the original matrix versus that of the ordination space). First, a pairwise distance matrix was calculated among all fossil (limited to samples between 8 ka BP to 17 ka BP at the seven sites) and modern samples, using the *matrix* function in R and squared-chord dissimilarity as the distance metric. The ordination was calculated with two dimensions and 9999 permutations, using the *isoMDS* function in the MASS library in R (Clarke 1993). The correlation between the abundance of each taxon and the NMDS values was calculated for Axes 1 and 2 in R using the *cor* function. The NMDS value for each modern site was then plotted and spatially interpolated using inverse distance weighting in the SpatialAnalyist Toolkit in ArcGIS.

Results

Minimum Vegetation Dissimilarity

Prior to 14.5 ka BP, SCD values are generally <0.3, with close modern analogs found in the boreal parklands of Canada (Fig. 4). By 14.5 ka BP, however, minimum vegetation dissimilarity from present increased above the 0.3 no-analog threshold, first at Chatsworth Bog, then at 14.2 ka at Crystal Lake, and followed by abrupt increases at Crystal, Appleman, and Silver Lakes from 14.0 ka to 13.7 ka BP. At Spicer Lake and Kirchner Marsh, which have later onset dates (14.0 and13.4 ka BP), SCD values are well above 0.3 for the lowermost pollen assemblages. At all sites, SCD values peak at >0.6, reaching the highest values (0.8) at Crystal Lake. Sites vary in the timing of the decline in SCD values, and in whether that transition was abrupt (Kirchner Marsh, Devil’s Lake, Spicer Lake, Appleman Lake) or gradual (Chatsworth Bog, Crystal Lake, and Silver Lake). For most sites, SCD values continued to decline into the early Holocene, with occasional excursions >0.3. Chatsworth Bog, Crystal Lake, and Silver Lake show a second weak peak in SCD >0.3 at 11.0 ka BP. At Spicer Lake, SCD values decline abruptly, but then remain high relative to other sites, remaining near or just above 0.3 until 8 ka. Across all sites, peak SCD values occur from 14.5 to 11.8 ka BP. The onset of this no-analog interval appears to be time-transgressive from west to east (within <1 ka), while the decline appears broadly synchronous across sites but differing in rate (Fig. 4).

Individual Taxa

In this section, I describe vegetation history across sites for selected pollen taxa, using both time series of relative pollen abundances (Figs. 5-10) to highlight temporal patterns and compositional maps (Figs. 12a-12e) to highlight spatial patterns in composition. At all sites, *Picea* is the most abundant (50 – 80%) pollen type in the basal sediments (Fig. 5). The transition from high *Picea* abundances to high *Quercus* abundances, with an intermediate period of high *Pinus* abundances in eastern North America corresponds to their spatial zonation in eastern North America at present, and can be understood as a series of plant associations forming in response to rising temperatures (Venables and Ripley 1999). The timing of the *Picea* decline varies across sites, as does its overall trajectory. *Picea* declines first at Chatsworth Bog (14 ka BP), then at Crystal, Silver, and Appleman Lakes (14 ka to 13. 8 ka BP), followed by declines at Spicer, Kirchner, and Devil's Lakes around 11.5 ka BP. At Crystal, Silver, and Appleman Lakes, *Picea* exhibits four stages: 1) high abundances during the late Pleistocene, 2) moderate abundances (15-40%) during the no-analog interval, 3) a second peak (Crystal and Silver Lakes only) and 4) declines during the early Holocene. At Kirchner Marsh, Devil's Lake, and Spicer Lake, at which the dated sediment record begins near or within the no-analog interval, *Picea* abundances remain fairly steady (40-60%) throughout the no-analog interval, until declining at 11.5 ka BP, coeval with the onset of the Holocene. At the southwesterly Chatsworth Bog, however, *Picea* is never a major component of the no-analog assemblages, and the *Picea* decline occurs at 14.3 ka BP, near the beginning of the no-analog interval.

Almost all sites show a brief interval of high *Pinus* abundances, generally beginning ca. 12 ka or a bit later, i.e. during the Younger Dryas$_{WL}$ or near its end. At the northernmost sites (Kirchner Marsh and Devil's Lake), *Pinus* establishes between 11.8 ka and 11.5 ka BP, but remains a larger component of the vegetation going into the Holocene than the sites further to the south and east. Chatsworth Bog in the southwest lacks a *Pinus* phase entirely. Crystal, Spicer, Appleman, and Silver Lakes each have a distinctive zone of high *Pinus* abundances from >12 ka to 10.5 ka BP, encompassing the end of the Younger Dryas and the early Holocene. At all sites, *Pinus* remains present at low abundances into the Holocene. *Quercus* establishes in a time-transgressive pattern from west to east, and is most important as a component of the vegetation at Chatsworth Bog, Crystal Lake, and Appleman Lake. *Quercus* establishes initially at Spicer and Crystal Lakes, but gradually, while at Appleman and Silver Lake, the increase in *Quercus* is more rapid at 12 ka BP. At the northernmost sites, *Quercus* increases at or after 11 ka BP, and is a minor component of the vegetation.

Fraxinus nigra-type and *Ostrya*-type pollen are two of the main deciduous components of the no-analog assemblages (Fig. 6). *Fraxinus* is an important component during the no-analog interval at all sites, but its history varies strongly among sites (Figs. 12a-12e). *Fraxinus* is a present in low-to-moderate abundances (2-10%) at Chatsworth Bog, Crystal Lake, and Appleman Lake as early as 17 ka BP. *Fraxinus* reaches its highest abundances at Chatsworth Bog (peaking above 50%) and Crystal Lake (30%) from 14 ka BP to 13.5 ka BP. With the exception of

Kirchner Marsh, *Fraxinus* is most abundant in the western sites, particularly those closest to Lake Michigan, decreasing in importance to the south and east. At Devil's and Crystal Lakes, *Fraxinus* has a second period of abundance from 11.5 to 10.3 ka BP, during which abundances of *Fraxinus* match or exceed those during the no-analog interval (18-20%). However this second peak occurs in association with high abundances of other deciduous taxa and *Pinus* and low abundances of *Picea,* keeping SCD values <0.3. At all sites except Kirchner Marsh, *Fraxinus* remains present at moderate to low (~5%) abundances into the Holocene. *Ostrya*-type pollen is generally more abundant in the southeastern half of the transect than in the northwestern sites. In the southeastern sites, the association between Fraxinus and Ostrya-type varies over time. During the no-analog interval, *Fraxinus* and *Ostrya*-type pollen abundances behave in a largely synchronous manner, but after 11ka, their abundances are uncorrelated. *Fraxinus nigra* is very shade-intolerant, while *Ostrya virginiana* is highly ranked with regard to shade for its ability to persist under climax canopies, aggressively reproducing when released from the understory (Grimm and Jacobson 2004).

Ulmus is present in low (~5%) abundances during the no-analog interval, increasing first at Kirchner Marsh, Appleman and Devil's Lakes at 11.5 ka BP, then at Spicer Lake at 11.0 ka BP, and finally at Chatsworth Bog and Silver Lake between 11.0 ka BP and 10.5 ka BP (Fig. 7). At Kirchner Marsh, Chatsworth Bog, and Crystal Lake, where *Ulmus* reaches its greatest abundances, the *Ulmus* phase lasts from 11.5 to 9.0 ka BP, with a gradual decline in *Ulmus* over this period (though *Ulmus* appears to be on the rise again at Kirchner Marsh), while at Spicer, Appleman, and Silver Lakes, *Ulmus* appears to expand and become incorporated into the existing deciduous forest, maintaining steady abundances thereafter. *Fraxinus nigra* and *Ulmus* *americana* are commonly found together today (Fowells 1965). Interestingly, the increase in *Ulmus* at 11.5 ka BP appears to be driven by early Holocene warming, and yet is present at only low abundance during the Bølling-Allerød$_{WL}$, believed to also be characterized by relatively warm climates in the Northern Hemisphere. The presence of *Ulmus* is sufficient, in combination with *Picea* and other deciduous taxa, to drive up SCD values during the no-analog interval, but it is not a major component, never reaching the high abundances of *Fraxinus* or *Ostrya*-type pollen in the southeastern sites. *Ulmus americana* is found throughout eastern North America today in a wide range of climates, but is more commonly found on flats and bottom lands, preferring well-drained loams (Fowells 1965). Growth is poor when the summer water table is high, which supports the hypothesis that the no-analog communities were wetter than present.

Both *Larix* and *Salix* were present at all sites during the no-analog interval until 11 ka BP (Fig. 8). Both *Salix* and *Larix* are commonly found together in modern bogs and water-logged soils (Fowells 1965), but *Larix* tends to be found in colder environments while *Salix* species have a wider aggregate climatic distribution (Fowells 1965). They show different histories during the no-analog period. At most sites, *Larix* appears to be more abundant before and after the no-analog interval, except at Kirchner Marsh and Spicer Pond. Conversely, *Salix* abundances tend to be higher during the period of no-analog vegetation. Both taxa display large fluctuations in their abundances, which is likely due to their low abundances and the sensitivity of their relative abundances to fluctuations in the more dominant types (particularly *Fraxinus*). For *Larix* in particular, values of >2% likely indicate that it was a significant component of the landscape in the sites with records >14.5 ka BP. Because *Salix* is not identified to species, and includes both dwarf/shrub tundra species and thermophilous tree species, the presence of *Salix* pollen in both Pleistocene and Holocene sediments likely represent different taxa at different times. At all sites, *Salix* is present into the early Holocene, while *Larix* is found only in trace abundances except at Kirchner Marsh and Devil's Lake, the northwestern-most sites.

Betula is closely associated with *Pinus* at all sites (Fig. 9). With the exception of Appleman Lake, which sustained low abundances of *Betula* throughout the no-analog interval, *Betula* was either absent or present in trace abundances until 13 ka BP, when it increased first at Kirchner Marsh and Devil's Lake. At these sites, *Betula* and *Pinus* overlapped as important components of the local vegetation during the end of the Younger Dryas cold interval, but their periods of greatest abundance were slightly offset. At Chatsworth Bog, *Betula* (as with *Pinus*) shows a slight increase during the Younger Dryas$_{\mathrm{WL}}$, but is a much smaller component of the pollen sum than at the other sites. At Crystal, Spicer, Appleman, and Silver Lakes, *Betula* and *Pinus* overlap during the Younger Dryas$_{\mathrm{WL}}$, though *Betula* remains at lower abundances than the sites to the northwest. As with *Ulmus*, one of the puzzles of *Betula* is why it becomes abundant after 12 ka, but not during the period of no-analog vegetation, when other hardwood taxa such as *Fraxinus* and *Ostrya/Carpinus* flourished.

Herb pollen (here defined as the sum of all non-arboreal pollen types) concentrations remain fairly stable at most sites before and during the no-analog interval, with the exception of Devil's and Spicer Lakes, approximating 10-15% of the upland pollen sum except at Kirchner Marsh, which has values of 25% during the no-analog interval (Fig. 10). The return to glacial conditions during the Younger Dryas$_{\mathrm{WL}}$ does not seem to have resulted in a marked increase in the herbaceous component of the pollen sum at any of the sites in the region. The two southeastern sites, Appleman and Silver Lakes, show a decline in herb abundances first at 12.3 ka BP, followed be declines in other sites by 11.5 ka BP, indicating a possible time-transgressiveness in the regional decline of nonarboreal pollen. Herb concentrations remain low during the early Holocene, increasing abruptly first at 11 ka BP at Kirchner Marsh (>40%) and at 9 ka BP at Chatsworth Bog, representing the migration of the prairie-forest ecotone. Increases at Crystal and Silver Lakes at 9.5 ka BP correspond with increased warming and drying in the mid-continent in the early Holocene. Poaceae is a moderate component of the herb sum and largely tracks the fluctuations in total herb percentages. Poaceae is the dominant herb type only at Chatsworth Bog during the early Holocene increase.

Fire History

Macroscopic charcoal records are available for Kirchner Marsh and Spicer, Appleman, and Silver Lakes. Fire activity is highly variable across sites (Fig. 11). For the two sites with records prior to 14.5 ka (Appleman and Silver Lakes), background CHAR levels were low, with few and generally small peaks, suggesting occasional fires with low amounts of biomass burnt. All sites show evidence of intensified fire regime during the no-analog interval, characterized by low backgrounds with several peaks in CHAR, including the highest-magnitude peaks in CHAR during the available record at Silver Lake. At Silver and Appleman Lakes, these peaks are associated with the decline in *Sporormiella* spores and the onset of no-analog vegetation (Fig. 1) (Thompson et al. 2000, Gill et al. 2009). Most sites suggest a further intensification in fire regime with the increase in *Pinus* abundances. Increases in background CHAR levels are observed at Spicer and Silver Lakes, while an increased frequency of fire events is seen at

Kirchner Marsh. At Appleman Lake, however, background CHAR and peaks are low at Appleman during the Pinus period. All sites show an increase in CHAR during the early Holocene, which is most pronounced at Appleman Lake. Appleman Lake and Kirchner Marsh show an increase in *Quercus* coeval with increases in charcoal, whereas at Silver and Spicer Lakes *Quercus* increased first and charcoal increased afterward.

Spatiotemporal patterns

Comparisons of the spatiotemporal patterns of the no-analog communities and their primary components show some inter-regional variability at millennial timescales, which suggests that intrinsic factors influenced their formation (Fig12 a – 11e). At 15 ka BP (Fig 12a), just before the no-analog interval, Kirchner Marsh, Devil's Lake, and Spicer Lake had not yet formed, though all sites were deglaciated by that point (Gill et al. 2012). *Picea* was the most abundant taxon at all sites, though at Chatsworth Bog herbaceous taxa were already a significant component. *Fraxinus* was already present in trace abundances, and SCD values were just under 0.3 at Crystal, Chatsworth and Spicer. By 14 ka BP (Fig 12b), Devil's and Spicer Lakes had formed, and all sites except the easternmost (Appleman and Silver Lakes) were fully within the no-analog interval. High SCD values at all active sites were driven largely by coexistence of boreal *Picea* with thermophilous deciduous types, particularly *Fraxinus*. However, at Chatsworth Bog, *Picea* was a much smaller component than at other sites, while abundances of *Fraxinus* were the highest (near 50%). Crystal and Spicer Lakes, both near the margins of Lake Michigan, show greater spatial coherency than their second-nearest neighbors (Devil's Lake and Appleman Lake). Silver Lake and Appleman Lake are more similar than Silver and Chatsworth

Bog, which is at approximately the same latitude. By 13 ka BP, all sites in the transect were active and compositionally novel, but showed considerable variation in the relative abundance of major types. *Picea* was still an important component of all but the southernmost sites (Chatsworth and Silver). The sites with assemblages most dissimilar from present were consistently Crystal Lake and Chatsworth Bog, driven in part by the highest abundances of *Fraxinus*, which does not reach such high abundances in modern pollen samples. *Ostrya*-type pollen increased in abundance along the transect to the southeast. By 12 ka BP (Fig 12e), only Silver and Spicer Lakes had SCD values >0.3; the assemblages at the remaining sites were no longer no-analog, despite the coexistence of *Picea* and hardwood deciduous taxa. At 12 ka BP, *Fraxinus* values were largely reduced, even at those sites (Crystal and Spicer Lakes) that remained compositionally novel. Finally, by 11 ka BP, Spicer, Chatsworth, and Silver lakes had SCD values just above 0.3, which corresponds with the second peak in dissimilarity noted above, but the remaining sites were in the early phases of early Holocene vegetation were no longer novel. The end of the no-analog interval (11.5 ka BP) dates to the end of the Younger Drays$_{WL}$ cold interval and the onset of the Holocene, with a marked increase in *Pinus*, occasionally *Betula*, and increased fire activity at several sites.

