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Diverse responses of vegetation and fire after pleistocene megaherbivore extinction across the eastern US

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ABSTRACT

Megaherbivores are keystone species whose removal from landscapes can cause cascading ecosystem changes, yet the consequences of Late Quaternary megaherbivore extinctions remain uncertain. This paper tests the Megaherbivory Release Hypothesis (MRH), which posits that the decline and extinction of megaherbivores (body size >1000 kg) during the last deglaciation in eastern North America contributed to the expansion of more palatable hardwood tree taxa, the development of vegetation assemblages with no modern analogue, and increased fuel load and fire activity. Coprophilous fungal spores in lake sediment records are used as proxies for megaherbivore abundance and are essential to testing the MRH through analyses of lead/lag relationships among vegetation composition, megaherbivore abundance, fire, and climate. Although some prior analyses of coprophilous fungal spores from individual sites have supported the MRH, these interpretations have been complicated by 1) discrepancies in the timing of coprophilous spore declines versus megaherbivore extinction timing based on dated vertebrate remains, 2) reliance on a single fungal taxon (*Sporormiella*) rather than a full suite of coprophilous fungi taxa, and 3) uncertainties in the taphonomic processes that influence fungal spore abundances. To examine the spatiotemporal relationships among megaherbivory, vegetation, and fire, we developed five new multi-taxon coprophilous fungal spore records for comparison with existing pollen, spore, and charcoal records from 14 sites across eastern North America. The MRH was well supported in the northeast and central US, with most sites showing a coprophilous spore decline by ~14.6 ka followed by a rise of hardwood taxa (~14.4 ka). However, changes in fire regime varied widely among northeast and central US sites and may have preceded spore declines. The MRH was not well supported in the southeastern US, where a smaller rise in hardwood taxa (~16.1−13.1 ka) generally preceded the decline in coprophilous spores at individual sites (~15.8−12.7 ka). These site-level and regional differences suggest spatial variations in the strength of couplings among late-Quaternary megaherbivore extinctions, vegetation composition and structure, and fire regime. Possible explanations for the differences between the northern and southeastern US include (1) differences in landscape heterogeneity of canopy openness and palatability, (2) net primary productivity and sensitivity to top-down trophic effects, (3) megaherbivore density, and (4) climate trends and seasonality at orbital to millennial timescales.

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1. Introduction

Paleoecologists have long debated the interactions among climate change, megafaunal extinctions, fire regime shifts, and vegetation dynamics during the end-Pleistocene deglaciation (e.g. Gill et al., 2009; Gill et al., 2012; Martin and Klein, 1984; Owen-Smith, 1987; Zimov et al., 1995). One hypothesis, which we term the Megaherbivory Release Hypothesis (hereafter MRH), posits that the loss of diverse guilds of Pleistocene megaherbivores (>1000 kg [Owen-Smith, 1987],) in eastern North America and elsewhere during the last deglaciation contributed to the expansion of more-palatable temperate deciduous tree taxa as they were released from megaherbivore suppression, increased fire activity as hardwood fuel loads increased, and the formation of vegetation associations with no modern analogue (Gill et al., 2009, 2012; Gill, 2014). The MRH is an example of trophic downgrading, in which removal of one or more top-level consumers affects lower levels of the food web (Estes et al., 2011). For instance, grazing typically increases plant species diversity (Hester et al., 2006), particularly in areas with high net primary productivity (Bakker et al., 2016). Megaherbivores can reduce fire fuel load (Bond and Keeley, 2005; Staver et al., 2009) and influence tree recruitment by increasing open space and reducing canopy density through both herbivory and trampling, which inhibits sapling and small plant growth. In riesponse to the growing recognition of the functional importance of megaherbivores, some conservation biologists are exploring rewilding strategies, in which functional analogues of extinct megaherbivores are introduced into contemporary ecosystems with the goal of reversing trophic downgrading and increasing biodiversity (Schowanek et al., 2021; Svenning, 2018; Svenning et al., 2016). Improved understanding of the effects of reduced megaherbivory on late-Pleistocene vegetation is thus of direct relevance to contemporary practice in conservation biology, and an example of the emerging field of conservation paleobiology (Barnosky et al., 2017; Dietl et al., 2015).

Testing the MRH is complicated by challenges in disentangling megafaunal effects from other past drivers of ecosystem dynamics. Post-glacial vegetation dynamics in North America and elsewhere are known to be strongly regulated by climate (Williams et al., 2004; Giesecke et al., 2019). The last deglaciation was characterized by multiple large and interlinked environmental changes, including rising temperatures and altered patterns of precipitation (Fastovich et al., 2020), a Northern Hemisphere peak in insolation seasonality at 11 ka, rising CO_2 and its effects on plant productivity and nutrient content (Faith, 2011; Prentice et al., 1991), and widespread changes in fire regime that were jointly regulated by changing climates, megaherbivore extinctions, and CO_2 (Karp et al., 2021; Marlon et al., 2009). Because many of these factors vary over both space and time, single-site studies usually cannot provide definitive evidence for or against causal hypotheses such as the MRH.

Establishing the timing of lead-lag relationships is central to testing hypotheses about past megaherbivore-vegetation-fire interactions. Much of the research testing the MRH has therefore been powered by records retrieved from lake and mire sediments, in which multiple proxies provide independent records of past vegetation composition (e.g. pollen, plant macrofossils, and sedimentary ancient DNA (sedaDNA)), fire history (e.g, sedimentary charcoal and other combustion byproducts), megaherbivore population declines and extinctions (e.g. coprophilous fungal spores, fecal sterols, and sedaDNA), and past climates (e.g. isotopes and biomarkers). Spores from coprophilous (dung-affiliated) fungi in association with other lacustrine paleoecological proxies are increasingly used to track local changes in megaherbivore abundances in different biomes, geographic regions, and times (Baker et al., 2013; Perrotti and van Asperen, 2019). In the northeast and central US, Robinson et al. (2005) and Gill et al. (2009, 2012) showed that declines in spores of coprophilous fungi (hereafter coprophilous spores or spores) coincided with or slightly preceded increases in fire activity and an increase in deciduous hardwood tree pollen at six sites. Other studies include Beringia (Graham et al., 2016; van Geel et al., 2011b; Monteath et al., 2021), Australia (Rule et al., 2012; van der Kaars et al., 2017), New Zealand (Wood and Wilmshurst, 2013), the Andes (Rozas-Davila et al., 2016), western North America (Davis, 1987; Davis and Shafer, 2006), eastern North America (Gill et al., 2009, 2012; Halligan et al., 2016; Robinson et al., 2005), Europe (Jeffers et al., 2018), and Africa (Ivory and Russell, 2016; van Geel et al., 2011a).

Using coprophilous spore records to test the MRH, however, is complicated by questions about the fidelity of coprophilous spores as indicators of megaherbivore abundance and extinction timing. For instance, the timing of coprophilous spore declines at several sites in North America precedes the final extinction of mastodon and mammoth by several thousand years (Feranec and Kozlowski, 2016; Fiedel, 2018; Widga et al., 2017). It is possible that declining spore concentrations indicate declining grazing pressure and functional extinction prior to final extinction (Gill et al., 2009), but many taphonomic factors can complicate the ecological interpretation of spore abundances. First, increases in pollen accumulation rates can depress the detection probability of spores if all samples are counted to the same pollen sum (Wood and Wilmshurst, 2013). Second, coprophilous spore dispersal can be highly localized, reflecting dung or large herbivore presence within 100 m (Baker et al., 2016; Gill et al., 2013), raising the possibility that spore representation in lake sediments is sensitive to factors such as distance to shoreline, and suggesting that spore presence may be more meaningful than absence (van Asperen et al., 2020). Hence, abundant spores are best interpreted to indicate high levels of grazing, near or at carrying capacity, and fluctuations in spore abundances may not directly represent fluctuations in megaherbivore abundances (Davies et al., 2022).

Several strategies have been proposed to enhance the ecological signals recoverable from coprophilous spore data. Coprophilous spores may work best as indicators of megaherbivory pressure in sediments collected from small basins with simple geometries (Baker et al., 2013). Absolute concentrations or accumulation rates are sometimes preferred when analyzing spore data (Perrotti and van Asperen, 2019), because coprophilous spores are frequently found in lower relative abundances than many terrestrial pollen types (e.g., 2%–8% of the terrestrial pollen sum), and percentages are sensitive to changes in the absolute concentrations of other taxa (Davis, 1963). However, concentration and accumulation rates are sensitive to changes in sedimentation rate and require well-constrained age-depth models, thus, simultaneously considering spore percent, concentration, and accumulation is recommended (Davis et al., 1984). Lastly, recent papers now recommend using multiple coprophilous spore taxa (Table 2) (Baker et al., 2016; Davies et al., 2022; Graham et al., 2016; Perrotti and van Asperen, 2019), to minimize the chance that spore abundance fluctuations result from environmental changes (e.g. Kuthubutheen and Webster, 1986) or other autecological characteristics.

To test the MRH and address the above challenges, we employ a multi-site, multi-proxy, and multi-spore-taxa research design. We examined 14 new and existing coprophilous spore records from across eastern North America, from the southern Great Lakes and New York State to peninsular Florida (Fig. 1). These spore records are analyzed alongside established records of pollen and charcoal spanning the eastern US to better understand the spatiotemporal

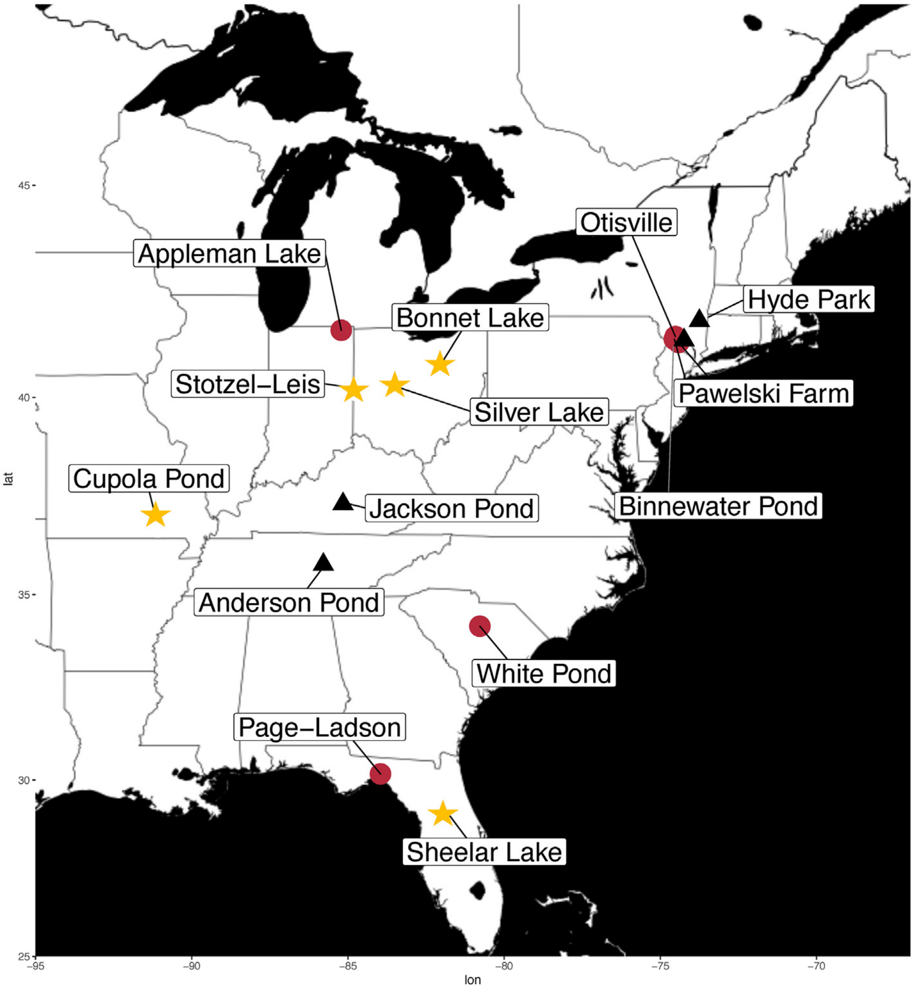


Fig. 1. Map of sites. Yellow stars indicate sites where we completed multi-taxa coprophilous spore recounts. Red circles indicate sites where we used existing coprophilous spore counts; these counts are for Sporormiella only, except White Pond, which includes counts for Sporormiella, Coniochaeta, Cercophora, and Podospora. Black triangles indicate sites not included in the time series analyses due to incomplete deglacial sediment sequences or insufficient chronological control.

patterns in deglacial megaherbivore abundance and declines, vegetation dynamics, and interactions with changing climates and fire regime. All sites include AMS radiocarbon chronologies, fossil pollen, and sedimentary charcoal indicators of past vegetation and fire histories. The existing coprophilous spore records from these sites have been limited to *Sporormiella* (Gill et al., 2009, 2012; Robinson et al., 2005). Hence, a cornerstone of this synthesis is five new records of multiple coprophilous fungal taxa alongside published multi-taxon coprophilous spore counts and *Sporomiella*-only records (Table 1). We assess the timing and strength of coprophilous spore declines across the eastern US and their timing relative to independent estimates of megaherbivore extinction based on direct bone dates. We then evaluate the MRH by examining the relative timing of spore declines, increases in deciduous hardwood tree abundances and no-analogue vegetation, and shifts in fire regime, focusing separately on sites in the northeast and central US (NECUS) and southeastern US (SEUS) to test for regional variations in megaherbivore-fire-vegetation-climate interactions. Records supporting the MRH are expected to exhibit a spore decline followed by an increase in hardwood pollen abundance, no-analogue pollen assemblages, and sedimentary charcoal.