NMDS

When the fossil and modern pollen samples are jointly ordinated using nonmetric multidimensional scaling (NMDS), the fossil pollen samples occupy a space of low density in modern assemblages (Fig 13). Axis 1 appears to sort taxa by their distributions along temperature gradients: taxa with the highest positive correlations with Axis 1 include boreal taxa, including *Picea*, *Alnus*, and Cyperaceae, while the taxa most negatively correlated are thermophilous tree taxa, including *Quercus*, *Ulmus*, and *Carya* (Table 3). A map of NMDS values for modern samples shows a strong latitudinal gradient, with steepest gradients corresponding to the transition between boreal forests to mixed hardwood forests in eastern North America (Fig. 14). Axis 2 appears to sort by taxa abundant in modern prairie and tundra communities and the late-glacial no-analog 'parklands' versus pollen types that are abundant in Holocene forests. Taxa most positively correlated with Axis 2 values include the herbs (*Ambrosia*, Poaceae, *Artemisia*) and *Fraxinus nigra*-type pollen, while negative values include arboreal taxa typically found in cool-temperate forests at present (*Betula*, *Pinus*, *Fagus*). Spatially, the NMDS values for Axis 2 are highest for modern in tundra and prairie samples (Fig. 14). No-analog fossil pollen assemblages occupy an NMDS space that is centrally located along in both axes, and in a space that is largely unoccupied by modern sites, consistent with their interpretation of representing parkland landscapes that are between closed and open landscapes, and with a mixture of boreal and temperate tree taxa. The presence of some modern assemblages in this space does not necessarily indicate close modern analogs, but rather likely reflects the fact that NMDS collapses variability to two axes. The NMDS solution has a stress value of 20.3, which potentially reflects a poor fit (Dyke 2004). However, large stress values are typical of NMDS solutions with a large number of samples (in this case, n = >3000), and a poor fit to some degree reflects the high dissimilarity between fossil and modern samples.

Silver Lake and Chatsworth Bog show representative time-transgressive trajectories through NMDS space during the no-analog interval (Fig. 15). Both sites start in the upper right quadrant, with samples clustered within high positive values along Axis 1 (correlated with boreal taxa) and Axis 2 values around 0.4 (indicating more open conditions). While both sites begin to move the area of low modern sample density prior to 14 ka BP, there is an abrupt movement between 13.9 to 13.6 ka BP to central no-analog space in the NMDS, remaining there until the early Holocene. By the start of the Holocene (11.7 ka BP at Silver Lake and 11.2 ka BP at Chatsworth Bog), samples are clustered tightly on the left side of the NMDS ordination space, indicating a transition to temperate deciduous forests.

Discussion

Timing and possible drivers of the no-analog plant associations

The no-analog interval reported here (14.5 to 11.8 ka BP) in the Great Lakes region is much more tightly constrained than prior estimates for eastern North America, which identified a broad peak in vegetational dissimilarity between 17 ka and 12 ka BP (Williams et al., 2001, Williams and Jackson 2007). One reason for the different time estimates is differences in spatial extent: the Williams et al. (2001) synthesis for eastern North America included southerly sites such as Cupola and Jackson Ponds where the period of no-analog vegetation began earlier (Jackson et al. in prep.). Another is improved temporal precision. Williams et al.'s (1993, 2001) estimates of the timing of the no-analog interval (17 ka BP to 12 ka BP) was based on older chronologies in the North American Pollen Database; The improved chronologies used in these sites, based on AMS radiocarbon dates of terrestrial plant macrofossils and avoiding materials potentially biased by the hardwater effect (Williams and Jackson 2007). Revising the start of the late-glacial no-analog communities in the upper Midwest to a time window spanning 14.5 ka BP to 13.8 ka BP places the regional timing squarely within the Bølling-Allerød$_{WL}$ and during the decline of the Pleistocene megafauna, which has implications for understanding the drivers of these novel plant associations.

The rough correspondence between the timing of the no-analog vegetation in the Great Lakes and the Bølling-Allerød interval at Greenland suggests the importance of millennial-scale variations in Northern Hemisphere climates on vegetation in the Great Lakes. The apparent offset between the onset of the Bølling-Allerød at Greenland at 14.7 ka BP (Grimm et al. 2009)) and the formation of the no-analog communities in the Upper Midwest (and particularly the rise of *Fraxinus nigra*; 14.8 ka to 13.8 ka BP, Figs. 2, 3) appears to be real and perhaps due to asynchronous climate changes between the central US and the North Atlantic, given that the Fraxinus rise is dated to 14.2 ka at the well-dated Crystal Lake record (Gonzales and Grimm 2009) and the close synchrony of local δ^{18}O and vegetation changes at White Lake (Yu 2007). The decline of the no-analog interval is more gradual and appears to be linked to the end of the Younger Dryas and the onset of Holocene warming; SCD values (Fig. 3) began to decline at 12.6 ka BP and reached values <0.3 by 11.8 ka BP. However, these millennial-scale oscillations alone cannot explain the no-analog assemblages because of the major compositional differences between late-glacial no-analog assemblages and early Holocene vegetation (Figs. 12a-12e). Other possible factors include higher-than-present seasonality of temperature and insolation during the late Pleistocene, changes in moisture availability due to changes in precipitation and lower-than-present CO_2 concentrations, and megafaunal browsing. I discuss each of these in turn.

The revised no-analog interval in the Great Lakes region still occurs during more-seasonal-than-present climates, though peak differences in seasonality extend into the early Holocene, and modeled climate dissimilarity begins as early as 17 ka BP (Rasmussen et al. 2006). These analyses were based on snapshot CCM1 and HadCM simulations at discrete intervals (Williams and Jackson, 2007); our results indicate the need for new climate-analog analyses based on transient climate simulations with meltwater forcing included (e.g. Liu et al 2009). Higher-than-present seasonality remains a viable hypothesis as a contributing factor of the late-glacial no-analog associations. *Fraxinus*' climate envelope may include warmer-than-present summers and colder-than present winters (Williams et al. 2001, Gonzales et al. 2009); increased seasonality and cold winters may explain why *Ulmus* is absent during the warmer temperatures of the Bølling-Allerød$_{WL}$ and only increases during the Holocene.

Pleistocene herbivores may have played an important role as a biotic driver of novel plant associations. Williams et al. (2001) hypothesized that the presence of novel (relative to modern) grazing and browsing megaherbivores may have contributed to the formation of no-analog plant associations, which was later explicitly tested by Gill et al. (Gill et al. 2009, 2012). Contrary to this hypothesis, at Silver and Appleman Lakes rises in SCD values follow the decline in spores to <2 % of the upland pollen sum. Gill et al. (2009) suggested that this pattern, along with an increase in fire activity, might be caused by herbivory release of palatable deciduous taxa (e.g. *Fraxinus*) following the functional decline in local megaherbivore populations (Davis 1987, Davis and Shafer 2006, Gill et al. 2009, Gill et al. 2012). *Sporormiella* records from upstate New York (Gill et al. 2012) indicate local increases in vegetation dissimilarity (though values remain <0.3) and deciduous taxa immediately following the decline in megafauna (inferred from the decline in spores <2% of the upland pollen sum). Broadly, the no-analog interval corresponds with the decline in megafauna in North America (Fig. 1), as indicated by the last appearance dates (Robinson et al. 2005) of taxa local to the region (though the LADs themselves are for North America broadly), as well as evidence for human presence (including Proboscidean kill sites) along the ice margin in the region (Overstreet and Kolb 2003, Johnson 2006, Joyce 2006, Faith and Surovell 2009). *Fraxinus* litter contains high relative abundances of leaf nitrogen (Johnson 2007) and is heavily browsed by deer today (Reiners and Reiners 1970); Pleistocene megaherbivores may have found *Fraxinus* an equally palatable source of micronutrients. Schweger et al. (2011) hypothesize that the loss of megaherbivores may explain why Holocene vegetation in northwest Canada is compositionally different than previous interglacials. Gill et al. (2012) presented a conceptual model where top-down climatic controls on Quaternary vegetation dynamics are mediated by biotic interactions, including herbivory; the end-Pleistocene megafaunal extinctions likely played an important role in the formation of the late-glacial no-analog communities by influencing plant community composition (particularly hardwood expansion), dispersal, ecosystem structure (resulting in less open landscapes) and ecosystem function (including nutrient cycling and fuel regimes) (Gill et al. 2009, 2012). Megaherbivory thus remains a viable contributing driver of the no-analog vegetation in the Great Lakes region. Our results support the further application of the *Sporormiella* proxy to further test linkages between megafaunal collapse and dissimilarity, particularly as related to the observed northwest-southeast time-transgressive pattern. Such analyses should be accompanied by mechanistic vegetation models of plant-megaherbivore interactions to test the influences of extinct megaherbivores on Pleistocene vegetation.

CO_2 concentrations were approximately 160 ppm lower than pre-industrial values during the no-analog interval, but were relatively stable during that interval. CO_2 concentrations influence the allocation of resources to growth, reproduction, and structure within plants (Field 1991, Johnson 2009). Lower partial pressure of CO_2 relative to modern concentrations would have lowered photosynthetic, and likely growth rates (Field et al. 1995). Decreased CO_2 results in a proportional decrease in photosynthesis under ideal growing conditions due to limited substrate for the carboxylation of Rubsico, particularly under high light environments (Cowling and Sykes 1999). CO2 interacts with temperature to affect the relative photosynthetic efficiencies of C3 and C4 plants (Ehleringer et al. 1997), so the effect of CO2 on photosynthetic efficiencies in the upper Midwest may have been relatively muted during the LGM, and more important during the warmer temperatures and more open canopies during the Bølling-Allerød (Sage and Kubien 2007). Lowered CO_2 concentrations would increase sensitivity to moisture deficits, as stomatal closure exacerbates the effect of reduced available CO_2 (Sage 1995). Decreased CO_2 also reduces plants' abilities to assimilate leaf nutrients, including nitrogen (which in turn limits Rubisco capacity), though there is some evidence that this is regulatory response of plants as an adaptation to the lower CO_2 concentrations that were predominant during the Quaternary (Sage and Coleman 2001). Therefore, it is likely that low CO_2 concentrations affected plant growth and community dynamics during the no-analog interval, although the importance of carbon dioxide concentrations to the formation of novel plant associations remains uncertain.

Were climates during the late-glacial no-analog interval wet or dry?

The role of moisture availability as a driver of the late-glacial no-analog vegetation composition has been something of a puzzle, due to conflicting lines of evidence that support either wetter-than-present or more mesic/xeric conditions during the Pleistocene-Holocene transition. Global climate model simulations from CCM1 suggest regional aridity during the no-analog interval from 14 ka to 10 ka BP, including the period of peak vegetation dissimilarity, due to anticyclonic flow from a persistent high-pressure cell located over the LIS, which would have displaced the polar jet, blocking moisture from the Gulf airmass (Sage and Coleman 2001). Webb et al (1991) compared the CCM1 model results with the regional pollen record, noting that the model overestimated July temperatures from 16 ka to 11 ka BP when compared with those inferred from the vegetation. CCM1 predicted drier-than-present climates during this interval, particularly in summer, but wetter-than-present springs due to increased snow depths relative to present, which Webb et al. found to be consistent with the pollen record. Using the Polar MM5 mesoscale climate model, Bromwich et al. (1998) simulated a steep thermal gradient along the southern LIS in the lower atmosphere caused by cold air from the ice sheet interacting with a warmer land surface, which delivered high levels of precipitation along the margins ice sheet. A regional climate model predicted a split jet stream caused by anticyclonic flow, but only during winter (November through April); precipitation totals were also maximized along the ice sheet margins in winter (Bromwich et al. 2005). In contrast with modeled circulation patterns, sedimentary features preserved in sand dunes from this interval indicate a predominantly westerly, rather than anticyclonic, wind direction (Bromwich et al. 2004), though westerly airflow may still have been reduced by anticyclonic anomalies over the LIS.

Moderate to high abundances of herbs, and particularly the presence of *Ambrosia* and *Artemisia* during the no-analog interval suggest landscape openness due to colder and/or drier climates (Webb et al. 2003, Mason et al. 2011). Regional dune activation, particularly from 13.3 ka to 11.1 ka BP in Indiana and Ohio, indicates dune formation in response to abrupt cooling during the late Pleistocene and Younger Dryas (Grimm and Jacobson 2004) but not the Bølling-Allerød, suggesting that climates were wet enough to support stabilizing vegetation. High evaporation driven by increased summer insolation would have resulted in increased moisture demands on vegetation, but the presence of hydric taxa such as *Fraxinus nigra* suggests the presence of a supplemental moisture source. *Fraxinus nigra* and *Picea mariana* grow in wet conditions today, and their coexistence in the no-analog paleorecord has been interpreted as indicating wetter conditions (Grimm and Jacobson 2004, Campbell et al. 2011). The main deciduous constituents of the no-analog assemblages, *Fraxinus nigra* and *Ostrya*-type, indicate different moisture regimes. *Fraxinus* has a shallow root compared to most deciduous trees, and is typically found on poorly-drained, riparian, or boggy sites, and is successful on sites that experience seasonal flooding (Gonzales and Grimm 2009). *Ostrya virginiana*, on the other hand, is found on mesic to xeric sites in the northern portion of its range, and is flooding intolerant. By the end of the no-analog interval, when *Fraxinus* and *Ostrya* are no longer in phase, fluctuations between them could represent a shift from soil-moisture controls to atmospheric or successional drivers.

Examining periglacial environments and the hydrological influence of the LIS during the Pleistocene-Holocene transition may help resolve these conflicting lines of evidence. Specifically, surface meltwater from the LIS, elevated groundwater, melting permafrost, and stagnant ice would all have provided local sources of moisture independent of atmospheric conditions. All sites were in close enough proximity to the LIS that their groundwater systems were likely strongly influenced by it (Fig 14a-e). Simulations of periglacial hydrology indicate that subglacial aquifers were not capable of evacuating the estimated basal water from the Lake Michigan Lobe, and that subglacial surficial drainage was necessary (Wright and Rauscher 1990). Groundwater recharge rates are estimated to have been as much as ten times that of modern levels as the LIS overran sedimentary basins—as much as 0.2% of the volume of the LIS itself—and subglacial infiltration likely accounted for as much as 5-10% of the meltwater generated (Breemer 2002). This meltwater is presumed to have drained into Paleozoic aquifers, reducing subglacial fluid pressures, inhibiting esker formation, and contributing to ice sheet stagnation (Person et al. 2007). Meltwater, permafrost, and preserved stagnant ice would all provide sources of moisture independent from the atmosphere; Yansa (2005, 2006a) refers to this additional moisture as the "residual meltwater effect." This additional moisture would have been variable in space and time, depending on landscape position relative to the water table (Yansa 2002) and the local amount of stagnant ice and permafrost (Smith et al. 1997). Release of this residual meltwater may have been triggered by warmer temperatures during the Bølling-Allerød. In the upper Midwest, Yansa (2008) suggests that meltwater-saturated conditions may have inhibited fire and prolonged the growth of *Picea*

Paleohydrology could also explain why regions of climatic dissimilarity were much more widespread than the no-analog plant communities. Models of LGM climate show extensive regions of high dissimilarity relative to modern, in contrast to pollen assemblages (Yansa 2006b), though these simulations were done at a coarse resolution, and so may not be suitable to pick up on finer-scale patterns of moisture variability. Highest modeled climatic dissimilarities were away from the ice sheets, while the highest vegetation dissimilarities were along the ice margins (Williams et al. 2001). The no-analog plant communities were a broader phenomenon in North America, found as far away as the southern US and Beringia; however, the expression and composition of those assemblages varied across the continent. Specifically, no-analog deciduous-coniferous communities in other regions were characterized by different co-dominants with *Picea*, including *Quercus* and *Carya* in the southeast, lower abundances of *Fraxinus* and higher abundance of other deciduous types in the mid-South (Williams et al. 2001), and high values of *Betula*, *Populus*, and *Salix* in Alaska (Delcourt 1979). In the northeastern United States, rates of vegetation change were high, responding to rapid fluctuations in climate, and yet novel plant assemblages were absent (Anderson et al. 1989, Williams et al. 2001). Differences in deglacial hydrology could also explain why the late-glacial no-analog communities were present in the Great Lakes region but were largely absent from New England (Anderson et al. 1989, Shuman et al. 2009), in spite of the presence of the taxonomic constituents of no-analog assemblages in different abundances. Bedrock conditions were not conducive to elevated water tables, and a lack of hummocky topography in large portions of the Northeast suggests that periglacial environments did not experience the same conditions as in the Midwest. Paleohydrology may thus have represented a strong regional control on the expression of no-analog communities, in conjunction with other drivers; seasonality in particular would have been stronger in the continental interior than at the coasts.

The no-analog pollen assemblages recorded at our sites may be “deep;” representing novel combinations of taxa growing together in local communities, or they may be “shallow,” representing landscape heterogeneity within the watershed that has no modern analog (Jackson and Williams 2004). In a “shallow” no-analog scenario, arid conditions would favor mesic trees such as *Ostrya* and herbaceous taxa such as *Ambrosia* and *Artemisia* on the well-drained uplands, hummocks and dunes, while *Picea mariana*, *Larix*, and *Fraxinus nigra*-type would have thrived in the saturated or seasonally flooded lowlands. If so, at the regional scale of pollen may homogenize heterogeneous landscapes in the deglaciated Midwest into what appear to be novel plant associations at the stand scale. Currently, the data are insufficient to resolve this question, though a “shallow” no-analog scenario may explain apparent disagreements among modeled and proxy indicators of moisture.

Future Research Directions

It is increasingly apparent that there are multiple environmental drivers of the late-glacial no-analog associations, as is generally true of dynamics in ecological and other complex systems (Williams et al. 2001), and that no single factor can explain their formation or decline. Novel plant assemblages in the Great Lakes emerged due to a combination of biotic and abiotic drivers, and were influenced by a combination of global climates and regional factors particular to the Great Lakes region during deglaciation. Rising temperatures, high insolation and temperature seasonality, increased moisture availability (perhaps linked to periglacial hydrology), lower CO_2, and megafaunal herbivory remain viable drivers. Periglacial and recently deglaciated landscapes are highly dynamic and heterogeneous, with marked local variation in hydrology, substrate, low-relief topography, and permafrost conditions (Scheffer and Carpenter 2003). In order to further test the relative influence of these drivers, the next critical steps are

1) mechanistic modeling of paleovegetation to test hydrology and megaherbivory influences, along with climatic factors, and 2) the expansion of the scope of analysis to include novel plant associations in other regions, in order to better characterize the spatiotemporal patterns of no-analog vegetation and the regional to continental-scale controls on their expression and dynamics.

Conclusions

New chronologies and fossil pollen records indicate that the late-glacial no-analog assemblages in the Great Lakes region of the Midwestern US were much more temporally constrained than previously reported in subcontinental-scale syntheses. This new timing (ca. 14.5 ka BP to 11.8 ka BP, with century-scale variation in timing among sites) places the regional genesis of the no-analog interval within the Bølling-Allerød$_{WL}$ warm period and its termination at the transition from colder climates during the Younger Dryas$_{WL}$ to the Holocene. The onset of the no-analog vegetation appears to be slightly time-transgressive from west to east, and individual sites show significant variability in composition and the timing of events. Both among sites and at the broader continental scale, however, variations in the response of vegetation to environmental change suggest some degree of intrinsic factors driving local differences. A multiplicity of causes, along with local site factors, may have contributed both to the variability across sites in this study, and the regional expression of no-analog vegetation that was particular to the Great Lakes. Viable factors include rising temperatures, high insolation and temperature seasonality, increased moisture availability (either for the entire region, or just in the lowlands where periglacial hydrology drove locally saturated conditions), lower CO_2, and declining megafaunal herbivory. More work is needed to test the relative role of these drivers, on vegetation dynamics and biotic interactions during the Pleistocene-Holocene.

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Table 1: Site Information

Site Name	**County, State**	**Coordinates**	**MSL (m)**	**Data Publication**
Kirchner Marsh	Dakota Cty, MN	44 50.00 N, 93 07.00 W	254	This paper
Devil's Lake	Sauk Cty, WI	42 24.53 N, 89 43.47 W	405	Maher, 1982; Grimm 2009
Crystal Lake	McHenry Cty, IL	42 14.07 N, 88 21.48 W	273	Gonzales & Grimm 2009
Chatsworth Bog	Livingston Cty, IL	40 40.33 N, 88 19.23 W	220	Nelson et al. 2004
Spicer Lake	St. Joseph Cty, IN	41 44.52 N, 86 52.19 W	237	This paper
Appleman Lake	LaGrange Cty, IN	41 62.37 N, 85 21.36 W	293	Gill et al. 2009
Silver Lake	Logan Cty, OH	40 21.15 N, 83 48.45 W	332	Gill et al. 2012

Table 1: Site data, including county, lat/long, elevation, and the reference publication for previously-reported methods or data.

Table 2: Radiocarbon Dates

Spicer Lake, IN

Lab #	Depth (cm)	14C Age	1−σ	Cal. Age range	Material
OS-65291	494.5	5370	35	6010 - 6230	bark
OS-65872	498.5	5270	130	5750 - 6300	wood
OS-65292	583.5	6210	35	7010 - 7250	wood
UGAMS-5973	667.5	5400	210	5740 - 6640	charcoal
UGAMS-5974	729.5	5120	360	4990 - 6670	charcoal
UGAMS-4653	861.5	9470	60	10570 - 11070	Pinus seed
UCIAMS-56655	887.5	5060	160	5480 - 6210	charcoal
UGAMS-4654	887.5	6730	300	7010 - 8180	charcoal
OS-65862	888.5	10100	140	11240 - 12370	plant macro
UGAMS-4655	914.5	7620	280	7880 - 9200	charcoal
UGAMS-56656	914.5	8940	80	9780 - 10240	charcoal
UGAMS-4656	915.5	10090	60	11370 - 11980	wood
UCIAMS-56652	957.5	12410	35	14130 - 14930	pollen
OS-79784	1029.5-1037.5	12150	35	13850 - 14150	wood
UCIAMS-56657	1039.5	10160	180	11250 - 12400	
UCIAMS-56653	1056.5	12740	35	14790 - 15550	pollen

Kirchner Marsh

Lab #	Depth (cm)	14C Age	1−σ	Cal. Age range	Material
OS-84104	480.5	4780	35	5330 - 5590	terrestrial plant
OS-79266	722.5	6530	35	7340 - 7560	terrestrial plant
OS-84458	827.5	7110	280	7470 - 8440	terrestrial plant
OS-84143	954.5	10150	40	11620 - 12000	terrestrial plant
OS-84107	995.5	8060	35	8780 - 9080	terrestrial plant
OS-79805	1013.5	675	35	560 - 680	terrestrial plant
OS-84206	1115.5	11500	55	13230 - 13480	terrestrial plant
OS-84143	1145.5	11450	60	13170 - 13440	terrestrial plant
OS-84157	1183.5	5090	35	5750 - 5910	terrestrial plant
OS-84141	1185.5	11600	50	13300 - 13600	terrestrial plant
UCIAMS-53575	1207.5	11505	25	13270 - 13440	wood
UCIAMS-53576	1230.5	11585	25	13300 - 13560	wood

Table 2: Radiocarbon dates, including lab accession numbers and the mean depth (cm) for point samples or ranges for samples that spanned >1 cm. Calibrated calendar age ranges are reported as the entire distribution of all probabilities. Two basal pollen dates from Spicer Lake resulted in anomalously old ages given the regional vegetation, and so were rejected.

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Figure 1: Drivers of late-glacial vegetation