2. Methods

2.1. Site selection and palynological analysis

Sites were chosen to trace the timing of the coprophilous spore declines across the NECUS (40.22N–41.78N, 73.89W–85.21W) and SEUS (−29.31N–37.50N, 82.00–91.09W) and span multiple vegetation formations (Fig. 1). Postglacial expansion of hardwood taxa across these regions was time-transgressive over several millennia (Williams et al., 2004), whereas some late-Quaternary extinctions, such as mammoth and mastodon (Widga et al., 2017), are believed to have occurred more quickly. The five sites selected for new analyses of coprophilous fungal spores (Table 1) were chosen based on temporal length of record, existence of both pollen and charcoal data, availability of pollen residues for recounts of coprophilous spores, and geographic distribution across the region. Established spore records were also reviewed here to further increase spatial coverage (Table 1). There are four other studies in the eastern US that explicitly included *Sporormiella* in their pollen analyses but were not included in our analysis (Table 1). Of these sites, Pawelski Farm and Hyde Park, New York (Robinson et al., 2005) report high

Table 1
Site names, data characteristics, and associated publications.

Site	Coprophilous Spores	Pollen	Charcoal	Comments
Hyde Park, NY	*Sporormiella* only; Robinson et al. (2005)	Robinson et al. (2005)	Microcharcoal[a]; Robinson et al. (2005)	Omitted from formal analysis due to inadequate chronological control
Binnewater Pond, NY	*Sporormiella* only; Robinson et al. (2005)	Robinson et al. (2005)	Microcharcoal[a]; Robinson et al. (2005)	
Otisville, NY	*Sporormiella* only; Robinson et al. (2005)	Robinson et al. (2005)	Microcharcoal[a]; Robinson et al. (2005)	
Pawelski Farm, NY	*Sporormiella* only; Robinson et al. (2005)	Robinson et al. (2005)	Microcharcoal[a]; Robinson et al. (2005)	Omitted from formal analysis due to inadequate chronological control
Appleman Lake, IN	*Sporormiella* only; Gill et al. (2009)	Gill et al. (2009)	Macrocharcoal; Gill et al. (2009)	
Bonnett Lake, OH	Multi-taxon; this study	Fastovich et al. (2020)	Macrocharcoal; Fastovich et al. (2020)	
Silver Lake, OH	Multi-taxon; this study	Gill et al. (2012)	Macrocharcoal; Gill et al. (2012)	
Stotzel-Leis, OH	Multi-taxon; this study	Watson et al. (2018)	Macrocharcoal; Watson et al. (2018)	
Jackson Pond, KY	*Sporormiella* only; Liu et al. (2013)	Liu et al. (2013)	Liu et al. (2013)	Omitted from formal analysis due to truncated deglacial record
Anderson Pond, TN	*Sporormiella* only; Liu et al. (2013)	Liu et al. (2013)	Liu et al. (2013)	Omitted from formal analysis due to truncated deglacial record
Cupola Pond, MO	Multi-taxon; this study	Jones et al. (2017)	Macrocharcoal; Jones et al. (2017)	
White Pond, SC	Multi-taxon; Moore et al. (2019)	Krause et al. (2019); Moore et al., (in prep)	Macrocharcoal; Krause et al. (2019)	
Page-Ladson, FL	*Sporormiella* only; Halligan et al. (2016)	Perrotti (2018)	Macrocharcoal unassociated with pollen[b]; Hansen (2006)	
Sheelar Lake, FL	Multi-taxon; this study	Krause et al. (in prep)	Macrocharcoal; Krause et al., (in prep)	

[a] Binnewater and Otisville charcoal analyses are based on microcharcoal, which represents a more regional or extra-regional source area relative to the more locally sourced macrocharcoal data from other sites.

[b] Page-Ladson charcoal samples are from archaeological excavation side-wall samples and are not directly associated with pollen and spore data.

levels of *Sporormiella* in Pleistocene sediments and a decline in the earliest Holocene. However, neither site had adequate chronological control to construct an age-depth model. Liu et al. (2013) included a search for *Sporormiella* in their analyses at Anderson Pond, TN and Jackson Pond, KY, but found few spores, and the sediment sequences were truncated during the late-glacial transition.

We used original pollen residues from Bonnett, Silver, Stotzel-Leis, Cupola, and Sheelar to produce new fungal spore counts. Palynological extraction methods for these residues are detailed in the original publications (Table 1). Sheelar was originally cored and analyzed for pollen by Watts and colleagues in the 1980's (Watts and Hansen, 1994; Watts and Stuiver, 1980), and was cored again by Krause and others in 2016; a paper describing the site, age-depth model, and pollen datasets is in preparation (SOM Section 1; Krause, pers. comm.).

Pollen residues were mounted on microscope slides and scanned (20 transects/slide) at 400x magnification. We counted the occurrence of 12 fungal spore types that are either primarily or often associated with dung substrates and are considered to be indicators of megaherbivore abundance in both modern and ancient settings (Table 2; SOM Fig. 44) (e.g. Perrotti and van Asperen, 2019) on one slide, alongside a tracer of known concentration (either *Lycopodium* spores or microspheres). This counting procedure, in which we searched for only coprophilous spores and tracers across a fixed number of transects, may reduce the sensitivity of spore detection probability to a fixed pollen sum. However, high accumulation rates of pollen can reduce the detection probability of both spores and tracers, which increases the uncertainty of spore concentrations.

Where possible, we report abundances as both absolute concentrations and percentages relative to a terrestrial pollen sum. Concentrations could not be calculated for two of the recounted sites - Bonnett and Stotzel-Leis - because the microsphere tracer used to estimate concentration was contaminated by a biofilm in the solution that caused clumping of the spheres (Jessica Heck, personal communication 2018). Instead, we calculated spore-to-pollen ratios for Bonnett and Stotzel-Leis using microsphere counts from the coprophilous spore recounts and the original pollen counts, under the assumption that the microsphere distribution would be constant within each individual pollen residue. We were thereby able to calculate coprophilous spore abundances as a percentage of the total pollen assemblage.

2.2. *Age-depth models*

Age-depth models were recalculated for each site using radiocarbon dates reported in the original site publications, primarily consisting of AMS dates on terrestrial plant macrofossils (SOM Tables 3–14). Radiocarbon dates were calibrated using the IntCal20 calibration curve for the Northern Hemisphere (Reimer et al., 2020). We constructed the age depth models using the Bayesian age-depth modeling package *rbacon* (version 2.4.3) (Blaauw and Christen, 2011) in the Rstats program (R Core Team, 2021) (SOM Figs. 1–7, 11-15). For sites with previously published Bayesian age-depth models, we used the reported priors.

2.3. *White Pond: aligning two cores and datasets*

At White Pond, two sets of cores (<25 m apart) were collected at different times in 2016 and analyzed by different teams (Krause et al., 2019; Moore et al., 2019), with different analyses for each core. Krause et al. (2019) completed a 30,000 year-long pollen record, anchored by 15 AMS radiocarbon dates (SOM Table 10), each based on materials of known terrestrial plant origin, and accompanied by analyses of branched glycerol dialkyl glycerol tetraethers

Table 2
Coprophilous fungi counted in this study. Modern taxonomic affinity for fungal types encountered in this study and substrates. Table modified from Perrotti and van Asperen (2019). Table is organized by strength of coprophilous association and alphabetically, with fungal taxa listed first that are strongly associated with herbivore dung (marked by asterisks), then less strongly associated taxa listed. Photos of select taxa are available in SOM Fig. 44.

Genus	Substrate	References
*Ascodesmis**	Primarily dung; occasionally soil or decaying vegetation	Doveri, 2007, p.492; Guarro et al., 2004, p.79
*Arnium**	Primarily dung; occasionally soil	Bell (1983), p.46, Doveri, 2007, p.872; Guarro et al., 2004, p.59)
*Bombardioidea**	Exclusively dung	Bell (1983), p.49; Doveri, 2007, p.870
*Delitschia**	Almost exclusively herbivore dung; occasionally soil and decaying wood	Bell (1983), p.51; Guarro et al., 2004, p.159
*Podospora**	Almost exclusively herbivore dung; occasionally soil	Bell (1983), p.14; Doveri, 2007, p.905, Guarro et al., 2004, p.340; Shlütz and Shumilovskikh (2017)
*Sordaria**	Almost exclusively dung; occasionally soil or vegetation	Bell (1983), p.36; Doveri, 2007, p.826; Guarro et al., 2004, p.383
*Sporormiella**	Mostly herbivore dung; occasionally soil or wood	Doveri, 2007, p.613
*Trichodelistchia**	Exclusively dung	Bell (1983), p.51
Apiosordaria	Primarily soil; occasionally dung	Krug et al., 2004; Guarro et al., 2004, p.59
Coniochaeta	Primarily soil; also dung and decaying wood	Bell (1983), p.39, Hanlin (1990); Doveri, 2007, p.810; Guarro et al., 2004, pp.132-142
Cercophora	Primarily decaying vegetation; occasionally charcoal, soil, and dung	Bell (1983), p.40; Doveri, 2007 p.847; Hanlin (1990), pp,46–47; Guarro et al., 2004, p.111
Chaetomium	Primarily decaying vegetation; also dung, soil, and other organic substrates	Bell (1983), p.33; Doveri, 2007, p.760; Guarro et al., 2004, p.118

(brGDGTs), magnetic susceptibility, macroscopic charcoal proxies, and analyses of *Sporormiella* abundance. Moore et al. (2019) focused on the interval from ca. 15.0 to 8.4 ka, anchored by 22 AMS radiocarbon dates (from mostly aquatic seeds of unknown taxonomic affinity, see SOM 11), and conducted multiple geochemical and other indicators of a hypothesized Younger Dryas impact event that included a multi-taxon search for coprophilous spores (*Sporormiella, Coniochaeta, Sordaria,* and *Podospora*). The Moore et al. (2019) record also has an unpublished fossil pollen record (Moore et al. in prep.).

Here we show summary pollen metrics from both cores, the multi-taxon coprophilous fungi data from Moore et al. (2019; hereafter called WHIT19-Moore), and charcoal data from Krause et al. (2019; hereafter called WHIT19-Krause). We primarily used the pollen metrics from WHIT19-Moore to assess lead-lag relationships with the fungal spore data from the same record. However, because the multi-taxon spore record is from WHIT19-Moore, and the charcoal record is from WHIT19-Krause, we relied on cross-correlation and alignment of the two cores based on three stratigraphic horizons (Table 3): 1) a rise in *Fagus* (beech) pollen abundances (WHIT19-Krause: 285 cm below sediment surface, WHIT19-Moore: 233 cm depth [SOM Fig. 8]), 2) a *Fagus* decline (WHIT19-Krause: 261 cm depth, WHIT19-Moore: 210 cm), and 3) a lithostratigraphic boundary that is close to the *Fagus* decline (WHIT19-Krause: 262 cm; WHIT19-Moore: 212 cm). The *Fagus* decline is associated with a mud-to-peat transition (WHIT19-Moore) and a transition from organic silty gyttja to brown gyttja with coarse organics and intermittent charcoal layers (WHIT19-Krause) and marks the top of Unit II in Moore et al. (2019) and the top of Unit 4 in Krause et al. (2019). Based on these stratigraphic benchmarks, several differences emerge between the WHIT19-Krause and WHIT19-Moore age-depth models. First, the estimated ages for the *Fagus* rise differs substantially between the two cores, with the WHIT19-Krause estimate 1500 years younger than for WHIT19-Moore. Second, WHIT19-Moore inferred a sedimentation hiatus at the top of Unit II and immediately above the *Fagus* decline at 211.5 cm, based on the abruptness of the lithological boundary and bracketing calibrated radiocarbon dates that are offset by ~2000 years. No hiatus was reported for WHIT19-Krause (Krause et al., 2019). The source of the potential hiatus detected by Moore et al. (2019) remains unclear and is not interpreted here to reflect a regional or site-wide event.

Given these discrepancies, we maintained separate age-depth models for the two cores and, when plotting these time series, indicated the age-depth model used. To better align and update the two records, we recalculated the age-depth models for each. For the Krause et al., (2019) core, we kept all dates and updated the calibration curve to IntCal20NH for a new age-depth model called Krause19-AP21. For the WHIT19-Moore core, we used all dates from WHIT19-Moore core WP-2016-3 (the WHIT19-Moore published model [see SOM Fig. 10] also included dates from nearby cores), included a hiatus at 211.5 cm as in Moore et al. (2019), and added as additional constraints the modeled ages of a *Fagus* pollen rise and decline from Krause19-AP21. We call this new model Moore-AP21.