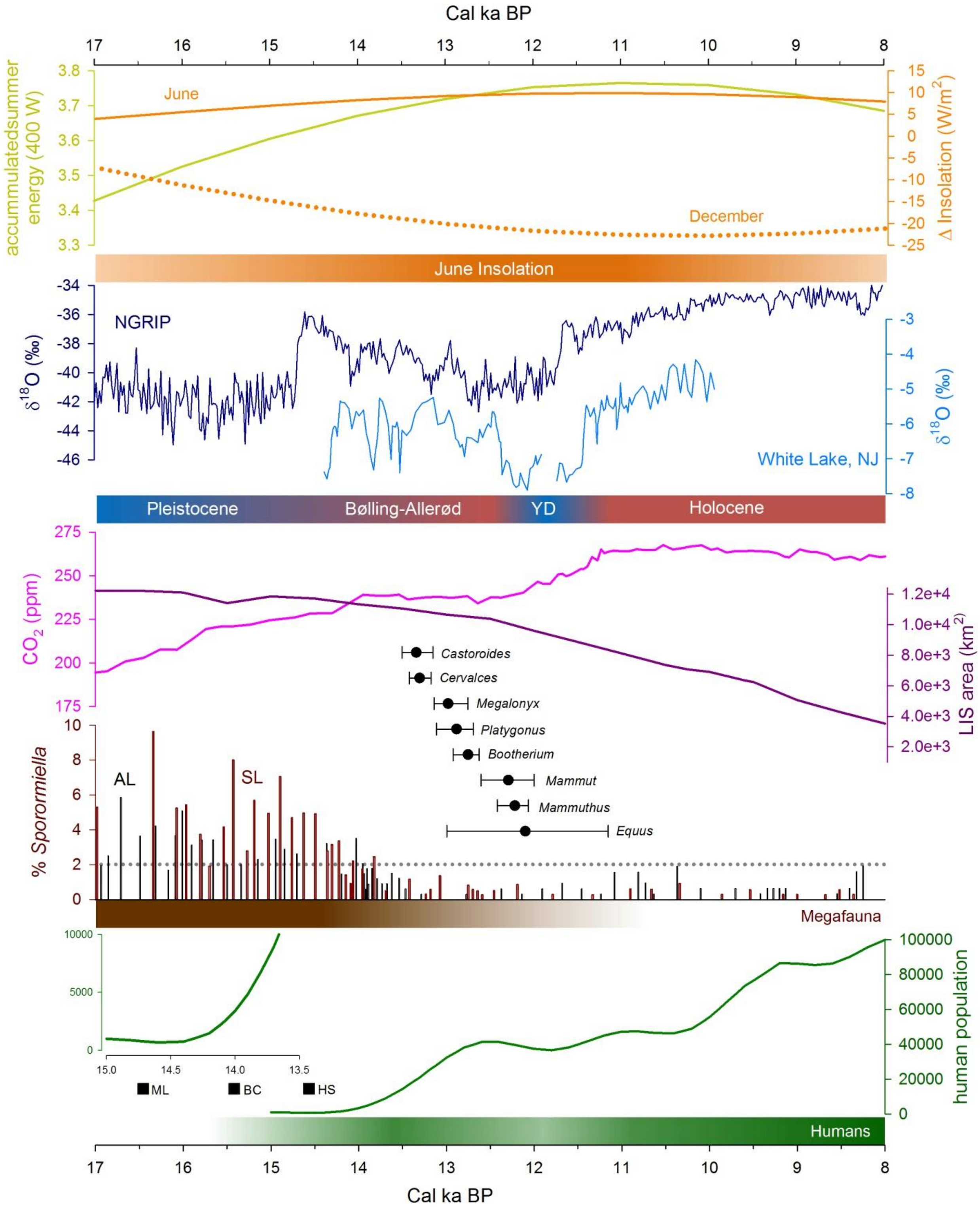


Figure 2: Site map

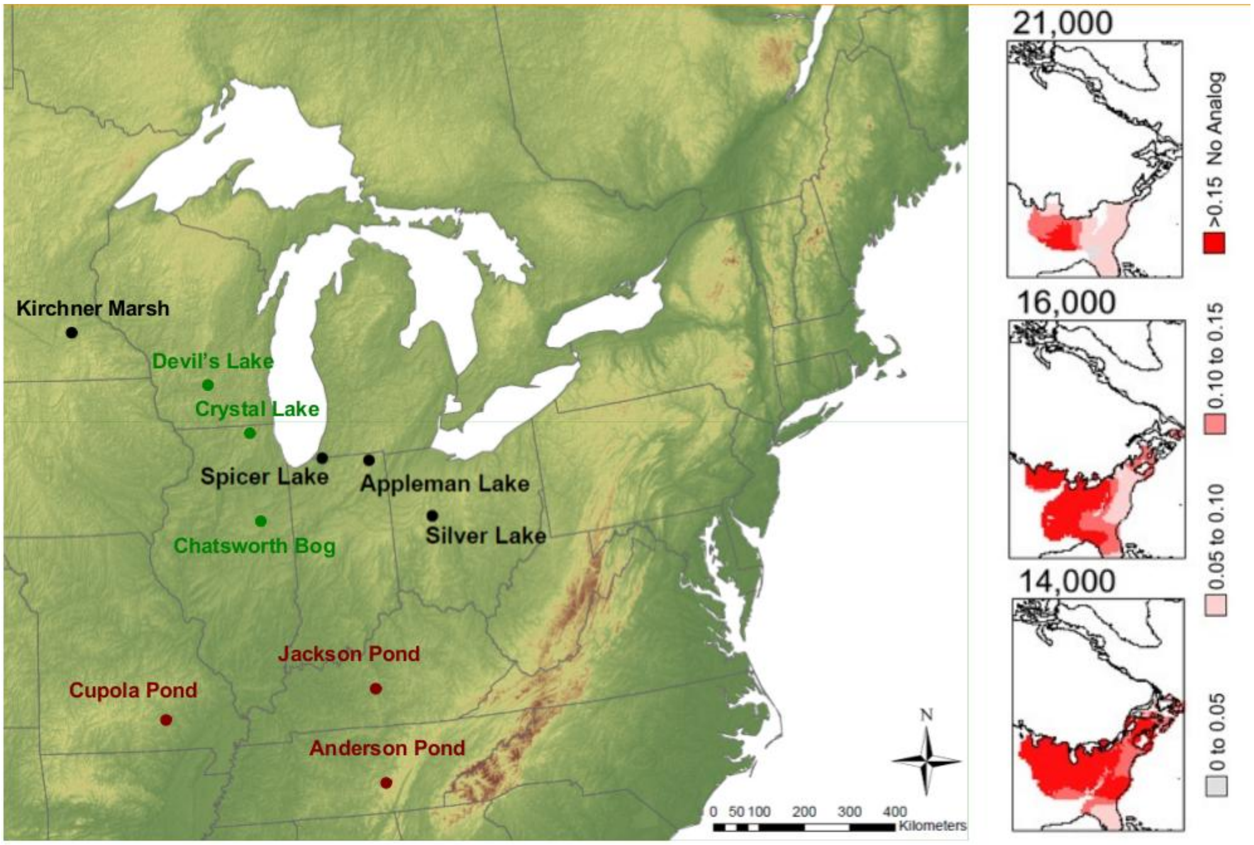


Figure 3A: Spicer Lake age model

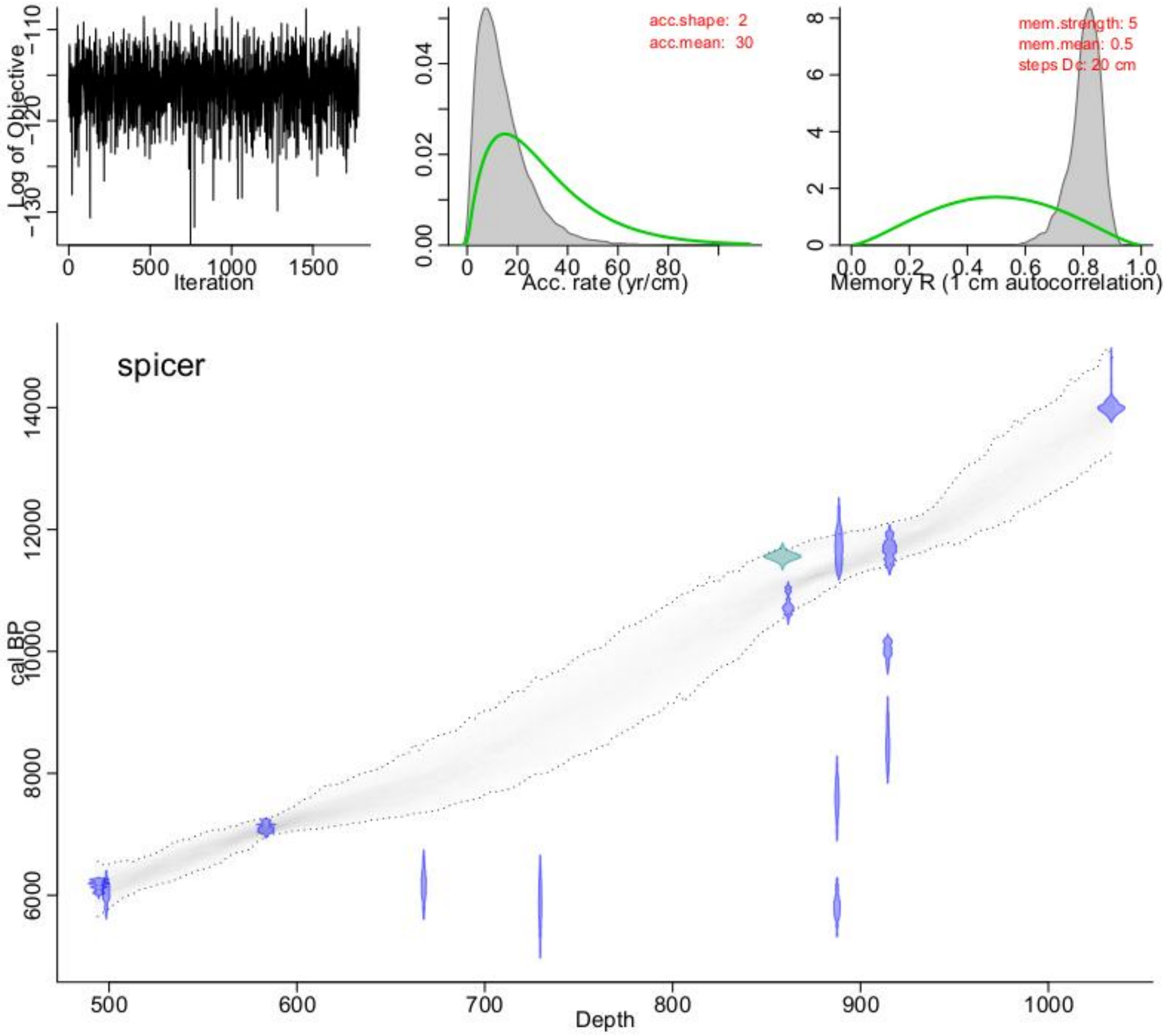


Figure 3b: Kirchner Marsh age model

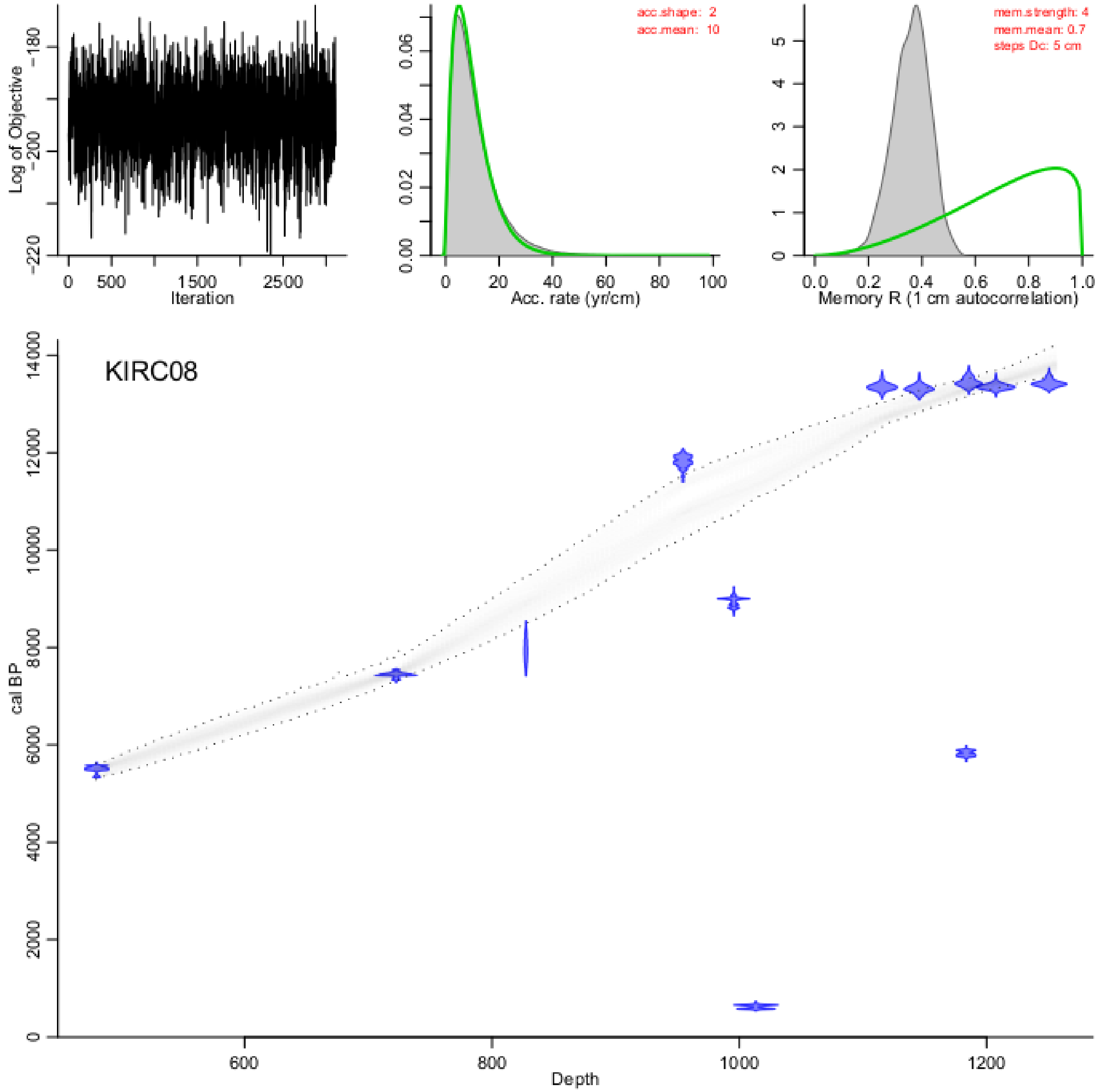


Figure 4: Minimum vegetation dissimilarity

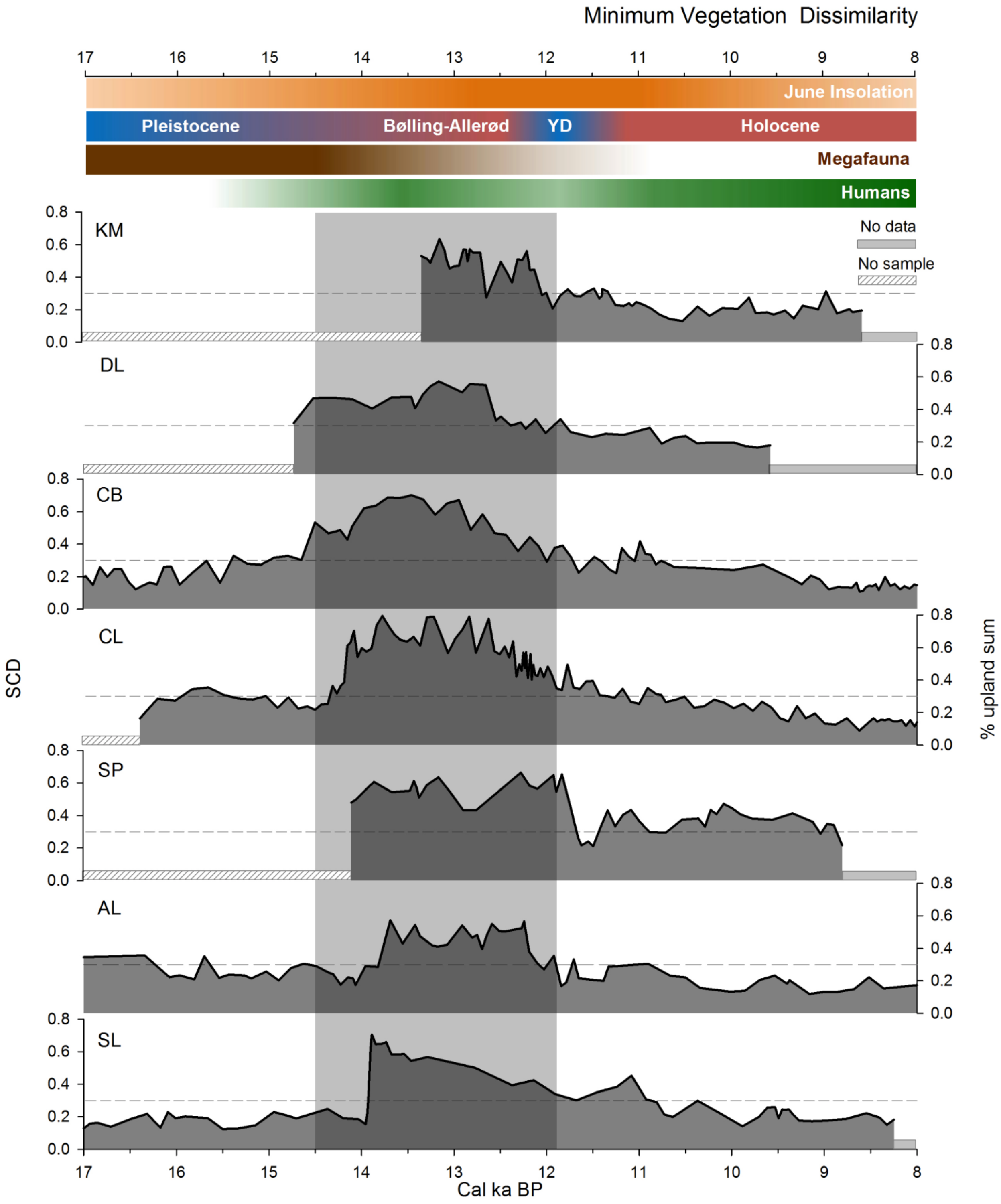


Figure 5: *Picea*, *Pinus*, and *Quercus*