2.4. Data processing and numerical analysis

For all the multi-taxon spore records, we calculated and analyzed the total abundance of strongly coprophilous spores, defined as exclusively or primarily utilizing dung as substrate (Table 2; Perrotti and van Asperen, 2019). For sites in which only *Sporormiella* was counted, we simply show *Sporormiella*; where available total coprophilous fungal spores are reported in the supplementary material (SOM Figs. 16–25). All spore data are presented as concentrations (spores/cm^3) except for Bonnett Lake and Stotzel-Leis due to the microsphere issues noted in Section 2.1. We also calculated spore percentages and accumulation rates as alternative representations of spore abundance, except for White (WHIT19-Moore), where raw counts and therefore percent data were unavailable. Coprophilous spore percentages were calculated relative to the total terrestrial pollen count. Fungal spore accumulation rates (spores/cm^2/yr^1) were calculated by multiplying spore concentration by sedimentation rates at each site and are shown for all sites in the SOM (Figs. 16–25).

Pollen data were summarized as percent abundance of hardwood pollen taxa (defined here as *Acer* (maple), *Alnus* (alder), *Betula* (birch), *Carya* (hickory), *Castanea* (chestnut), *Cornus* (dogwood), *Corylus* (hazelnut), *Fagus* (beech), *Fraxinus* (ash), *Juglans* (walnut), *Liquidambar* (sweetgum), *Morus* (mulberry), *Nyssa* (black gum), *Ostrya/Carpinus* (hophornbeam/ironwood), *Platanus* (sycamore), *Populus* (poplar), *Quercus* (oak), *Salix* (willow), *Tilia* (basswood), and *Ulmus* (elm). For all sites, vegetation novelty and no-analogue pollen assemblages were assessed by calculating the minimum dissimilarity of published pollen datasets (Table 1) to modern pollen assemblages in North America (Whitmore et al., 2005) using the minimum squared-chord distance metric (minSCD). We used the analogue package in R (Simpson, 2007; Simpson and Oksanen, 2020), using the 64-taxon list, and used 0.3

Table 3
White Pond stratigraphic benchmarks from Krause et al. (2019) and Moore et al. (2019). Unit 4 Top (WHIT19-Krause) and Unit II Top (WHIT19-Moore) are interpreted as the same stratigraphic horizon. See SOM Tables 10–11, SOM Figs. 9–12 for dates and age-depth models from each White Pond core.

Benchmark	Core/ Model	Approx. Depth cm below sediment surface	Rounded Median Modeled Age (ka)	95% CI	Comments
Fagus Rise	Krause19-AP21	285	12.10	11,199–12,959	
	Moore-AP21	233	13.35	13,169–13,612	
Fagus Decline	Krause19-AP21	261	10.25	10,025–10,508	
	Moore19-AP21	210	10.35	10,269–10,487	
Unit 4 Top	Krause19-AP21	262	10.20	10,105–10,638	Closest date: 260.5 cm, 9140 ± 30
Unit II Top	Moore19-AP21	212	12.74/10.40	10,458–12,735	Bracketed by dates of 8870 ± 30 and 9230 ± 30 at 210.5 cm and 10,900 ± 30 at 212 cm. Probable hiatus at 211.5 cm

minSCD as a standard threshold for identifying no-analogue vegetation (Williams and Shuman, 2008).

At each site, we used Bayesian Change Point detection (BCP) to assess the timing of changes in coprophilous fungal spore concentrations (or percent at Bonnett Lake and Stotzel-Leis), hardwood pollen percent abundance, and minSCD. We used the 'bcp' package in R (Erdman and Emerson, 2007; Wang and Emerson, 2015), which calculates the posterior probability of a change in mean fungal spore abundance by fitting piecewise linear functions through the data points. We used 10,000 iterations of Markov-Chain Monte Carlo sampling after an initial burn-in of 1000 iterations. We used the recommended parameter of 0.2 in the uniform prior on the signal-to-noise ratio (Barry and Hartigan, 1993), and used $p0 = 0.07$, where p0 is the prior estimate of change point probability. We define change points as intervals where the posterior probability of a change point exceeds 0.3 based on our observation that change points of >0.3 accompany visually apparent declines in spore abundances. This threshold is lower than most standard tests for significance, so this is an operational criterion rather than a formal demonstration of statistical significance. We used visual inspection of the BCP posterior probabilities of a change point and the original time series to define a probable time range for spore declines at each site. When BCP analysis indicated a single significant change point that corresponded with a visual signal (spore decline or pollen, minSCD, or macrocharcoal increase), the result of the BCP analysis was selected as the timing of the change. When BCP analysis indicated multiple significant change points, the last spore decline or the first hardwood pollen, minSCD, or macrocharcoal increase were selected as conservative estimates of the timing of changes. When BCP analysis did not identify a significant change point, the last visually notable spore decline or first visually notable hardwood pollen, minSCD, or macrocharcoal increase were selected. We did not include BCP posterior probabilities for the charcoal data because the highly episodic nature of charcoal accumulation data results in many changepoints detected (see SOM Figs. 36–43) but consulted the posterior probability curves when determining charcoal record changepoints. Many of the changes occur over centuries, so when reporting results, we both present estimates of change points and their temporal ranges.

After updating the age-depth models for each site using the IntCal20 radiocarbon calibration curve, we re-calculated macrocharcoal accumulation and background charcoal deposition rates were calculated using CharAnalysis (Version 1.1; see SOM Table 15 for parameters) (Higuera et al., 2010), except for Binnewater and Otisville, where microcharcoal concentrations are presented.

For all events, we sequentially assessed both depth uncertainty and age uncertainty. Depth uncertainty is caused by discontinuous sampling. Age uncertainty is caused by uncertainties in radiocarbon dating and other age controls that create a range of possible ages for any given depth. For each event, we assessed a range of possible depths through inspection of the *bcp* output and the original proxy measurements, treating this as a uniform probability within this range. We then assigned ages to each depth using the *rbacon* output and report event ages as medians (median age estimate for the median depth, minima (youngest 95% CI age for the uppermost depth) and maxima (oldest 95% CI age for the lowermost depth). When discussing the timing of events, we reference rounded, median modeled ages and age ranges based on minima and maxima.

3. Results

3.1. Timing of declines in coprophilous fungal spore abundances

Of the fourteen sites considered, eleven exhibit coprophilous spore presence and decline in terminal Pleistocene-early Holocene sediments (Fig. 2, Fig. 3). Of the eleven, Pawelski and Hyde Park have spore records with abundant spores in the Pleistocene sediments that decline about the Pleistocene/Holocene boundary but have insufficient chronological control to confidently assess the timing of this shift. Of the three sites that do not show a spore decline, Jackson and Anderson are *Sporormiella*-only and consist of truncated deglacial records. Stotzel-Leis is a multi-taxon record that shows a single large peak at 11.0 ka, but with otherwise moderate spore abundance (up to ~13%) throughout.

No sites show a continuous increase in coprophilous spores from the Pleistocene to Holocene. Hence, individual site-level coprophilous spore records either show trends consistent with declining megaherbivory pressure during the late Pleistocene or show no signal. We interpret the no-signal records as indicating that megaherbivores were not consistently present near these sites in large enough numbers to strongly influence the vegetation, or that spore representation was limited by analytical or taphonomic factors such as the short dispersal distance of coprophilous spores.

The inferred timing and uncertainty vary among the records with coprophilous spore declines (Fig. 2; Fig. 3; SOM Table 17). Most records exhibit a gradual spore decline. At Binnewater, we place the decline at 16.6 ka (range: 17.9–15.8 ka) based primarily on BCP analysis of *Sporormiella*-only percentages. *Sporormiella* spores comprise a proportion of about 5% of the total pollen assemblage and gradually decline from 18.0 ka until 16.6 ka, after which they fall below 2% of the total pollen assemblage until becoming nearly absent from the record at 16.0 ka. BCP detects a changepoint shortly before spores fall below the 2% threshold. The ~2000-year uncertainty in the timing of the spore decline at Binnewater results from

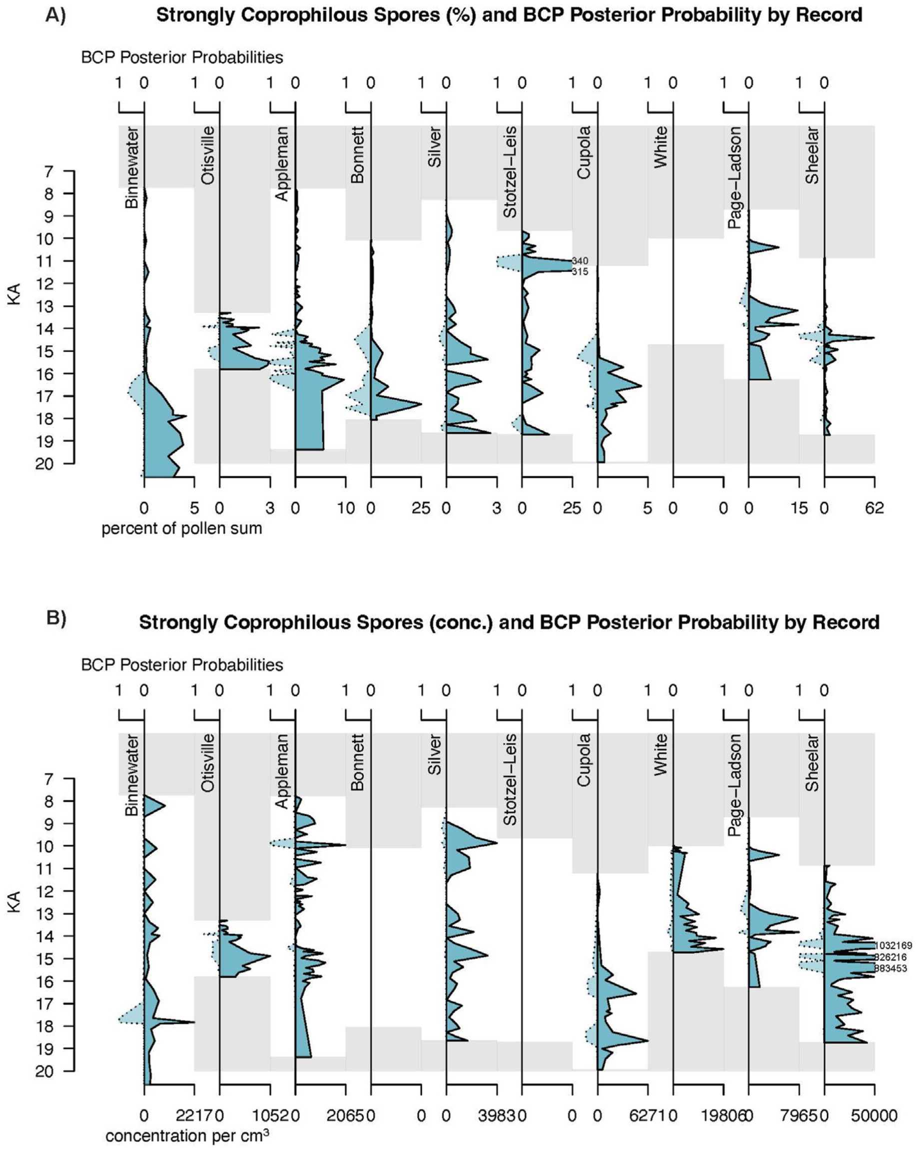
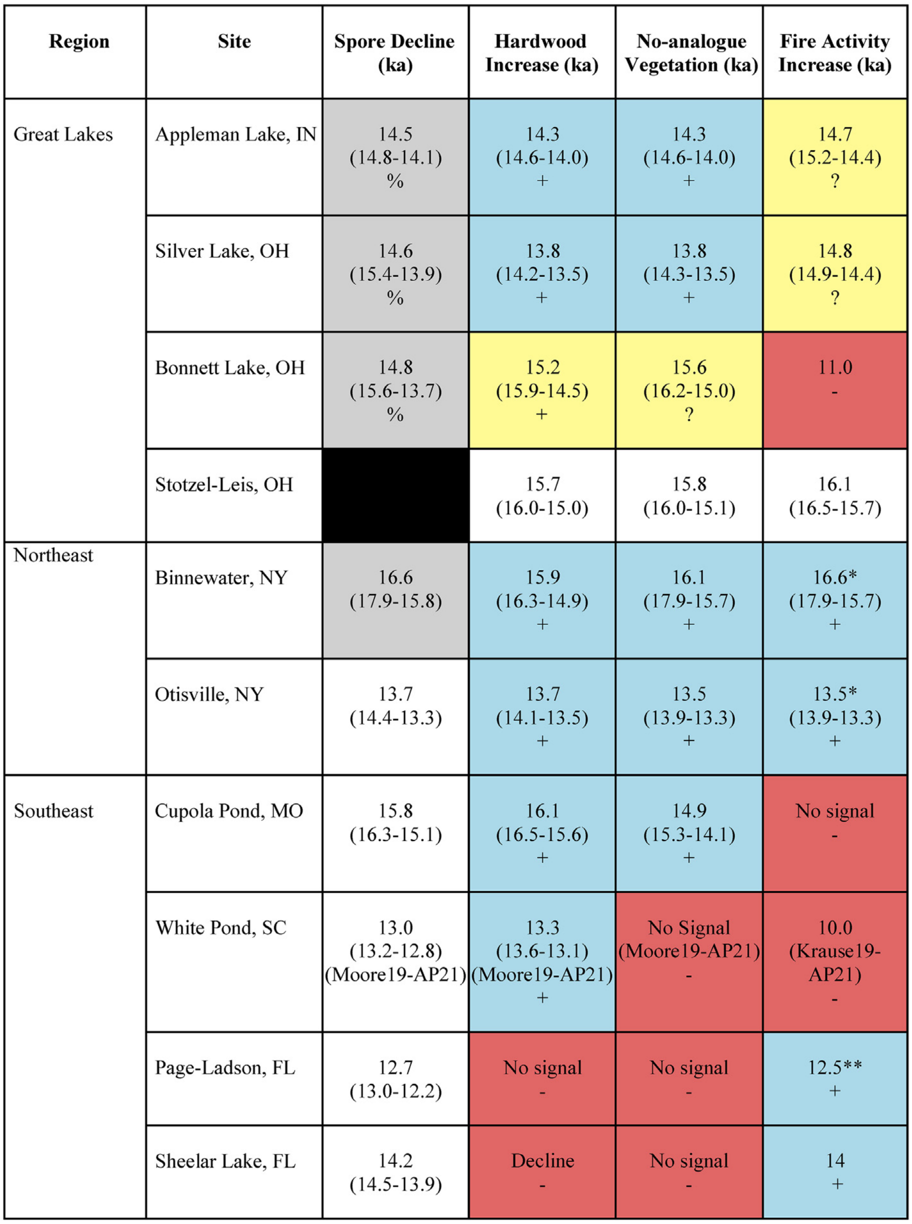


Fig. 2. Trends in strongly coprophilous spore abundances across all sites. Abundances are represented as a percentage of terrestrial pollen (Fig. 2A) and as concentrations (spores/cm^3, Fig. 2B), except for sites where either percentage or concentration data were not available. For each site, the BCP-detected posterior probability of an abrupt changepoint in spore abundance means are on the left side of each axis, with concentration or percentage on the right side of each axis. Sites are arranged longitudinally, with northernmost sites at left. Time periods that were analyzed for coprophilous spores have a white background and are bounded by transparent gray boxes. Note the x-axis scale differences. Individual samples with anomalously high spore concentrations at Stotzel-Leis and Sheelar Lake have been plotted off the x-axes and values noted on the plots. See Table 1 for data sources.

coarse sampling resolution and consequent depth uncertainty as well as age-depth model uncertainty. Spore concentration and accumulation metrics do not reflect a similar pattern, which we interpret to result from an increase in pollen concentration in the late Pleistocene-early Holocene aged sediments, which resulted in a reduction in tracer counts that increased variability in concentration and accumulation estimates.

At Otisville, we place the spore decline at 13.7 ka (range: 14.4–13.3 ka) based on *Sporormiella* concentrations. *Sporormiella* concentrations peak at over 1000 spores/cm^3 shortly before gradually declining after 14.8 ka until the end of the record. BCP indicates a changepoint at ~13.7 ka, after which spore concentration exhibits a final decline. Spore percentages show a similar pattern, strengthening the interpretation that fewer spores were being deposited into the basin in the end-Pleistocene sediments.

At Appleman, we place the decline at 14.5 ka (range: 14.8–14.1 ka) based primarily on BCP analysis of *Sporormiella*-only percentages. The spore decline is variable and gradual, beginning after 16.2 ka with spore abundance above 9%, until it falls below 2% at 14.3 ka. BCP analysis of spore concentration data also suggests a final change point at 14.5 ka. A comparison of spore concentration, accumulation, relative percent to total pollen, and raw counts at Appleman (SOM Fig. 18) shows similar patterns except for differences between measures of spore concentration/accumulation and percent. All metrics show a decline at 14.5 ka, but the percentage data show no return to high abundances, while the concentration and accumulation data show variably high abundances between 13.0 and 9.0 ka. As at Binnewater, highly variable concentrations after the 14.5 ka decline are believed to be due to an increase in pollen concentration, which resulted in fewer *Lycopodium* tracers counted and greater variance in estimated spore concentrations. The placement of the decline at 14.5 ka is consistent with Gill et al. (2009), with a minor adjustment in timing based on the age-depth model developed here.



Region	Site	Spore Decline (ka)	Hardwood Increase (ka)	No-analogue Vegetation (ka)	Fire Activity Increase (ka)
Great Lakes	Appleman Lake, IN	14.5 (14.8-14.1) %	14.3 (14.6-14.0) +	14.3 (14.6-14.0) +	14.7 (15.2-14.4) ?
	Silver Lake, OH	14.6 (15.4-13.9) %	13.8 (14.2-13.5) +	13.8 (14.3-13.5) +	14.8 (14.9-14.4) ?
	Bonnett Lake, OH	14.8 (15.6-13.7) %	15.2 (15.9-14.5) +	15.6 (16.2-15.0) ?	11.0 -
	Stotzel-Leis, OH	■	15.7 (16.0-15.0)	15.8 (16.0-15.1)	16.1 (16.5-15.7)
Northeast	Binnewater, NY	16.6 (17.9-15.8)	15.9 (16.3-14.9) +	16.1 (17.9-15.7) +	16.6* (17.9-15.7) +
	Otisville, NY	13.7 (14.4-13.3)	13.7 (14.1-13.5) +	13.5 (13.9-13.3) +	13.5* (13.9-13.3) +
Southeast	Cupola Pond, MO	15.8 (16.3-15.1)	16.1 (16.5-15.6) +	14.9 (15.3-14.1) +	No signal -
	White Pond, SC	13.0 (13.2-12.8) (Moore19-AP21)	13.3 (13.6-13.1) (Moore19-AP21) +	No Signal (Moore19-AP21) -	10.0 (Krause19-AP21) -
	Page-Ladson, FL	12.7 (13.0-12.2)	No signal -	No signal -	12.5** +
	Sheelar Lake, FL	14.2 (14.5-13.9)	Decline -	No signal -	14 +

Fig. 3. Summary of timing of events relevant to the Megaherbivore Release Hypothesis (MRH) for all sites in this study with a well-dated record of spore declines and associated indicators of vegetation composition and fire regime. Event placement was determined through both BCP analysis and visual inspection. Blue shading and a + symbol indicate an event timing that is consistent with the MRH. Yellow shading and a ? Symbol indicates an ambiguous lead-lag relationship that may or may not support the MRH. Red shading and a - symbol indicates either no signal or an event time inconsistent with the MRH. In the coprophilous spore column, white background indicates spore declines that are confirmed across multiple coprophilous spore taxa and in both percentage and concentration representations. Gray shading and a % symbol indicate a signal of coprophilous spore declines but ambiguities due to either a disagreement among the spore quantification metrics or an inability to calculate concentrations. At White Pond, pollen-based event timings are based on the WHIT19-Moore record in order to correlate with the spore data from the same record. See SOM Table 17 for more precise depth and age-model uncertainty.

At Bonnett, the decline is placed at 14.8 ka (range: 15.6–13.7 ka) based primarily on BCP analysis of the multi-spore percentage data (Fig. 2a). Bonnett exhibits an initial spore decline after a peak of nearly 25% at ~17.0 ka, with a final decline by ~14.8 ka, after which spores remain below 2% of the total pollen assemblage.

The multi-spore record from Silver is interpreted to show a spore decline at 14.6 ka (range: 15.4–13.9 ka) that is most strongly apparent in the percentage data (Fig. 2a) and weakly signaled in the concentration data (Fig. 2b) and other measures of abundance (SOM Fig. 20). The percent data indicate a variable, gradual decline from 15.6 ka, with spores declining below 2% at 14.6 ka. The inferred timing is similar to that reported by Gill et al. (2012), who reported a decline in *Sporormiella* percentages at 14.5 ka. However, the timing of the decline in spore concentration or accumulation values is confounded by a second peak in spore abundances between 11.5 and 9 ka. As with Appleman and Binnewater, the early Holocene concentrations are more uncertain because of the higher pollen concentration, in fewer tracers counted, and a bigger uncertainty for concentration estimates. Hence, the uncertainty associated with the timing of the decline at Silver Lake is high relative to other sites.

Sites in the SEUS also vary in the timing of coprophilous spore declines and the timing at some sites is later than at the northern sites (Fig. 2, Fig. 3). At Cupola, the final decline is placed at 15.8 ka

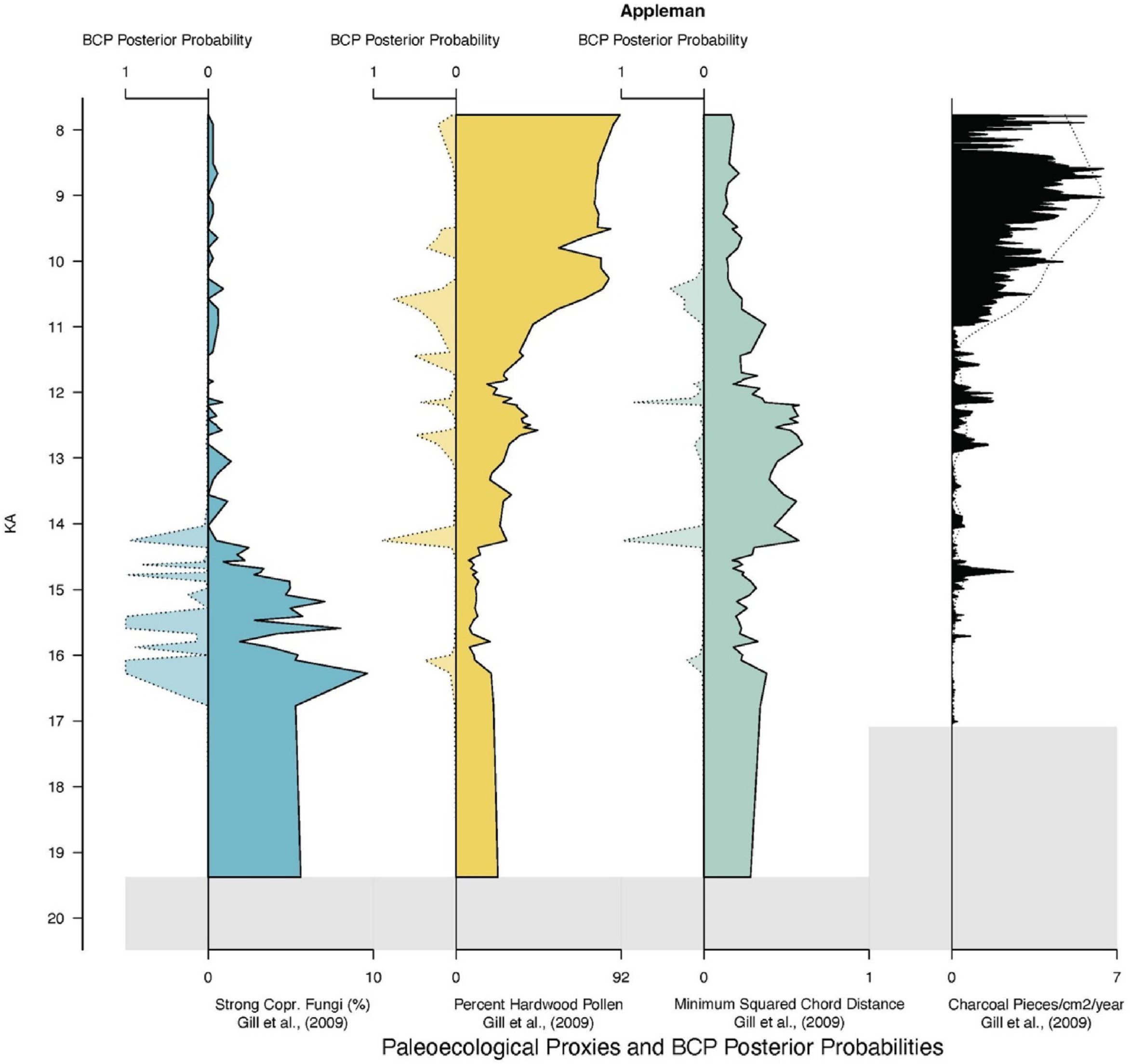


Fig. 4. Coprophilous spore percentages, summary pollen metrics, and charcoal accumulation from Appleman Lake, IN. The left plot (blue) shows the percentage of coprophilous fungi relative to a total pollen sum, the second plot (yellow) shows a percentage sum of all hardwood tree taxa, the third plot (green) shows the minimum squared chord distance (unitless) as an index of community novelty relative to modern pollen assemblages, and the fourth plot shows charcoal accumulation rates (spores/cm^2/year) with background charcoal accumulation smoothed with a 700-year window (dashed line). All data are from Gill et al. (2009). All pollen and spore plots include a left-side plot of the posterior probability of a change point. As in Fig. 2, areas with white background indicate time periods for which samples have been counted.