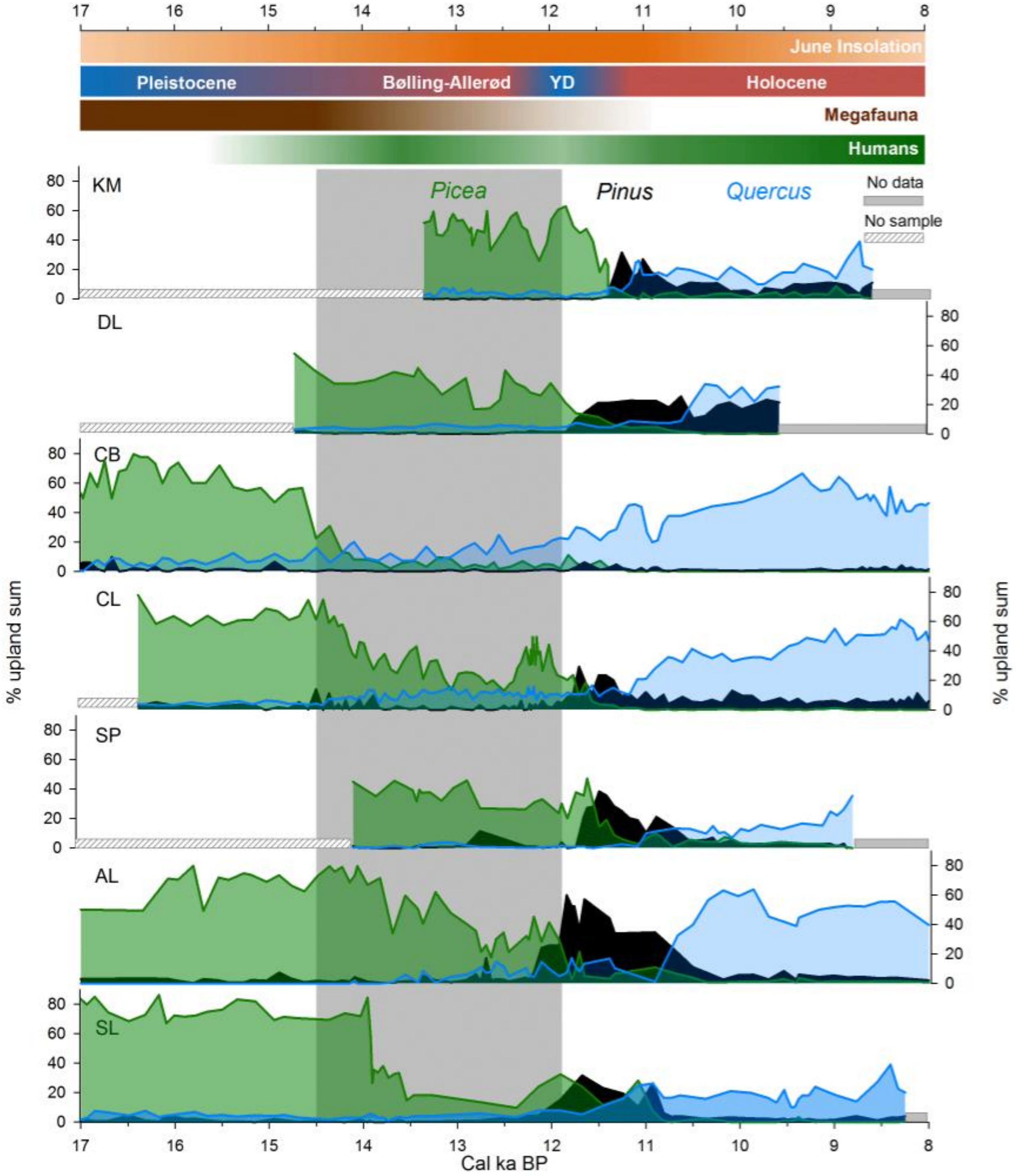


Figure 6: *Fraxinus nigra* and *Ostrya*-type

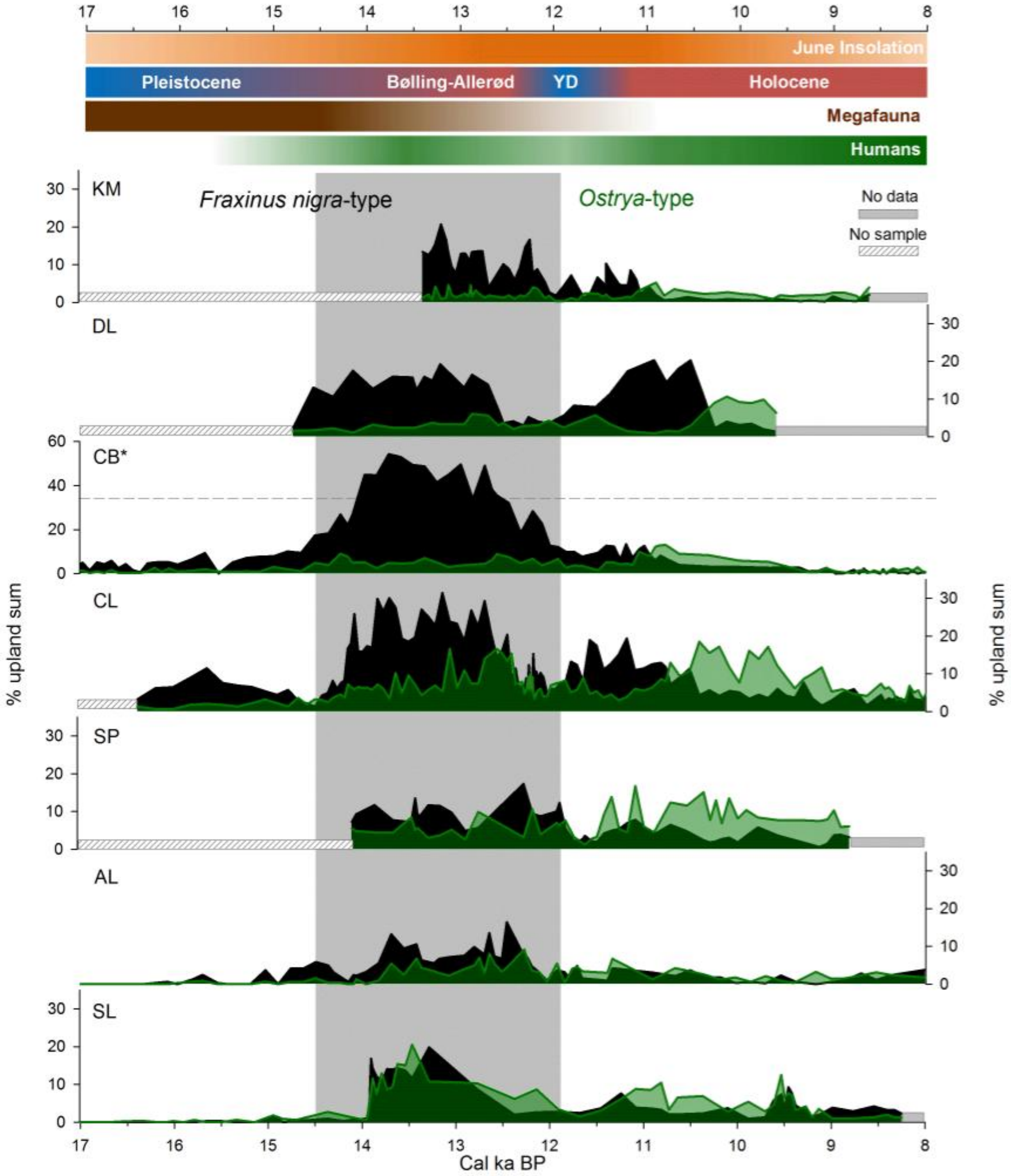


Figure 7: *Ulmus* and *Fraxinus nigra*

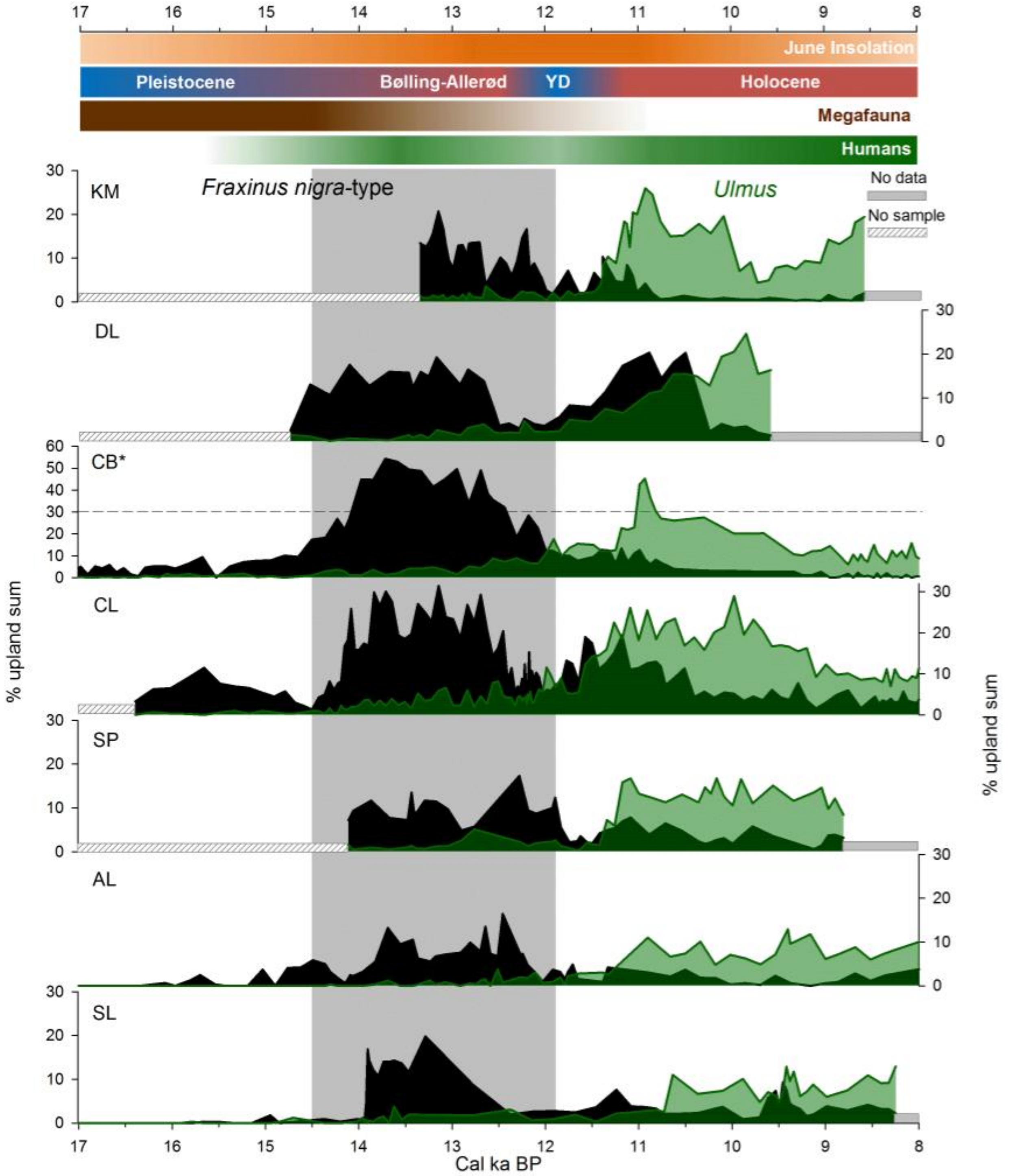


Figure 8: *Larix* and *Salix*

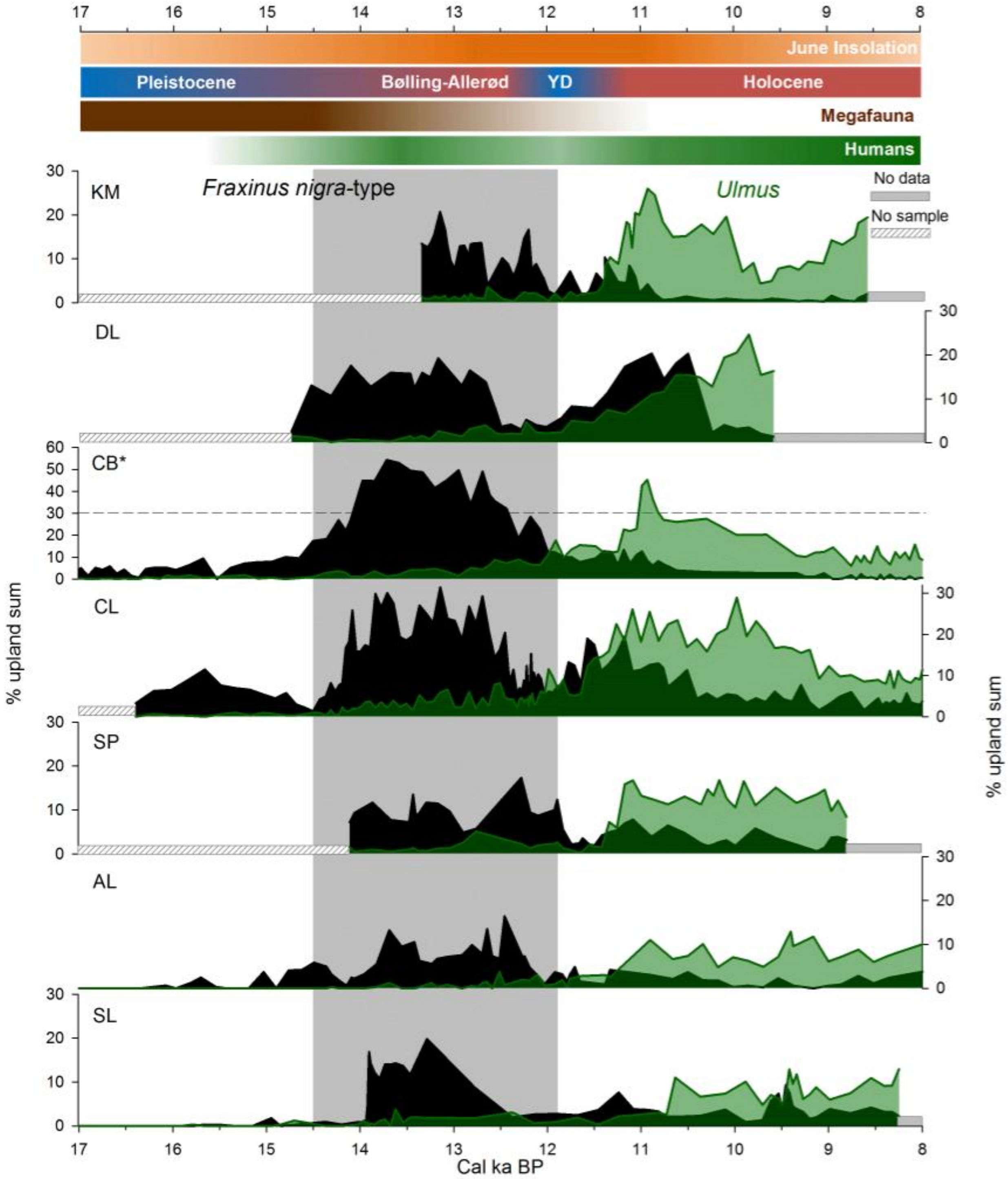


Figure 9: *Betula* and *Pinus*

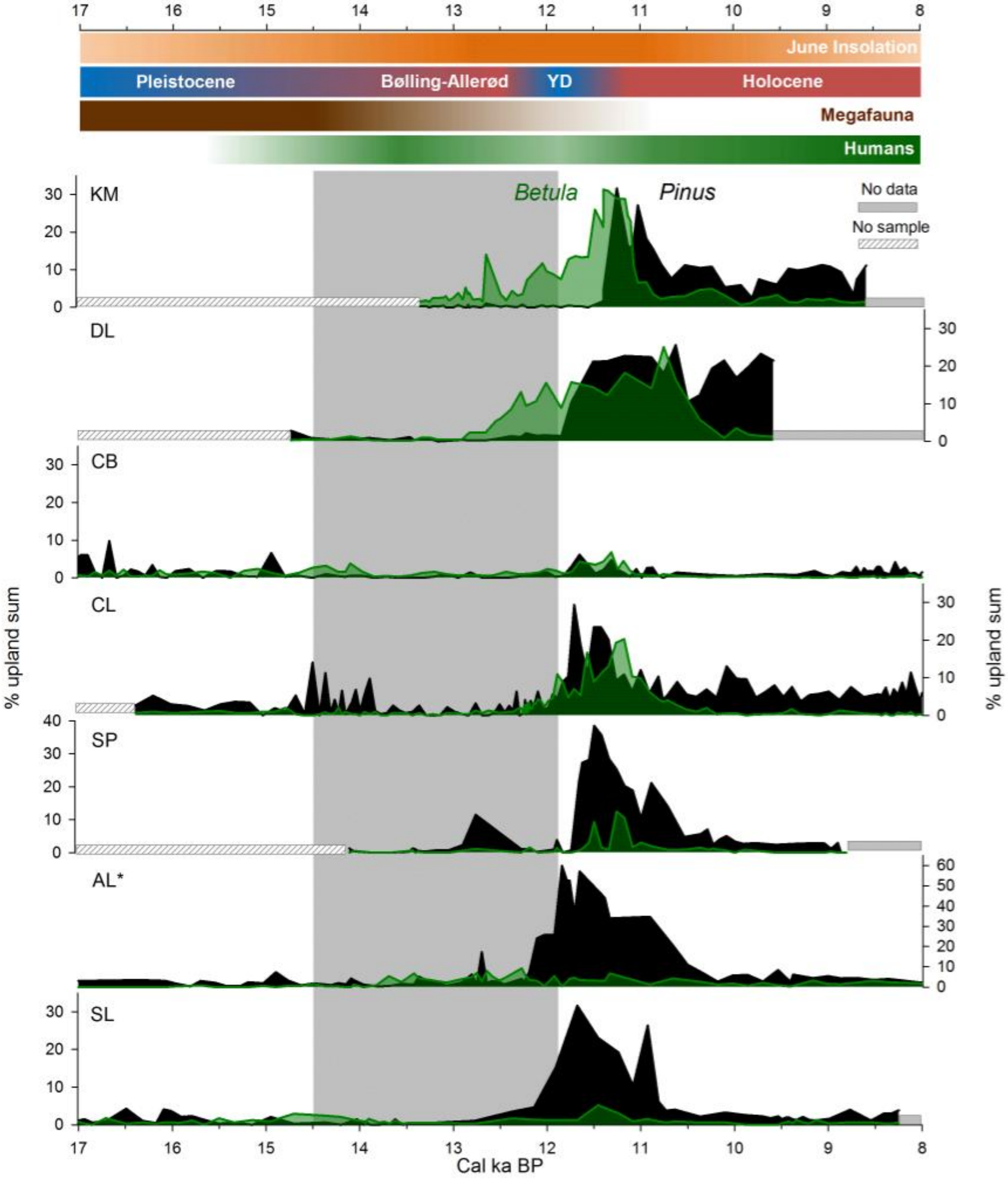


Figure 10: Non-arboreal pollen (herbs)