(range: 16.3–15.1 ka), based on spore concentrations and percentages that fluctuate and gradually decline but remain between 2000–6000 spores/cm^3 until ~15.5 ka (Fig. 2b; SOM Fig. 22). BCP analysis suggests that the final decline in coprophilous fungal spore abundance occurs at ~15.8 ka.

At White, the timing of the final decline is placed at 13.0 ka (range: 13.2–12.8 ka) based on three strongly coprophilous fungi taxa (*Podospora, Sordaria,* and *Sporormiella*). The spore decline is variable and gradual beginning ~14.8 ka, after concentration values up to 20,000 spores/cm^3 in the WHIT19-Moore core. With no BCP-indicated changepoints, interpretations at White are based on visual inspection.

At Page-Ladson, the decline is placed at 12.7 ka (13.0–12.2 ka) based on variable but high *Sporormiella* concentrations of up to 8000 spores/cm^3 until ~12.7 ka, after which *Sporormiella* gradually declines. BCP analysis indicates a peak probability of a change point at 12.7 ka. However, Page-Ladson has a brief resurgence of up to 4000 *Sporormiella*/cm^3 in early Holocene sediments dating to 10.8 to 10.3 ka. The source of the Holocene *Sporormiella* resurgence is unknown (Halligan et al., 2016).

At Sheelar, the multi-taxon spore record also demonstrates a late-Pleistocene signal of spore abundance and decline, with the decline placed at 14.2 ka (range: 14.5–13.9 ka). Spore concentrations between 15.5 and 14.2 ka are highly variable, with three spikes that are nearly 600% of concentrations found in the rest of the core. In sediments older than 15.5 ka, spore concentration is consistently between 30,000–50,000 spores/cm^3. BCP analysis suggests a final decrease in coprophilous fungal spores at 14.2 ka, and spore concentrations remain low (below 10,000 spores/cm^3) for the remainder of the record.

3.2. *Vegetation and fire responses to megaherbivore declines*

Strength of support for the MRH varies by region, with more consistent support in the northern sites (Fig. 3). A gradual and early spore decline by 16.6 ka at Binnewater is followed by an increase in

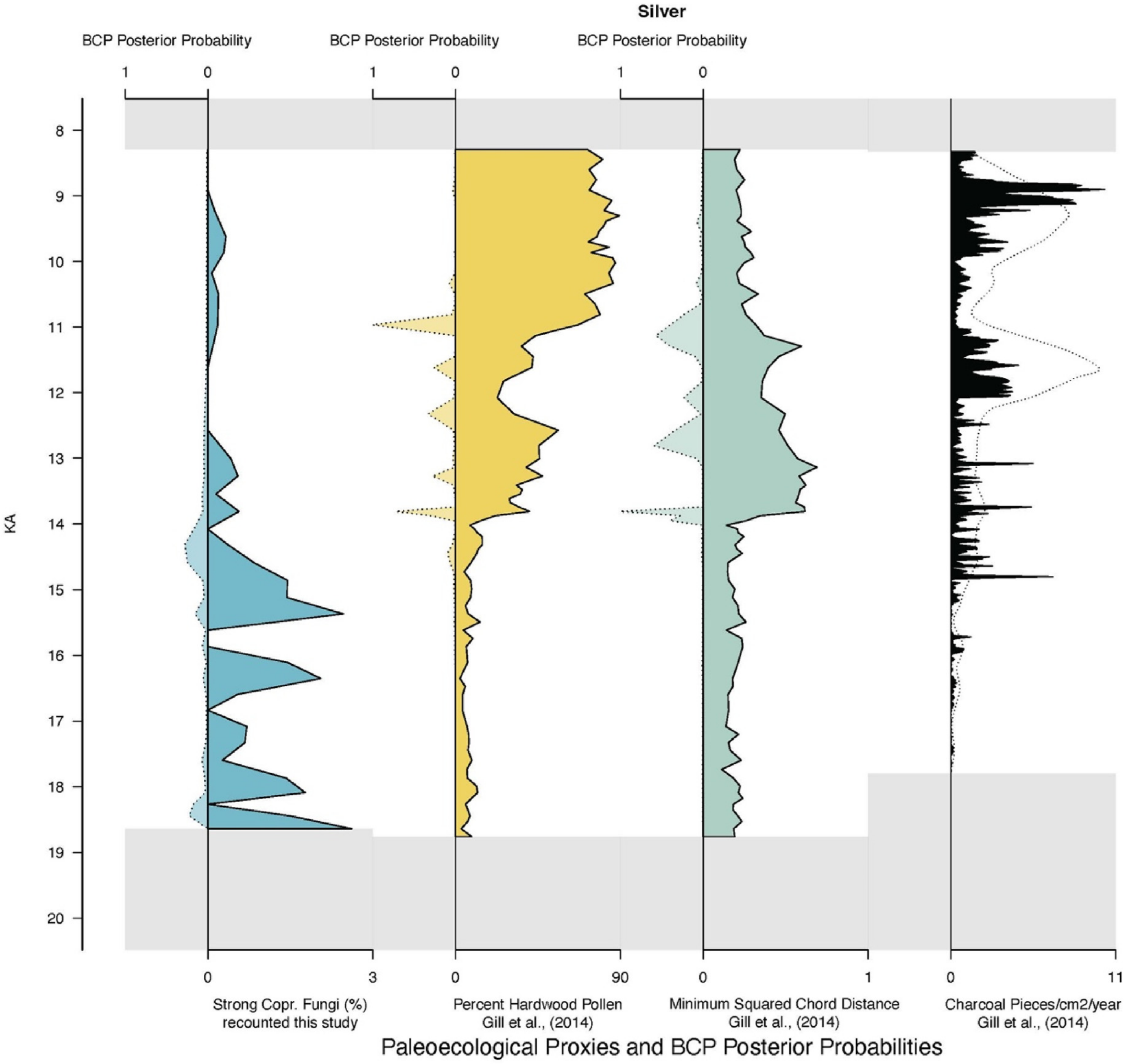


Fig. 5. Coprophilous spore percentages, summary pollen metrics, and charcoal accumulation from Silver Lake, OH. Figure design follows Fig. 4. Pollen and charcoal data are from Gill et al. (2012). Spores were recounted for this study.

hardwood pollen by 15.9 ka (range (16.3–14.9 ka) and gradual and modest increases in no-analogue vegetation by 16.1 ka (range: 17.9–15.7 ka). In the original study, Robinson et al. (2005) collected microcharcoal data, which is transported farther than macrocharcoal, and therefore provides a more extra-regional signature than macrocharcoal (Whitlock and Larsen, 2001). Microcharcoal increases at 16.6 ka (range: 17.9–15.7 ka), after *Sporormiella* declines.

At Otisville, a gradual spore decline at 13.7 ka is followed by an increase in hardwood pollen by 13.7 ka (range: 14.1–13.3 ka) and an increase in no-analogue vegetation at ~13.5 ka (range: 13.9–13.3 ka). As with Binnewater, only microcharcoal data is available and increases alongside the *Sporormiella* decline at 13.5 ka (range: 13.9–13.3 ka). Microcharcoal increases at 13.5 ka (range: 13.9–13.3 ka).

At Appleman, a gradual spore decline underway by 14.5 ka is followed by a two-step increase in hardwood pollen and no-analogue pollen assemblages beginning ~14.3 ka (range: 14.6–14.0 ka). A first peak in charcoal begins at ~14.7 ka (range:15.2–14.4 ka), which is interpreted as the onset of a new fire regime at Appleman (Gill et al., 2009), characterized by infrequent but large charcoal peaks against a background of low charcoal deposition. This onset overlaps with but appears to slightly precede the final spore decline (Fig. 4).

At Silver, the final coprophilous spore decline begins by 14.6 ka and is followed by an increase in hardwood pollen and no analogue pollen assemblages by 13.8 ka (range: 14.2–13.5 ka). An increase in charcoal at ~14.8 ka (range: 14.9–14.4 ka) overlaps with but appears to slightly precede the final spore decline (Fig. 5). Hence, at Appleman and Silver, an increase in hardwood taxa and no-analogue associations generally follows the spore declines, consistent with the MRH, whereas the timing of fire regime changes is more ambiguous. As noted in Section 2.4, however, these signals occur over centuries, creating some overlap between megaherbivory decline and increased fire activity.

Bonnett and Stotzel-Leis exhibit more mixed signals, but each supports some elements of the MRH. At Bonnett, the decline in coprophilous fungal spores is underway by 14.8 ka, which overlaps

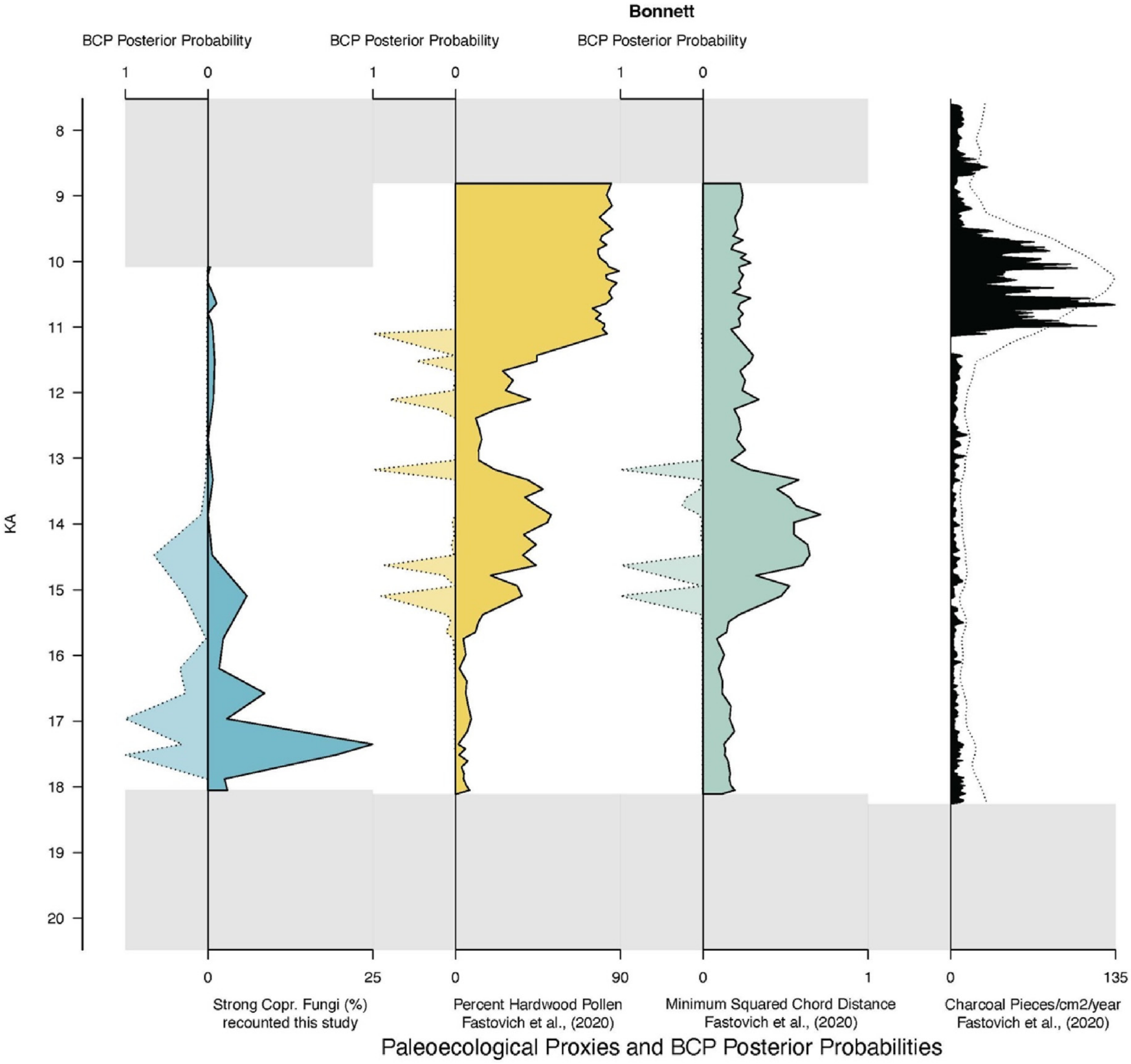


Fig. 6. Coprophilous fungi concentration, summary pollen metrics, and charcoal accumulation from Bonnett Lake, OH. Figure design follows Fig. 4. Pollen and charcoal data are from Fastovich et al. (2020). Spores were recounted for this study.

with both the initial increase in hardwood pollen at ~15.2 ka (range: 15.9–14.5 ka) and an increase in no-analogue pollen assemblages at ~15.6 ka (range: 16.2–15.0 ka). Although both vegetation changes appear to precede the final spore decline (Fig. 6), the precise lead-lag assessment is difficult because spore abundances decline gradually until 14.8 ka. Charcoal accumulation remains steady and low throughout most of the core, with no increase until after 11.0 ka, long after the decline in spore abundances and pollen record transformation. At Stotzel-Leis, coprophilous spores are minimally present throughout the record except for a brief spike at 11.4 ka. Despite a lack of a clear spore signal, there is a rapid increase in hardwood pollen at ~15.7 ka (range: 16.0–15.0 ka), with previous increases in hardwood pollen occurring as early as 16.0 ka. No-analogue pollen assemblages increase at ~15.8 ka (range: 16.0–15.1ka) and persist until ~11.2 ka. The earliest increases in hardwood pollen and no-analogue pollen assemblages co-occur with an uptick in charcoal at ~16.1 ka (range: 16.5–15.7 ka). These vegetation and fire shifts are earlier than similar changes at other sites in the region (Fig. 3), which may be caused either by inaccuracies in radiocarbon dating or by a heterogeneous expansion of hardwood taxa across the NECUS. A lack of coprophilous spores does not always indicate an absence of megaherbivores (van Asperen et al., 2020), so we cannot reject the hypothesis that changes at Stotzel-Leis resulted from megaherbivory release.