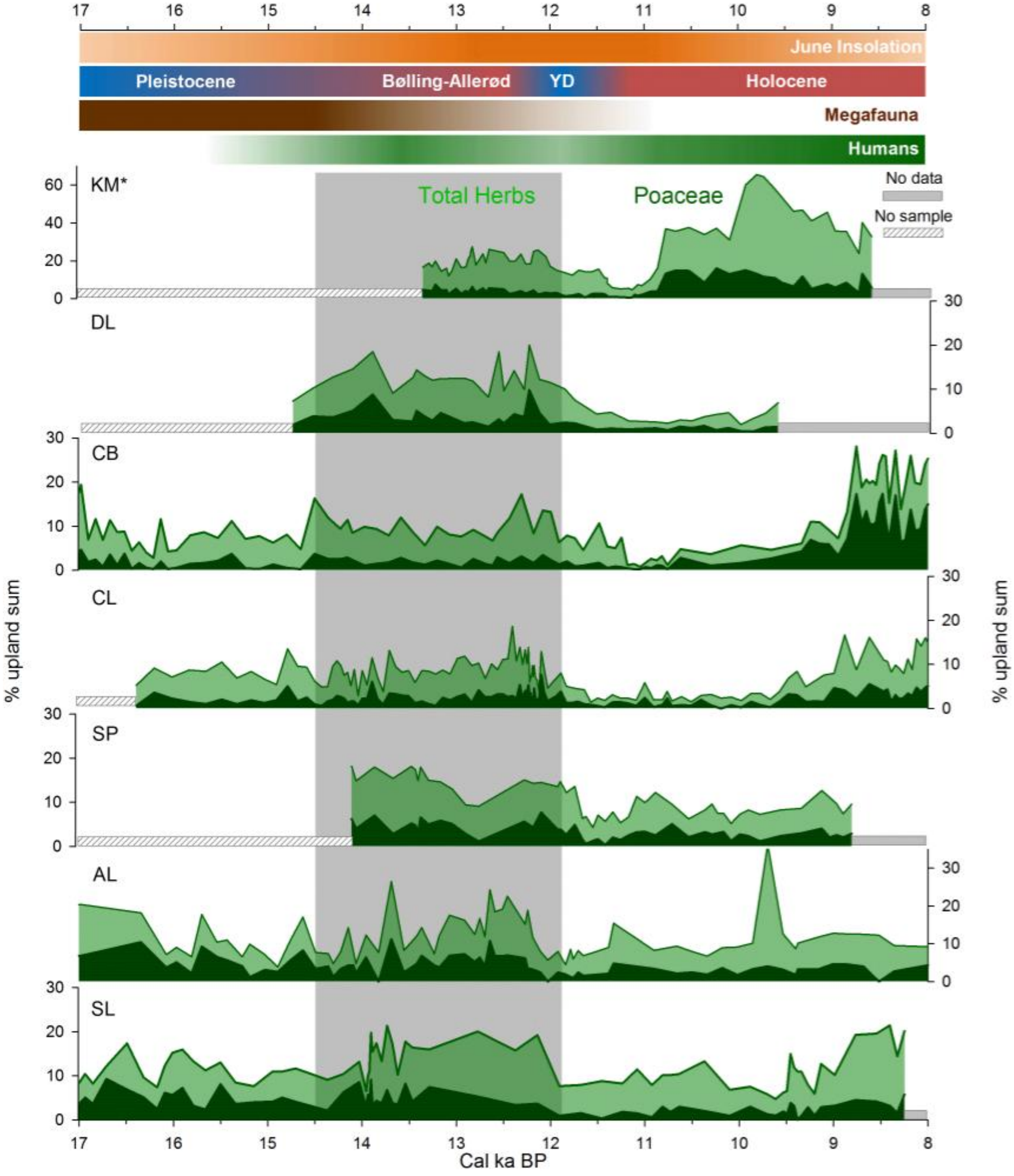


Figure 11: Fossil charcoal, *Quercus* and *Pinus*

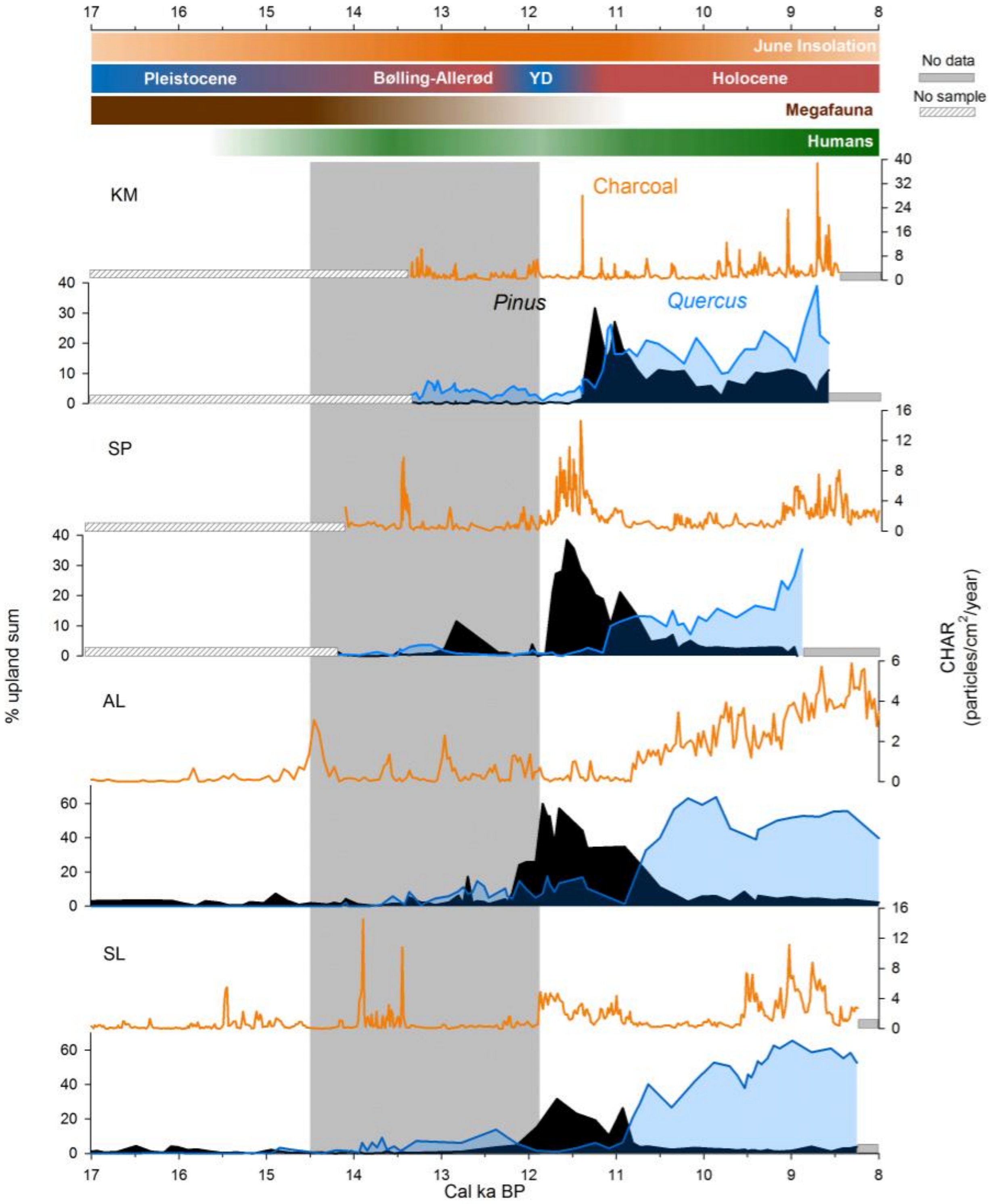


Figure 12a-b: Site composition, 15,000 BP & 14,000 BP

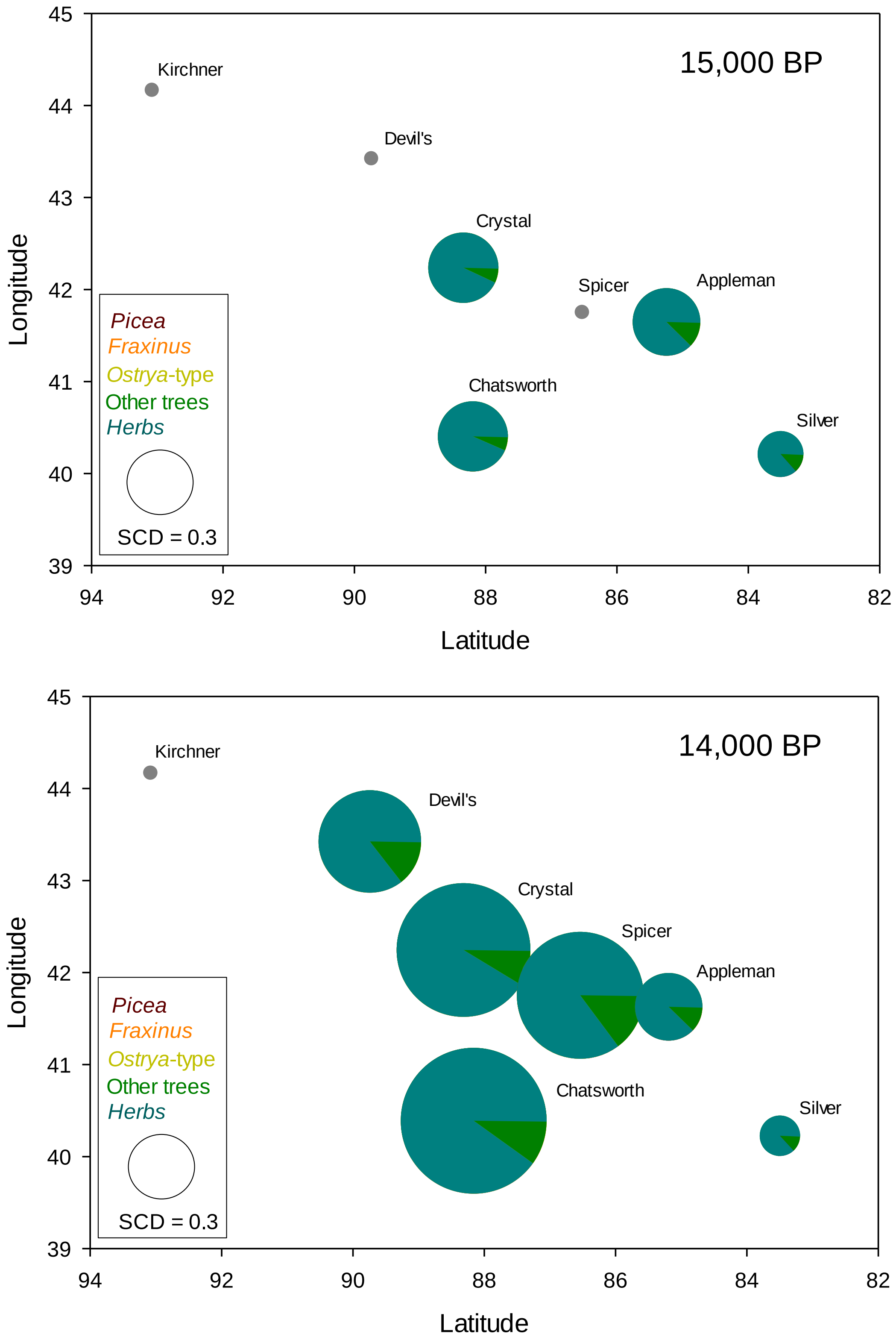


Figure 12c-d: 13,000 BP and 12,000 BP

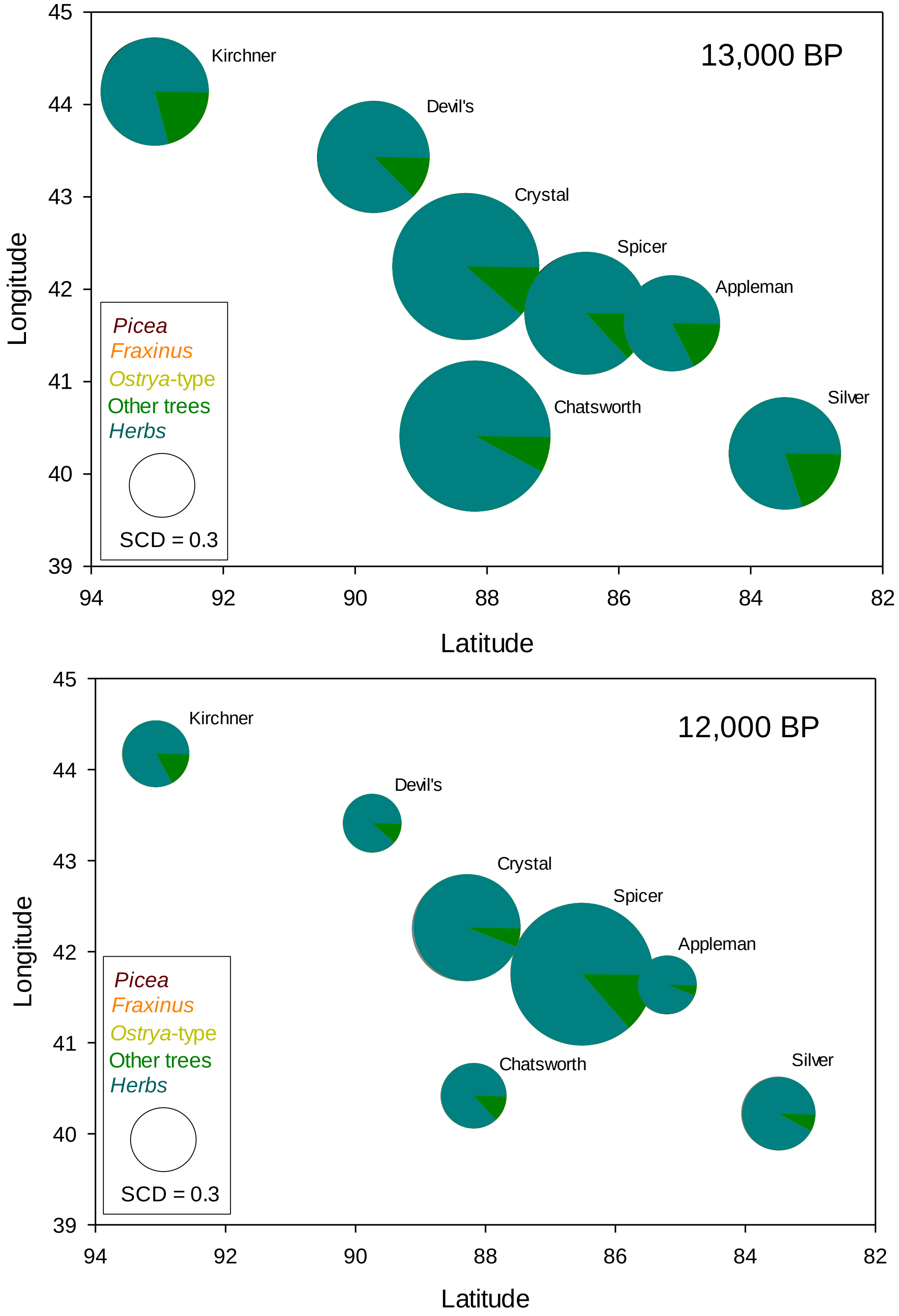


Figure 12e: 11,000 BP

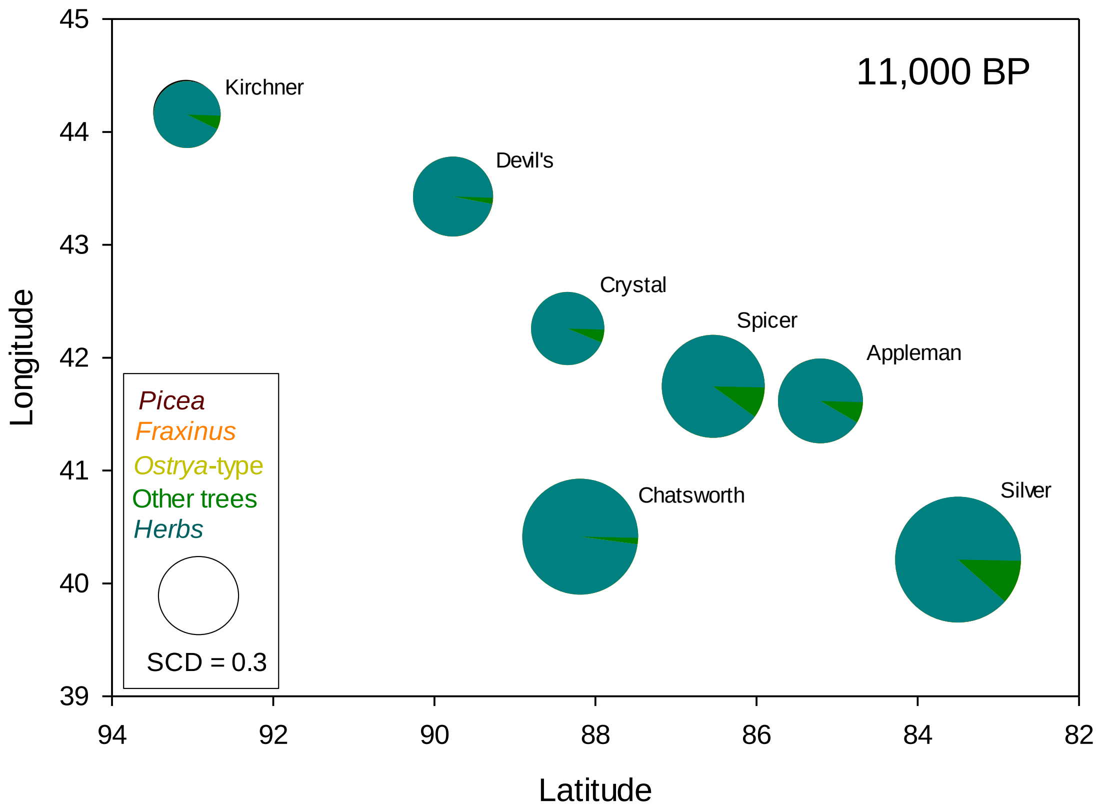


Figure 13: NMDS – Modern and no-analog fossil samples

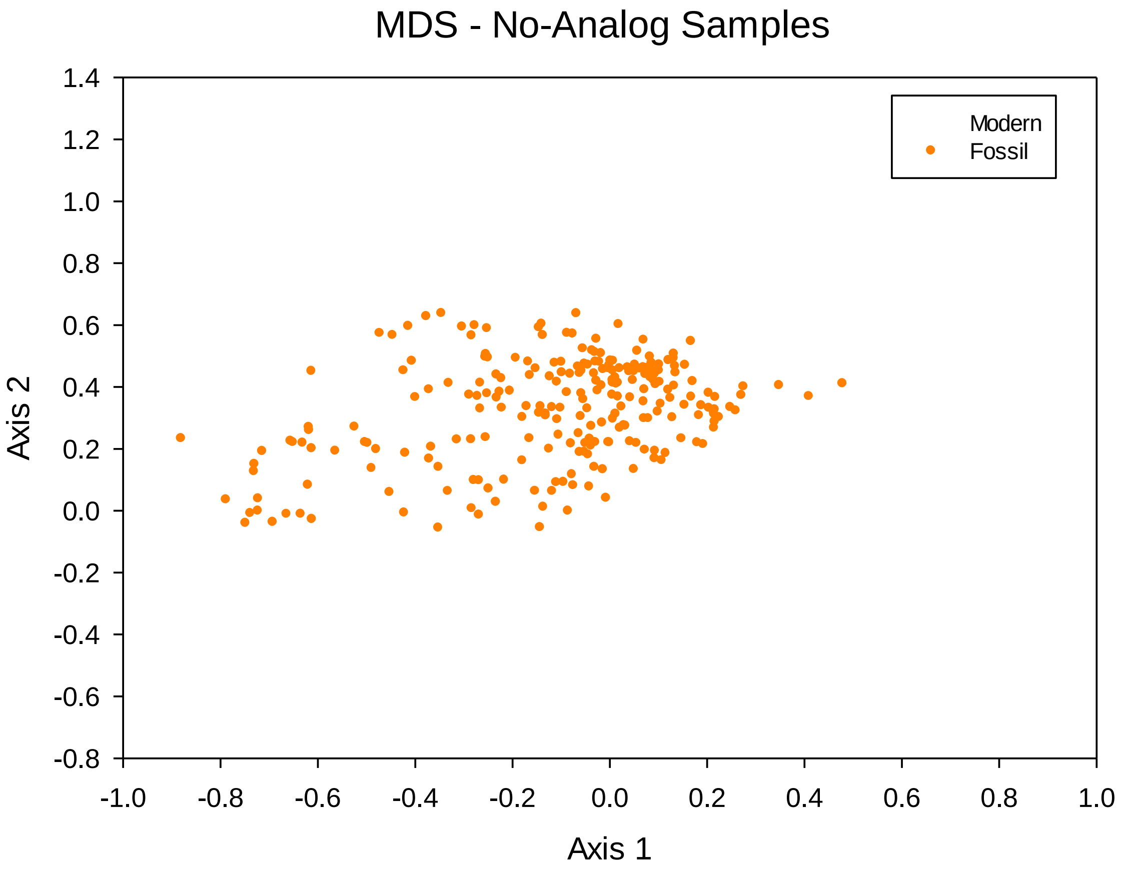


Figure 14: NMDS axis maps

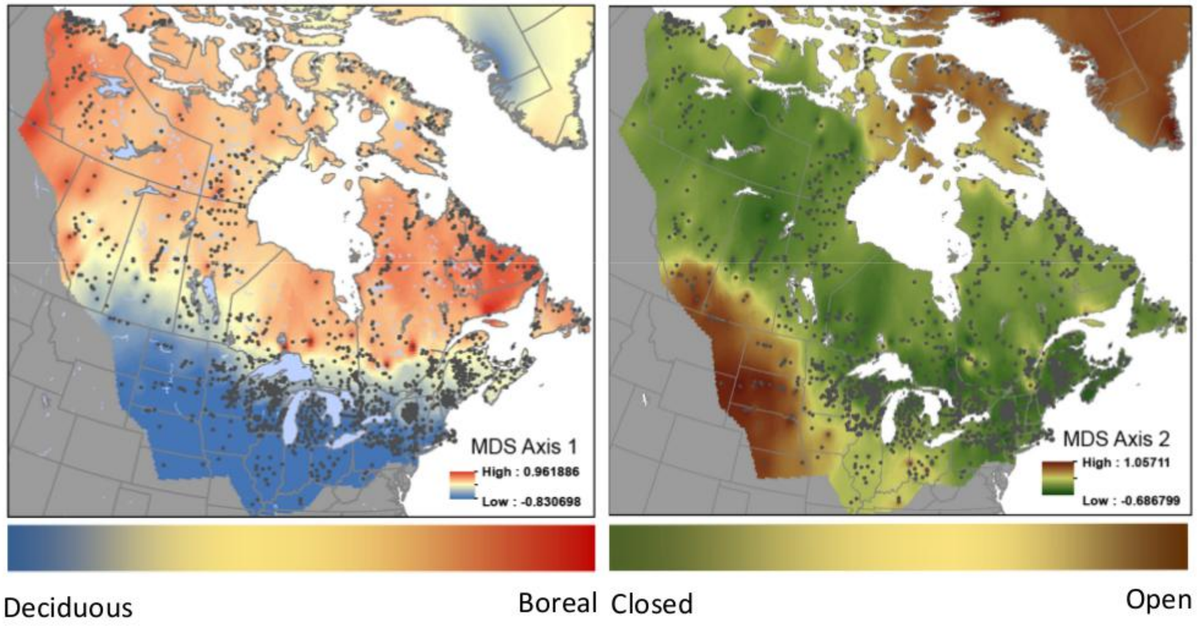
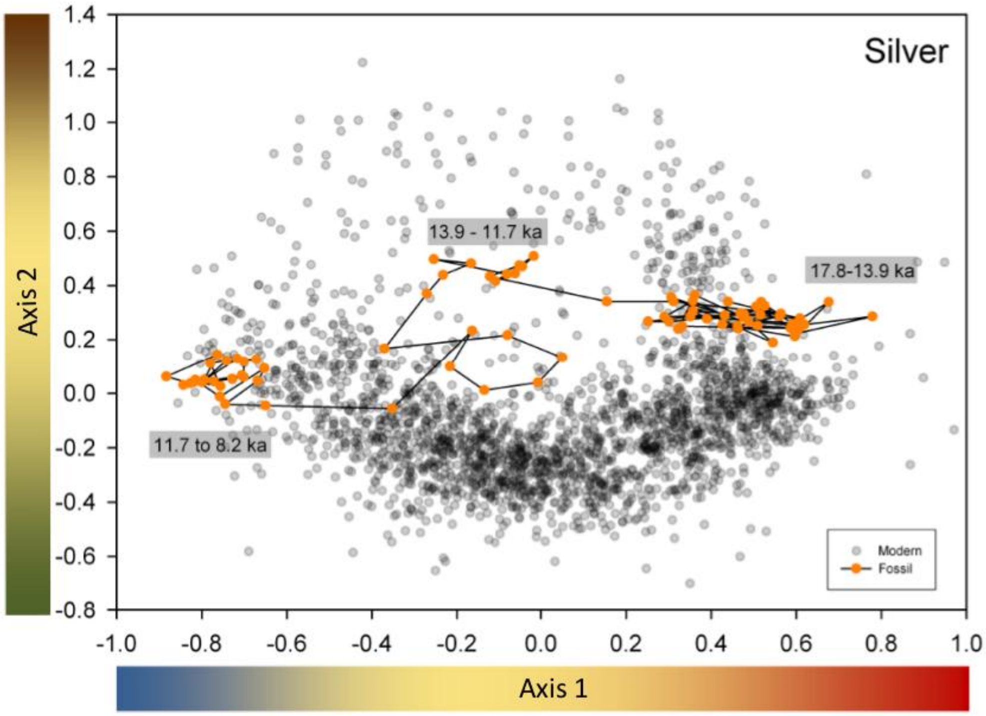


Figure 15: Site trajectories through NMDS space



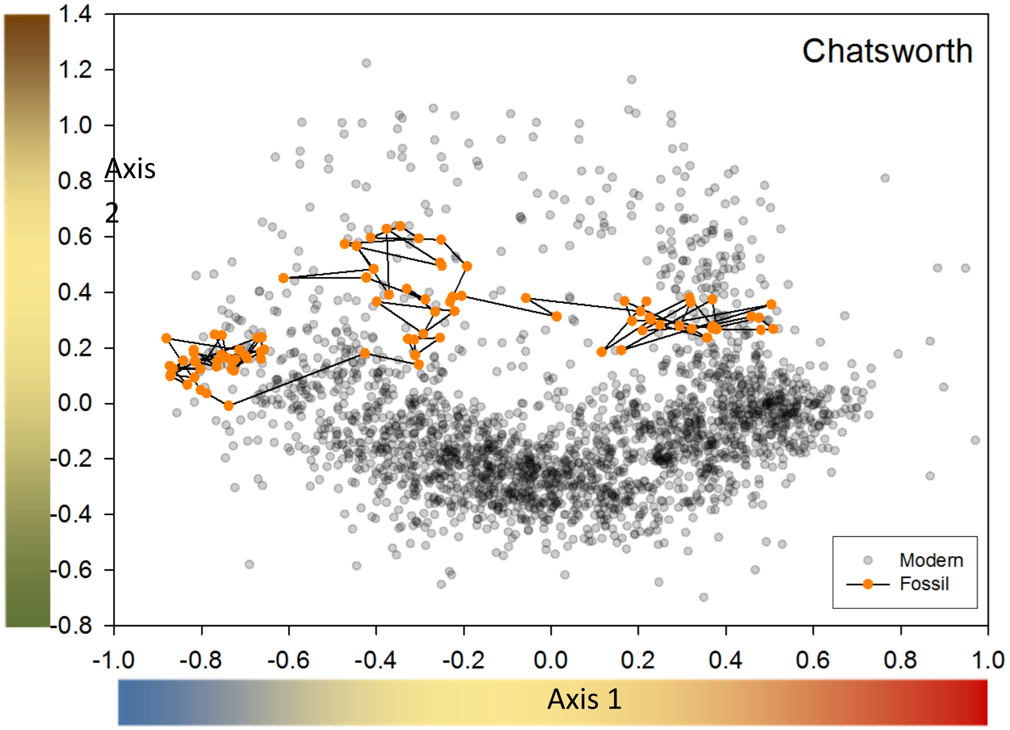


Figure Legends

Figure 1: Drivers of vegetation change during the Pleistocene-Holocene transition (17 ka to 8 ka BP) Top panel: solar energy, shown as accumulated summer solar energy (yellow line), using a the 400 W threshold (Matthews 1992) and June insolation (solid orange line) and December (dashed orange line) insolation, expressed as differences from modern values (W/m^2) (Berger & Loutre (2006). Second panel: changes in atmospheric circulation, temperature, and precipitation, represented by: oxygen isotope data from the more distal NGRIP ice core (Berger and Loutre , Andersen et al. 2006) and the relatively nearby White Lake, NJ (Andersen et al. , Yu 2007). Third panel: atmospheric CO_2 concentrations (pink line) from the Vostok ice core (Yu 2007), and ice volume (purple line) estimated from Dyke et al. (1999) by B. Shuman (pers. comm.). Fourth panel: the functional and final extinctions of Pleistocene megafauna, indicated by a) last appearance dates in the bone record (black circles with 2-sigma whiskers) based on direct dating of bones, for megafauna local to the Great Lakes region (Dyke 2004) and by b) declines in *Sporormiella* spore abundances at Appleman Lake (black bars) and Silver Lake (brown bars) (Faith and Surovell 2009, Gill et al. 2009). Last panel: the arrival and increase in human populations, represented as population estimates (green line) from Peros et al. (2012) and dates of earliest human presence (black boxes) Mud Lake (ML), Buttermilk Creek (BC), and the Heboir and Schaefer mammoth sites (HS) (Johnson 2006, Joyce 2006, Peros et al. 2010). The information in each panel is qualitatively summarized by gradient bars, which are used as for reference purposes in Figs. 3-10.

Figure 2: Bayesian age models for Kirchner Marsh (a) and Spicer Lake (b) based on the probability density function of each calibrated radiocarbon age (main panel). Age model probability is represented by a grayscale cloud, bounded by dotted-line error ranges. Inset figures show the prior (lines) and posterior densities (area fills) for the mean accumulation rate ("acc.shape," aka sedimentation rate) and memory ("mem.strength"; autocorrelation strength at 1 cm intervals), the two prior estimates in the age model. Bacon assumes linear accumulation, rejecting any outliers that violate this assumption.

Figure 3: Site map indicating the modern position of the sites analyzed for this paper. Sites in black indicate new data contributions, while green sites are previously-published records. Brown sites are those being analyzed as part of a broader analyses of the late-glacial no-analog associations by Stephen T. Jackson, a co-PI on the grant that supported this work. Maps on the right are modified from Williams et al 2007, indicating the location of peak vegetation dissimilarity in red.

Figure 4: Minimum vegetation dissimilarity from present for all sites in the transect, from northwest to southeast: Kirchner Marsh, MN (KM), Devil's Lake, WI (DL), Crystal Lake, IL (CL), Chatsworth Bog, IL (CB), Spicer Lake, IN (SP), Appleman Lake, IN (AL) and Silver Lake, OH). Squared-chord distance (SCD) values were calculated for all sites by comparing each fossil pollen sample with its closest matches in a subset of the Modern Surface Sample Dataset (Waters et al. 2011). Samples with SCD >0.3 are interpreted as having no modern analog. The transparent vertical grey bar indicates the no-analog interval. The horizontal hatched bar

indicates that no core material is available for that interval. The solid hatched bar indicates that data are not available from that interval.

Figure 5: *Picea* (green), *Pinus* (black), and *Quercus* (blue) pollen from all sites in the transect, in order from northwest to southeast: Kirchner Marsh, MN (KM), Devil's Lake, WI (DL), Crystal Lake, IL (CL), Chatsworth Bog, IL (CB), Spicer Lake, IN (SP), Appleman Lake, IN (AL) and Silver Lake, OH). Pollen data are represented as a percentage of the upland pollen sum. The transparent vertical grey bar indicates the no-analog interval. The horizontal hatched bar indicates that no core material is available for that interval. The solid hatched bar indicates that data are not available from that interval. All plots are on the same y-axis, except when indicated by a star.

Figure 6: *Fraxinus nigra*-type (black) and *Ostrya*-type (green) pollen from all sites in the transect, in order from northwest to southeast: Kirchner Marsh, MN (KM), Devil's Lake, WI (DL), Crystal Lake, IL (CL), Chatsworth Bog, IL (CB), Spicer Lake, IN (SP), Appleman Lake, IN (AL) and Silver Lake, OH). Pollen data are represented as a percentage of the upland pollen sum. The transparent vertical grey bar indicates the no-analog interval. The horizontal hatched bar indicates that no core material is available for that interval. The solid hatched bar indicates that data are not available from that interval. All plots are on the same y-axis, except when indicated by a star.

Figure 7: *Fraxinus nigra*-type (black) and *Ulmus*-type (green) pollen from all sites in the transect, in order from northwest to southeast: Kirchner Marsh, MN (KM), Devil's Lake, WI (DL), Crystal Lake, IL (CL), Chatsworth Bog, IL (CB), Spicer Lake, IN (SP), Appleman Lake, IN (AL) and

Silver Lake, OH). Pollen data are represented as a percentage of the upland pollen sum. The transparent vertical grey bar indicates the no-analog interval. The horizontal hatched bar indicates that no core material is available for that interval. The solid hatched bar indicates that data are not available from that interval. All plots are on the same y-axis, except when indicated by a star.

Figure 8: *Larix* (green) and *Salix* (black) pollen from all sites in the transect, in order from northwest to southeast: Kirchner Marsh, MN (KM), Devil's Lake, WI (DL), Crystal Lake, IL (CL), Chatsworth Bog, IL (CB), Spicer Lake, IN (SP), Appleman Lake, IN (AL) and Silver Lake, OH). Pollen data are represented as a percentage of the upland pollen sum. The transparent vertical grey bar indicates the no-analog interval. The horizontal hatched bar indicates that no core material is available for that interval. The solid hatched bar indicates that data are not available from that interval. All plots are on the same y-axis, except when indicated by a star.