The SEUS records provide only limited support for the MRH. At the northern SEUS sites (Cupola and White), there is a broad correspondence between spore declines and hardwood pollen increases, but the hardwood rise appears to precede the spore decline and there is no clear relationship with charcoal variations. At Cupola, a final decline in spores from ~16 ka to 15.5 ka is accompanied by an increase in hardwood pollen abundance that begins gradually by ~16.1 ka (range: 16.5–15.6 ka) (Fig. 7). Although the variable, gradual spore decline precedes a gradual increase in hardwood pollen, the individual change points at 15.8 ka (spores) and 16.1 ka (hardwood pollen) suggest that the increase in hardwood pollen slightly leads the spore decline (Fig. 3). The hardwood-pollen rise and spore decline are also accompanied by an increase in palynological novelty at ~14.9 ka (range: 15.3–14.1 ka), which corresponds with a second, larger increase in hardwood pollen

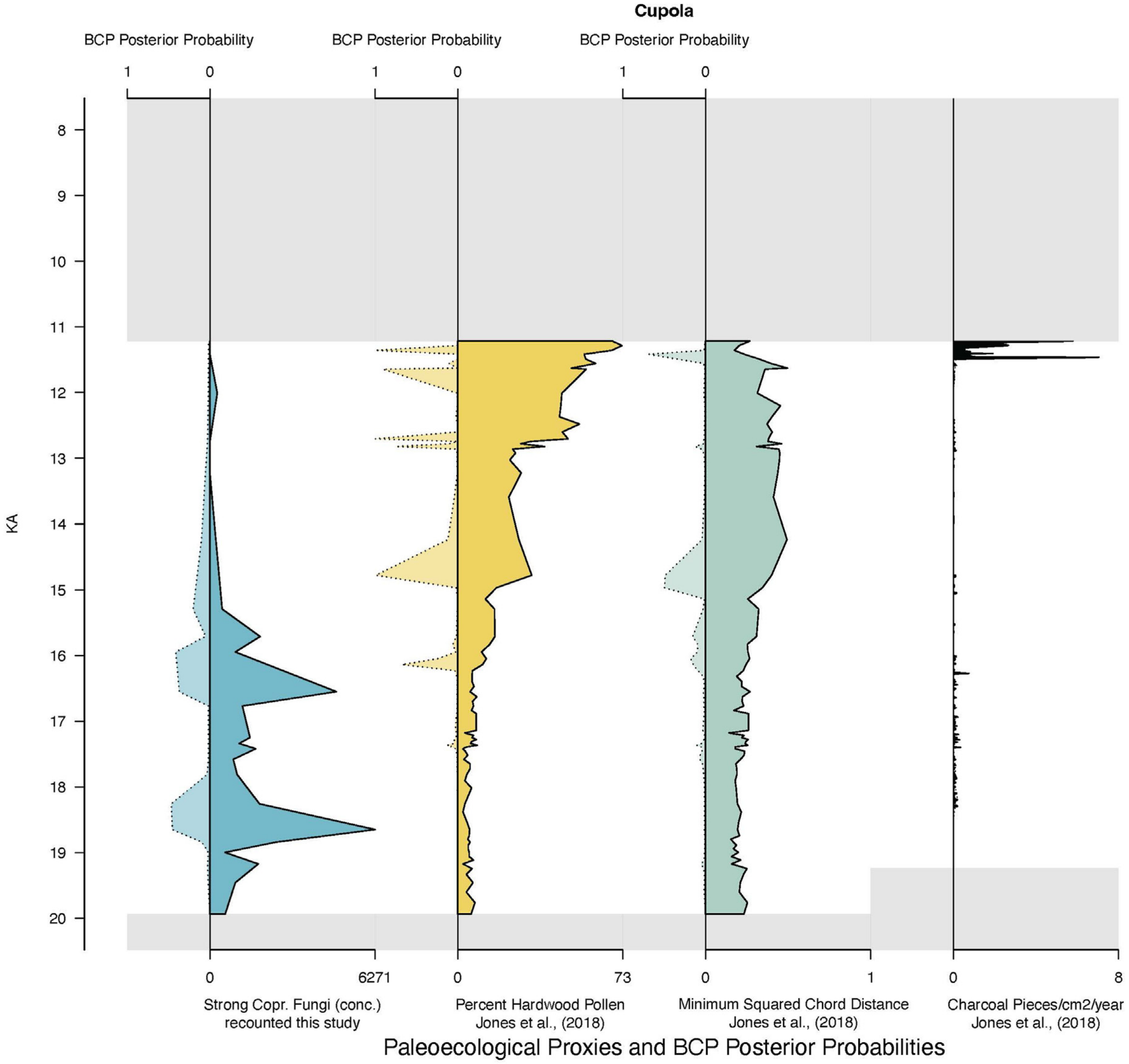


Fig. 7. Coprophilous fungi concentration, summary pollen metrics, and charcoal accumulation from Cupola Pond, MO. Figure design follows Fig. 4. Pollen and charcoal data from Jones et al. (2017). The background charcoal curve is not visible because it is below 0.03 throughout the entire record. Spores were recounted for this study.

abundance as well as a near absence of coprophilous spores. Charcoal abundances are low during this period of hardwood pollen rise and spore decline, and do not rise until 11.5 ka. Thus, gradual trends in the spore and pollen records at Cupola leave some potential for support of the MRH, but the lead-lag relationships generally do not support the MRH.

At White, the variable and gradual spore decline between ca. 14.8–13.0 ka co-occurs with a gradual increase in hardwood pollen, with a changepoint detected at 13.3 ka (range: 13.6–13.1 ka, WHIT19-Moore, Fig. 8). Although there is an age and depth discrepancy between palynological signals in the WHIT19-Moore and WHIT19-Krause cores, the increase in hardwood pollen in both cores occurs gradually. As with Cupola, the lead-lag relationships between the spore (13.0 ka) and hardwood changepoints (13.3 ka) are not consistent with the MRH, but the long duration of both trends leaves open the possibility of causal relationships. No-analogue vegetation assemblages are not well expressed at White Pond, and charcoal abundance remains very low or absent until 10.0 ka.

At the two Florida sites (Page-Ladson and Sheelar), the charcoal records are consistent with the MRH, but neither site shows an increase in hardwood vegetation or no-analogue pollen assemblages after coprophilous fungi decline. Page-Ladson does not exhibit clear signals of hardwood pollen abundance changes throughout the record, because many of the vegetation changes at Page-Ladson represent changes in abundance among hardwood taxa, with declines of temperate deciduous tree taxa such as *Fraxinus* and *Ostrya/Carpinus* in the Pleistocene and high abundances of *Quercus* in the Holocene sediments. Pollen-assemblage novelty is low throughout the record at Page-Ladson (SOM Fig. 29). At Page-Ladson, charcoal abundances decline at 12.5 ka, after a final spore decline at 12.7 ka. However, the Page-Ladson macrocharcoal record is compiled from several archaeological excavation unit sidewall samples adjacent to coring sites, and so there is uncertainty in the timing relative to the pollen and spore data.

At Sheelar, hardwood pollen decreases after the final spore decline by 14.2 ka (range: 14.5–13.9 ka) (Fig. 9). Pollen-assemblage novelty reaches moderate values (0.46 SCD), temporally tracking the hardwood proportions, but also declines after the spore decline at ~14.0 ka. At Sheelar, charcoal abundances decline at 14 ka, after

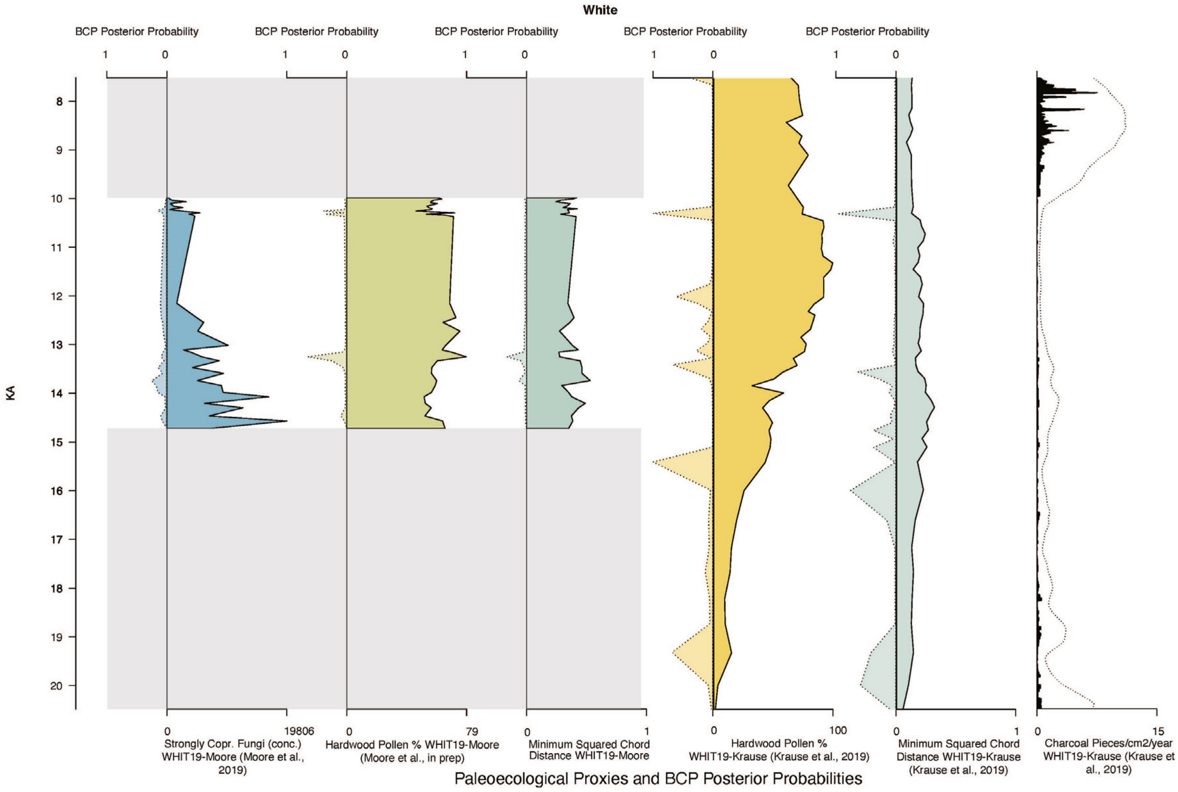


Fig. 8. Coprophilous fungi concentration, summary pollen metrics and charcoal accumulation from two cores from White Pond, SC. Figure design follows Fig. 4. WHIT19-Krause pollen and charcoal data from Krause et al. (2019). WHIT19-Moore pollen and spore data from Moore et al. (2019), and Moore et al. in prep.

the spore decline and are consistent with the MRH (Fig. 3, Krause et al. in prep).

Despite variations among sites in the magnitude and timing of spore declines and other signals, clear signals emerge when sites are grouped regionally (Fig. 10). The predictions of the MRH are generally supported by sites in the NECUS (Fig. 10a), with spore declines either closely coincident with or preceding the rise of hardwood tree taxa and emergence of no-analogue vegetation communities (Fig. 10a). This pattern is consistent regardless of whether the median, maximum, or minimum age estimates are analyzed. Moreover, five of six sites in the NECUS show the expected signals. However, relationships with charcoal record increases are more ambiguous and are either coincident with or preceding the spore declines. Conversely, in the SEUS, sites generally do not support the MRH (Fig. 10b), with fewer sites showing the expected signals and the changes in hardwood abundance generally preceding the decline in coprophilous spore abundances.

4. Discussion

4.1. Site-level and regional patterns of spore declines and megaherbivore extinction

A late-Pleistocene decline in coprophilous fungal spore abundances is widely documented across the NECUS and NEUS, with 11 of 14 sites exhibiting an apparent spore decline in the terminal Pleistocene sediments (Fig. 2, Fig. 3). In addition to the sites shown, the Hyde and Pawelski sites have a late Pleistocene spore decline but are not included in formal analysis due to insufficient chronological control. Despite the impacts of taphonomic processes on coprophilous spores (Baker et al., 2016; Raper and Bush, 2009; Wood and Wilmshurst, 2013), the consistent presence of a late-Pleistocene decline across sites supports the hypothesis that these spore declines record widespread declines in abundance of megaherbivores in eastern North America. However, the strength and timing of the spore declines vary among sites and regions. In the northern region, sites with a detectable spore decline indicate a median timing of decline between 16.6 ka and 13.8 ka. In the southern region, sites indicate a median timing of decline between 15.8 and 12.7 ka (Fig. 2).