Figure 9: *Betula* (green), and *Pinus* (undifferentiated; black) pollen from all sites in the transect, in order from northwest to southeast: Kirchner Marsh, MN (KM), Devil's Lake, WI (DL), Crystal Lake, IL (CL), Chatsworth Bog, IL (CB), Spicer Lake, IN (SP), Appleman Lake, IN (AL) and Silver Lake, OH). Pollen data are represented as a percentage of the upland pollen sum. The transparent vertical grey bar indicates the no-analog interval. The horizontal hatched bar indicates that no core material is available for that interval. The solid hatched bar indicates that data are not available from that interval. All plots are on the same y-axis, except when indicated by a star.

Figure 10: Herb pollen (light green), with the Poaceae component indicated in dark green, from all sites in the transect, in order from northwest to southeast: Kirchner Marsh, MN (KM), Devil's Lake, WI (DL), Crystal Lake, IL (CL), Chatsworth Bog, IL (CB), Spicer Lake, IN (SP), Appleman Lake, IN (AL) and Silver Lake, OH). Pollen data are represented as a percentage of the upland pollen sum. The transparent vertical grey bar indicates the no-analog interval. The horizontal hatched bar indicates that no core material is available for that interval. The solid hatched bar indicates that data are not available from that interval. All plots are on the same y-axis, except when indicated by a star.

Figure 11: CHAR (particles/cm^2/year; orange line), *Pinus* pollen (solid black area) and *Quercus* pollen (transparent blue area) for from all sites in the transect, in order from northwest to southeast: Kirchner Marsh, MN (KM), Devil's Lake, WI (DL), Crystal Lake, IL (CL), Chatsworth Bog, IL (CB), Spicer Lake, IN (SP), Appleman Lake, IN (AL) and Silver Lake, OH). Pollen data are represented as a percentage of the upland pollen sum. The transparent vertical grey bar indicates the no-analog interval. The horizontal hatched bar indicates that no core material is available for that interval. The solid hatched bar indicates that data are not available from that interval. All plots are on the same y-axis, except when indicated by a star.

Figure 12a-e: A map showing all sites as pie charts indicating the relative abundance of *Picea*, *Fraxinus*, *Ostrya*, other trees, and herbs at each sample at 15 ka, 14 ka, 13 ka, 12 ka, and 11 ka BP. The white area is the margin of the Laurentide Ice Sheet, from Dyke et al. (2005).The relative size of each pie chart is proportional to the SCD score of its respective pollen assemblage. Small grey circles at 15 ka and 14 ka BP indicate sites that have not yet begun sedimentation.

Figure 13: Two-dimensional NMDS of all modern pollen samples (transparent grey circles) and no-analog fossil samples (solid orange samples). Axes 1 and 2 are oriented such that the NMDS is positioned similarly to the scores of the samples in geographic space (Fig. 14).

Figure 14: Map of inverse-distance-weighted interpolations NMDS values for Axis 1 (top) and Axis 2 (bottom).

Figure 15: Spaghetti plots showing the trajectories of Crystal Lake and Chatsworth Bog through NMDS space from sample to sample. Transparent grey circles are the modern pollen samples, ad solid orange circles represent the fossil pollen samples through time, linked in chronological order with black lines. Color bars indicate inverse-weighted interpolations of the NMDS values from figure 14.

Appendix I

All new data collected for this dissertation has been attached in a supplemental electronic file (with an accompanying metadata file), which may be downloaded along with this .pdf file. Data will also be deposited in appropriate databases pending publication, including Neotoma (pollen, radiocarbon dates, LOI), the Global Charcoal Database (charcoal), and Dryad (for geochemical and geophysical data).