The timing of the coprophilous spore declines (16.6–12.7 ka, Fig. 3), although variable, generally occurs before the last known dates of megaherbivore extinction, suggesting that the spore data have recorded declines in megaherbivory pressure and populations that were a precursor to final extinction. Widga et al. (2017) estimated an extinction window of 13.46–12.16 ka for mammoth and 12.79–12.52 ka for mastodon in the Great Lakes region (Fig. 10), whereas Feranec and Kozlowski (2016) estimate extinction dates in the NECUS US of 12.4 ka and 13.3 ka for mammoth and mastodon, respectively. Though reliably dated faunal records are sparse in the SEUS due to poor bone collagen preservation, it appears that mastodon and mammoth persisted for centuries or millennia after most spore decline records (Widga et al., 2022). If so, the combination of spore records and bones can help provide a more nuanced understanding of extinction trajectories. Spores may serve as indicators of the major changes in megaherbivore abundance and therefore herbivory pressure, while bones provide a better indicator of local presence and final extinction, after correcting for sampling (Bradshaw et al., 2012; Signor and Lipps, 1982).

Others have noted the discrepancy in the timing of megaherbivore declines recorded by spores and bones. Gill et al. (2009, 2012) hypothesized that the spore declines, alongside pollen records (i.e. Jackson and Williams, 2004), indicate a ‘functional extinction’ where megaherbivore populations were substantially

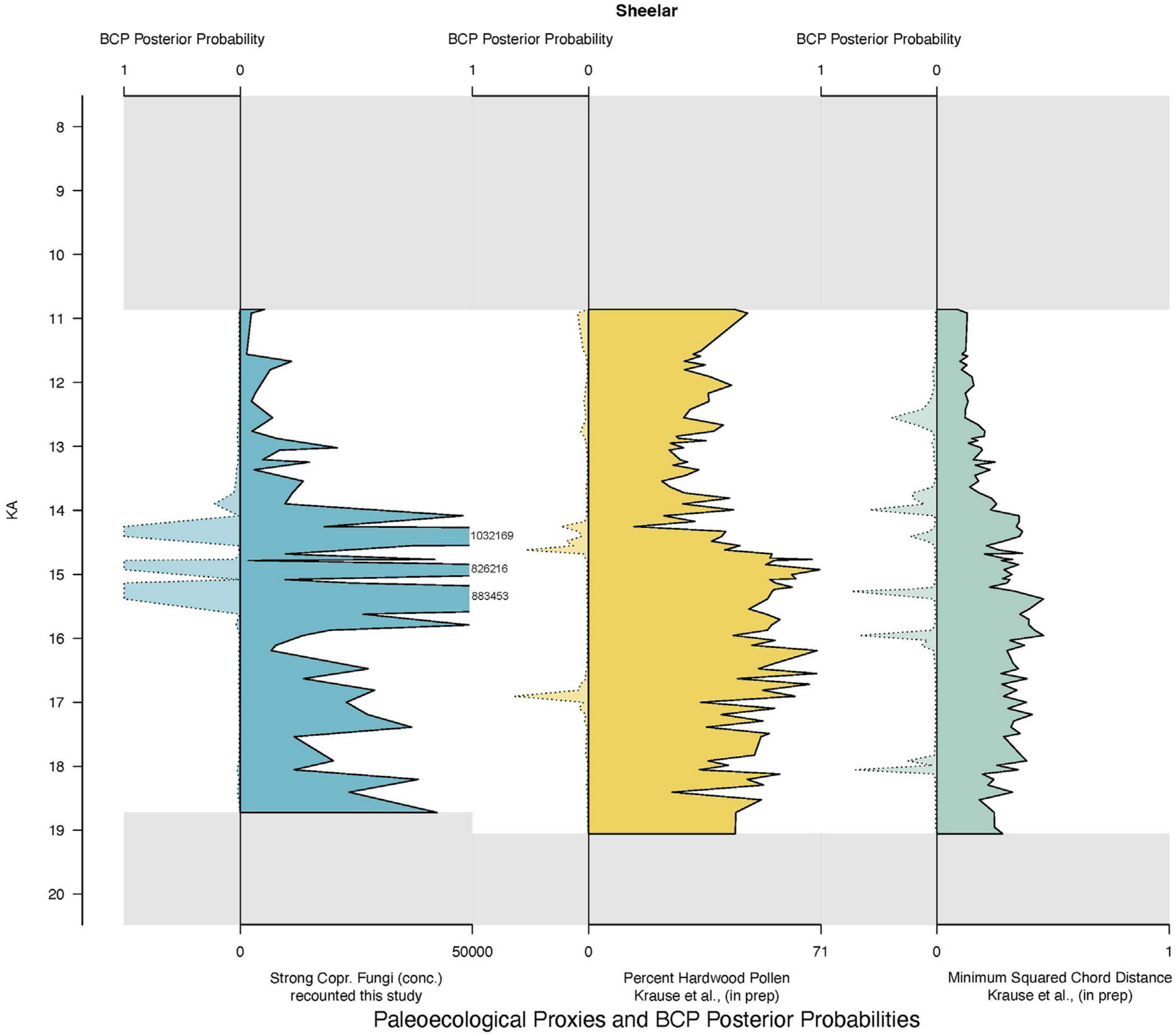
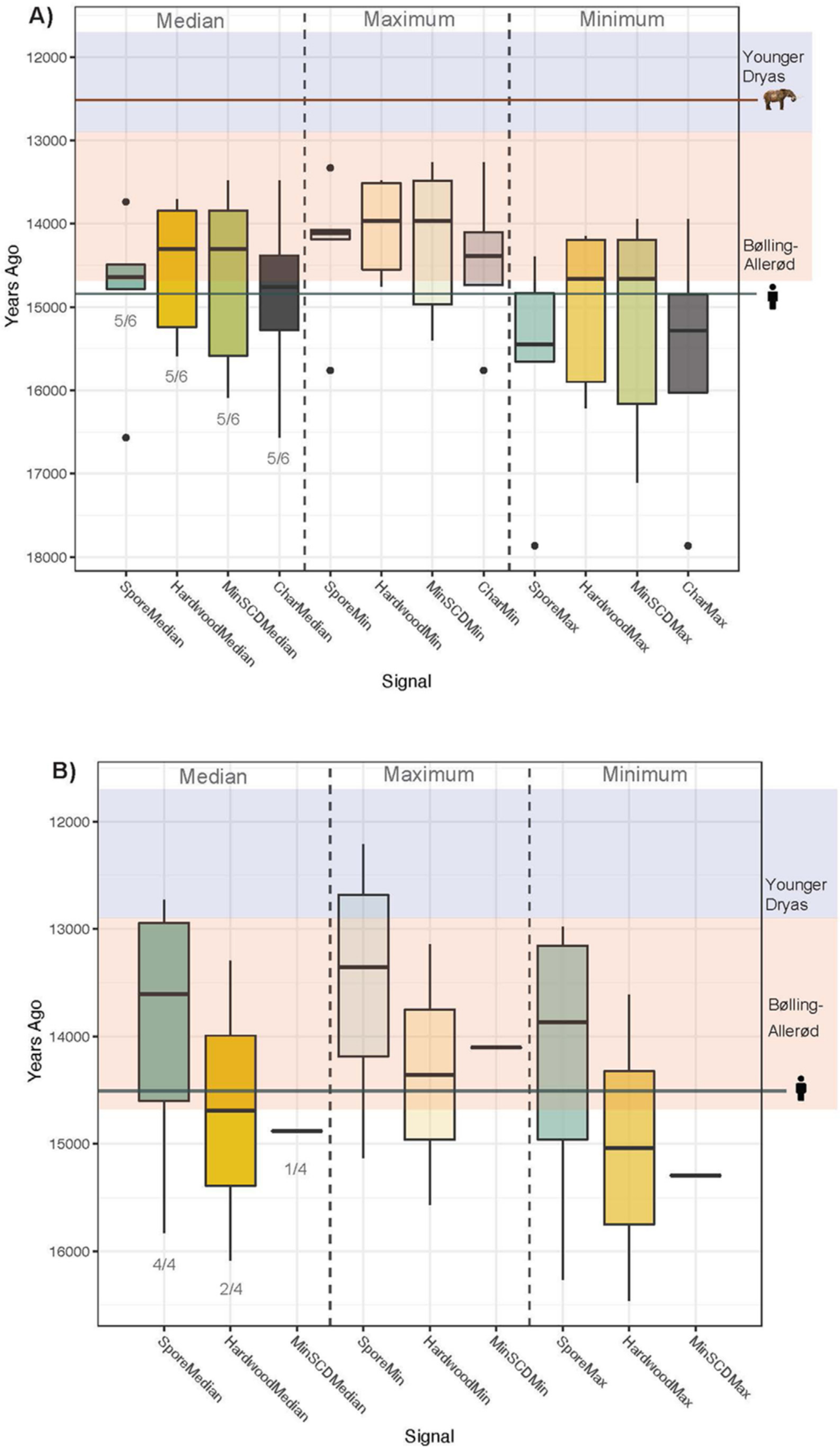


Fig. 9. Coprophilous fungi concentration and summary pollen metrics from Sheelar Lake, FL. Figure design follows Fig. 4, except that the unpublished charcoal data for Sheelar are not shown (Krause et al. in prep.). A few peaks in concentration values are too large for display; for these peaks their concentration values are shown. Pollen data from Krause et al., (in prep.) Spores were recounted for this study.

reduced and fractured into isolated disjuncts, pre-dating the final extinction recorded by bones. Fiedel (2018) challenged this hypothesis, noting that Widga et al. (2017) show an increase in mammoth and mastodon ^{14}C-dated remains at 14 ka, suggesting that population abundances increased prior to abrupt extinctions. This rise in recovered mastodon remains, however, could be influenced by taphonomic processes improving bone preservation, in particular an increased prevalence of wetland environments between 14.6 and 12.8 ka (Byun et al., 2021). The timing of the spore declines is also consistent with the known record of human arrival and dispersal in the Americas, given that humans were south of the Laurentide Ice Sheet by at least 15.5 ka and possibly as early as 23 ka (Bennett et al., 2021; Waters, 2019). Megaherbivore remains in the Great Lakes Region are often preserved in sediment characteristic of small lakes or wetlands, and strong circumstantial evidence suggests that humans cached body parts of mastodons and mammoths in ponds in the Great Lakes Region (Fisher, 1995, 2021; Fisher et al., 1994; Lepper et al., 1991), which would increase the likelihood of bone preservation. Another, more speculative, possibility is that humans may have altered megafaunal behavior and thereby affected both bone and spore-based representation records of megaherbivores. For example, if lakes and ponds were frequented by early humans (e.g. Halligan et al., 2016), they may have created a “landscape of fear” that drove megaherbivores away from these areas, [e.g. Clinchy et al., 2016]) further reducing spores deposited on lake margins.

Coprophilous spore records are also sensitive to taphonomic factors (Parker and Williams, 2012; Raper and Bush, 2009; van Asperen, 2017; van Asperen et al., 2020; Wood and Wilmshurst, 2013). Dispersal distances within terrestrial landscapes are on the order of 25–100 m (Gill et al., 2013), and spore concentration within lakes appears to reflect herbivore concentrations close to (potentially within 10 m of) the shoreline (Baker et al., 2016). Spore concentration can decline within 20 m to the shoreline, particularly in flat-bottomed lakes (Raper and Bush, 2009), but most of the cores used in this study with observed spore declines are more than 20m from shoreline (SOM Table 16), so distance to shoreline does not appear to be a definitive barrier. Note too that the largest total fungal spore accumulation, concentration, and raw counts are found in the SEUS sites, consistent with prior evidence that many coprophilous fungi species grow better in warmer, wetter environments (e.g. Kuthubutheen and Webster, 1986; Spano, 2020) despite generally having wide ecological tolerances.

In summary, a variety of ecological and taphonomic processes


A)
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5/6
5/6
5/6
SporeMedian
HardwoodMedian
MinSCDMedian
CharMedian
SporeMin
HardwoodMin
MinSCDMin
CharMin
SporeMax
HardwoodMax
MinSCDMax
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Fig. 10. Assessing the Megaherbivory Release Hypothesis via box plots of the intersite estimates in the timing of the coprophilous spore declines, rise of hardwood tree taxa, increase in vegetation novelty, and increase in fire activity for sites in the northeast and central US (NECUS, Fig. 10a, top panel) and southeastern US (SEUS, Fig. 10b, bottom panel). Because each event carries both depth and age uncertainty at each site, the intersite estimates are shown for the median (left panel), 95% credible interval maximum (middle panel), and 95% credible interval minimum (right panel) estimates of timing. Transparent blue and red polygons denote the Younger Dryas (12.9–11.7 ka) and Bølling-Allerød (14.7–12.9 ka) respectively. In Fig. 10a, brown line with mastodon icon indicates the estimated time of extinction of mastodon in the NECUS at 12.52 ka as modeled by Widga et al. (2017). Gray line with human icon indicates earliest available evidence of human occupation in the region at 14.85 ka from the Hebior site in Wisconsin (Joyce, 2006). In Fig. 10b, we omitted the brown line indicating megaherbivore extinction because of poor regional chronological control in the faunal record. The gray line with human icon indicates the earliest available evidence of human occupation in the region at 14.55 ka from the Page-Ladson site in Florida (Halligan et al., 2016). In the fractions below box plots, the denominator indicates the total number of sites in the region with a proxy record and adequate chronological control, while the numerator indicates the number of sites that show the specific signal predicted by the Megaherbivory Release Hypothesis. Charcoal is omitted from Fig. 10b because the two sites that exhibit a charcoal increase after spore decline (Page-Ladson and Sheelar) do not possess published, continuous charcoal records that are closely associated with the pollen/spore records.

contribute to the variation in coprophilous fungal spore abundances among our study sites and the apparent magnitude and timing of the spore declines. Nonetheless, despite these complexities, strong signals persist: ~80% of the study sites display late Pleistocene spore declines, and there is reasonable intraregional consistency in the timing of spore declines in the NECUS and SEUS (Fig. 3, Fig. 9). We infer that these records are detecting a common signal of the late-Quaternary megaherbivore population declines.

4.2. Regional variations in megaherbivore-vegetation-fire interactions and support for the MRH

We observe clear differences between the NECUS and SEUS in the temporal relationships among fungal spore decline, vegetation compositional changes, and fire regime shifts, suggesting the effects of megaherbivory and the trophic effects associated with the megaherbivore decline vary among ecosystems. Here, we review the different vegetation characteristics and climatic histories of these two regions to gain insight into why megaherbivore-vegetation-fire-interactions might differ between the NECUS and SEUS. We do not attempt definitive answers but rather a series of working hypotheses suitable for further investigation.

Overall, the MRH is better supported in the NECUS (Fig. 3, Fig. 9). Postglacial ecosystems in the NECUS were characterized by a mixture of open and forested landscapes, with a major regional transition from dominance of boreal conifers (*Picea, Abies, Larix*) (Fastovich et al., 2020; Jackson et al., 2000; Jensen et al., 2021; Robinson et al., 2005; Watson et al., 2018; Williams et al., 2004) to communities with no modern analogue consisting of increasing deciduous hardwoods (*Fraxinus, Ostrya/Carpinus, Ulmus, Quercus*) intermixed with boreal conifers. *Pinus* was absent or in low abundances during this period and wetlands were common in the poorly drained postglacial landscapes (Byun et al., 2021). Low to moderate abundances of prairie forbs such as *Ambrosia* (ragweed) in the NECUS between 16 and 13 ka suggest at least local areas of open upland vegetation (Williams et al., 2004; Wright et al., 1963), perhaps due to regional fire disturbance or periods of lower precipitation causing water stress. Our data suggest that megaherbivore-fire-vegetation feedbacks may have been most strongly expressed in these mixed parklands.

We hypothesize four distinct but connected mechanisms that could explain the high sensitivity of NECUS parkland and no-analogue ecosystems to megaherbivory release. First, strong spatial heterogeneity in light availability within the mosaic of open, semi-open, and closed vegetation in the NECUS likely amplified the ability of megaherbivory to regulate competitive balances among plant taxa, as they do in contemporary spatial mosaics of temperate woodlands (Olff et al., 1999). The loss of megaherbivores may have triggered vegetation closure (i.e. Olofsson et al., 2004) which would help shade-tolerant tree genera such as *Ulmus, Carpinus,* and *Ostrya* outcompete lower-stature plants such as grasses and forbs (Gill, 2014; Vera, 2000). Second, trophic effects of megaherbivores are expected to be highest where megaherbivore populations are densest (Bakker et al., 2016), so the semi-open woodlands of the NECUS may have supported larger populations of megaherbivores with a range of dietary preferences and hence stronger combined trophic effects. Third, evergreen conifers and deciduous hardwoods differ in palatability, because palatability to herbivores is inversely correlated to leaf lifespan (Southwood et al., 1986) and positively correlated to specific leaf area, which differs between gymnosperms and deciduous angiosperms on average by a factor of three (Poorter et al., 2009). Hence, these interspecific differences in palatability, combined with a spatial mosaic of plant functional types in the mixed parklands of the NECUS, may have amplified the importance of megaherbivory on vegetation composition. Fourth, the lower temperatures and consequent lower net primary productivity of vegetation in the NECUS between 16 and 12 ka (Wang et al., 2021), relative to more southerly ecosystems, may have made northern systems more sensitive to reductions in megaherbivory pressure with the late-Quaternary extinctions (e.g. Bakker et al., 2016).

Although the lead-lag relationships observed between decline in megaherbivory pressure (as signaled by coprophilous spores) and vegetation generally support the MRH in the northern sites, the relationships between megaherbivory and changes in fire regime (as signaled by changes in the abundance of sedimentary charcoal and frequency of peak occurrences) are more ambiguous (Fig. 2, Fig. 3; Gill et al., 2009, 2012). At four of the five northern sites with an observed decline in coprophilous spores, background charcoal deposition rates increased roughly contemporaneous with the spore declines (consistent with the MRH) but at two of these sites (Appleman and Silver), the increase in charcoal appears to slightly lead the decline in spores, albeit with substantially overlapping ranges (Fig. 3). We thus view the lead-lag relationships for charcoal and spores as weakly consistent with the MRH. If in fact increases in fire activity led megaherbivore decline, it could suggest additional influences on fire regimes in these ecosystems, such as changes in ignition sources related to climate or human activity.

Evidence for the MRH in the NECUS is not evidence against the known effects of climate variations on vegetation changes during the deglaciation (Prentice et al., 1991; Webb et al., 1993, Williams and Jackson, 2007). Individual sites in the NECUS suggest a close relationship between local temperatures and the formation of no-analogue plant communities (Fastovich et al., 2020). Increased fire activity appears to have accelerated the loss of *Picea* (spruce) forests and woodlands at some sites (Jensen et al., 2021). Given the mid-continental position of the NECUS, the high insolation seasonality between ca. 14 and 8 ka probably increased temperature seasonality (Kutzbach and Guetter, 1986; Williams et al., 2001), which may have allowed the commingling of boreal conifers and temperate hardwoods into communities with no modern analogue (Jackson and Overpeck, 2000; Jackson and Williams, 2004; Veloz et al., 2012; Williams and Jackson, 2007). The ecological consequences of reduced megaherbivory in the NECUS should be viewed as part of an interacting hierarchy of controls on deglacial vegetation dynamics (Gill et al., 2012), in which climate change exerted strong direct effects on vegetation, while also interacting with the effects of expanding human populations, megaherbivore declines, and shifts in fire regime.

The MRH is not well supported in the SEUS, where most sites either exhibit a decline in hardwood pollen abundance after coprophilous spores decline, or an increase in hardwood pollen abundance that precedes the coprophilous spore decline (Fig. 9b). Additionally, no-analogue pollen assemblages are not as common across the SEUS as in the NECUS. Much of the northern SEUS was covered by coniferous forests dominated by boreal and cool-temperate *Picea* and *Pinus* species (Jackson and Weng, 1999; Liu et al., 2013; Jackson et al., 2000; Jones et al., 2017), with boreal forest taxa declining in abundance after ~15 ka. In this region, most of the ecosystem transitions were among closed or semi-closed forest types (Jackson et al., 2000; Watts, 1980), in which light competition and fuel load may have been less heterogeneous than in the NECUS parklands, so the effects of megaherbivore population declines may have been smaller. Cupola Pond is an exception to this, with prominent late-glacial *Ambrosia* and Poaceae (grass) pollen, although notably, this site lies at the intersection of the northern SEUS and the NECUS. Because of these differences in vegetation composition and structure in the northern SEUS, deglacial warming and other climatic controls may have had more influence on plant community composition than disturbance by megaherbivores.

Northern Florida ecosystems at the last glacial maximum were characterized by a mixture of hardwoods and thermophilous pines, whereas open *Pinus* and *Quercus* savannas oscillated in central Florida (Grimm et al., 1993, 2006; Watts et al., 1992; Watts, 1975; Watts and Hansen, 1994). The rise in hardwood taxa abundances well before spore declines suggests that reduced megaherbivory was not a factor. However, fire activity appears to increase after spores decline at the two Florida sites in this study, which may be due to reduced megaherbivory and increased fuel load in the more flammable *Quercus* savanna or *Pinus* forest ecosystems or increased ignition by humans or lightning. Hence, it remains possible that in the heterogeneous and fire-prone landscapes of northern Florida, megaherbivores played some role in regulation of fuel load and fire regimes.

Overall, we find that the relationships among megaherbivore declines, vegetation change, and fire regimes vary regionally, indicating variable support for the MRH. The NECUS sites generally support the hypothesis that megaherbivore declines may have contributed to changes in vegetation composition but have a weak or influence on fire regime, whereas northern SEUS sites are generally inconsistent with the MRH. The reasons for these inter-regional variations are not yet definitively known, but potential contributing factors include differences in climate (temperature, precipitation, and their seasonality) that influence the distribution of vegetation communities and ecosystem structure, differences in fuel load, and potentially differences in ignition sources (lightning regimes and human activity). Hence, this work shows that scaling upwards from individual records to networks of sites at a subcontinental scale can provide insight to the differential impacts of the late Quaternary megaherbivore extinctions within and across ecosystems. Key next steps are to elucidate the underlying mechanisms through mechanistic vegetation models with megaherbivory processes incorporated (Pachzelt et al., 2015) and to examine other regions with dense networks to further understand the patterns and processes governing the differential impacts of megaherbivore functional extinctions across landscapes.

5. Conclusions

The majority of sites in this study demonstrate a widespread decline in coprophilous spore abundance in the terminal Pleistocene and early Holocene sediments, consistent with the hypothesis that these spores record declines in megaherbivory pressure in eastern North America prior to extinction. Overall, the timing of spore decline in the eastern US occurs between 16.6 and 12.7 ka and, in general, pre-dates last appearance ages based on bones. Possible explanations for the earlier timing of spore declines relative to last bone dates include functional extinction or local extirpation of megaherbivores prior to their final extinction or shifts in megaherbivore behavior in response to human presence.

At most NECUS sites, the coprophilous spore, pollen, and charcoal data support the MRH, wherein a release from megaherbivory recorded by spore declines contributed to the encroachment of hardwood vegetation, formation of no-analogue vegetation assemblages, and fire activity increase. Sites in the northern SEUS, conversely, do not exhibit a consistent signal of hardwood, no analogue vegetation, and charcoal increase after spore declines. The Florida sites, Page-Ladson and Sheelar, also do not support an increase in deciduous hardwood trees and no-analogue vegetation assemblages after spore declines but do show evidence of an increase in fire alongside declining herbivory. These regional differences imply that the strength of couplings and feedbacks among vegetation composition, megaherbivory pressure, and fire regime also varied regionally. The reasons for these interregional variations remain somewhat unclear, but possible hypotheses include regional differences in heterogeneity of vegetation openness and palatability, spatial variations in the densities of megaherbivores, and lower regional net primary productivity and consequent sensitivity to top-down trophic effects.

This paper brings together over a decade of previous research on the interactions among megaherbivory, vegetation, fire, and climate. By synthesizing this existing data alongside new proxy records for megaherbivore abundance and decline, we have provided some of the first evidence that ecosystem sensitivity to the late Quaternary megaherbivore population declines and extinctions varied among ecosystems. Hence this paper both provides partial support for the Megaherbivory Release Hypothesis and suggests that the strength of effects associated with trophic downgrading varied among regions. Sources of uncertainty include potential heterogeneities caused by intersite variations in taphonomic factors, and the focus on a time interval of rapid global environmental change, during which multiple factors including abrupt climate change and human population expansion may have influenced ecosystems. Future research should involve further investigation of the mechanisms influencing differential responses to megaherbivory release and development of regional-scale networks in other regions with dense paleoecological proxy networks such as Beringia or Europe. Another promising avenue forward is to further explore the hypothesized mechanisms for spatial variations in megaherbivory effects, including spatial heterogeneities in vegetation openness and light competition, density of megaherbivore populations, vegetation palatability, and climatic influences on vegetation productivity and sensitivity to megaherbivory.

Data availability

New, multi-taxon spore records have been submitted to the Neotoma Paleoecology Database (https://www.neotomadb.org/). Data and code used in BCP analysis and stratigraphic diagrams are available at https://github.com/perrangie/Perrotti_et_al._QSR_MRH.

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Author contributions

AP: Conceptualization, Methodology, Formal Analysis, Investigation, Writing; original draft, Writing; review and editing, Visualization. CK: Writing; review and editing, Visualization. JR: Writing; review and editing, Supervision. STJ: Writing; review and editing. JG: Writing; review and editing. GR: Formal Analysis, Writing; review and editing. TK: Writing; review and editing. JWW: Conceptualization, Writing; review and editing, Supervision, Project Administration, Funding Acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quascirev.2022.107696.

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