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Late Quaternary vegetation, climate, and fire history of the Southeast Atlantic Coastal Plain based on a 30,000-yr multi-proxy record from White Pond, South Carolina, USA

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Abstract

The patterns and drivers of late Quaternary vegetation dynamics in the southeastern United States are poorly understood due to low site density, problematic chronologies, and a paucity of independent paleoclimate proxy records. We present a well-dated (15 accelerator mass spectrometry ^{14}C dates) 30,000-yr record from White Pond, South Carolina that consists of high-resolution analyses of fossil pollen, macroscopic charcoal, and *Sporormiella* spores, and an independent paleotemperature reconstruction based on branched glycerol dialkyl tetraethers. Between 30,000 and 20,000 cal yr BP, open *Pinus-Picea* forest grew under cold and dry conditions; elevated *Quercus* before 26,000 cal yr BP, however, suggest warmer conditions in the Southeast before the last glacial maximum, possibly corresponding to regionally warmer conditions associated with Heinrich event H2. Warming between 19,700 and 10,400 cal yr BP was accompanied by a transition from conifer-dominated to mesic hardwood forest. *Sporormiella* spores were not detected and charcoal was low during the late glacial period, suggesting megaherbivore grazers and fire were not locally important agents of vegetation change. *Pinus* returned to dominance during the Holocene, with step-like increases in *Pinus* at 10,400 and 6400 cal yr BP, while charcoal abundance increased tenfold, likely due to increased biomass burning associated with warmer conditions. Low-intensity surface fires increased after 1200 cal yr BP, possibly related to the establishment of the Mississippian culture in the Southeast.

Keywords: Southeastern United States; Pollen; Macroscopic charcoal; brGDGT; White Pond, SC; No-analog vegetation; Holocene; Glacial; Deglacial

INTRODUCTION

Over the last 30,000 yr, North America experienced profound ecological changes, including species range shifts and the compositional turnover of terrestrial communities (Williams et al., 2004, Blois et al., 2013), megafaunal extinctions (Koch and Barnosky, 2006), and changing fire regimes (Marlon et al., 2009). Much interest has focused on better understanding the underlying climatic and non-climatic drivers of vegetation change over this time period and the causal mechanisms that ultimately resulted in contemporary plant communities (Blois et al., 2013; Ordonez and Williams, 2013; Gill, 2014; Jackson and Blois, 2015). In the eastern United States, particular attention has been directed at the late-glacial expansion of temperate hardwood species, development of plant communities lacking modern analogs, linkages to millennial-scale climate events in the North Atlantic and Greenland, late Pleistocene megafaunal extinctions, and changing fire regimes (Jackson and Williams, 2004; Grimm et al., 2006; Gill et al., 2009, 2012; Gonzales and Grimm, 2009; Liu et al., 2013; Jones et al., 2017; Watson et al., 2018).

The Southeast has long been a region of biogeographic and paleoecological interest due to its species-rich flora and its likely role as a refugium for many temperate taxa during glacial periods (Soltis et al., 2006), with evidence for low geographic separation among southeastern refugia (Lumibao et al., 2017; Bemmels and Dick, 2018). Previous

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paleoecological studies indicate extensive dominance of boreal coniferous trees across the region during the last glacial period, from the Carolina Coastal Plain to the southern fringes of the Appalachians and interior highlands (Whitehead, 1964, 1965, 1981; Watts, 1970, 1980a, 1980b; Delcourt, 1979; Royall et al., 1991; Delcourt and Delcourt, 1994). The contrast between glacial (boreal conifers) and Holocene (temperate and subtropical hardwoods and conifers) periods highlights the sensitivity of terrestrial ecosystems to climate change. Most late Quaternary pollen records from the Southeast, however, were collected more than three decades ago and generally consist of relatively poorly dated, single-proxy (pollen) records of vegetation, limiting our understanding of millennial-scale events and relationships between climate, herbivory, and vegetation changes in the region. Since that time, new paleoecological, paleoclimatic, and geochronological techniques have emerged and others have been refined. For example, sedimentary indicators of megafauna (coprophilous fungal spores) and fire (macroscopic charcoal) enable multi-trophic studies of past ecological changes (Gill et al., 2009, 2012; Higuera et al., 2009), while accelerator mass spectrometry (AMS) ^{14}C dating of terrestrial macrofossils has made sediment chronologies more accurate and precise (Grimm et al., 2009). New geochemical indicators of past climates developed for lake sediments, including organic biomarkers such as branched glycerol dialkyl glycerol tetraethers (brGDGTs; Zink et al., 2010; Fawcett et al., 2011; Loomis et al., 2012, 2015, 2017; Niemann et al., 2012; Woltering et al., 2014; Watson et al., 2018) provide paleoclimatic signals independent from fossil pollen proxies. At the same time, our understanding of hemispheric-scale climate trends during the last deglaciation has been sharpened by multiple high-resolution paleoclimate records from marine sediments, speleothems, and ice cores (Shakun et al., 2012; Buizert et al., 2014).

For these reasons, paleoecologists have recently begun to reinvestigate classic fossil pollen sites in the Southeast using new sediment cores, robust chronologies, and high-resolution multi-proxy analyses (Grimm et al., 2006; Liu et al., 2013; Jones et al., 2017). One area of emergent research involves understanding how millennial-scale North Atlantic climatic events were manifested across the Southeast and the degree to which they drove the postglacial expansion of hardwood taxa, formation of no-analog vegetation, and other ecological changes (Grimm et al., 2006; Liu et al., 2013; Jones et al., 2017). Both the regional expression of these climatic events in the southeastern United States and their effect on vegetation remain uncertain, however, with varying signals among Southeast paleoecological records. For example, warm Dansgaard-Oeschger interstadials and cold Heinrich events (including the Younger Dryas) recorded in the North Atlantic (Bond et al., 1993; Buizert et al., 2014) were expressed as alternating oak-scrub/prairie and pine phases at Lake Tulane in peninsular Florida, indicating cold/dry and warm/wet conditions, respectively. This suggests high vegetation sensitivity to millennial-scale climate changes, and that these regional climate variations were antiphased to the North Atlantic (Grimm et al., 2006). In contrast, fossil pollen data from Jackson and Anderson ponds in the interior Southeast show little sensitivity to millennial-scale climate events in the North Atlantic between 25,000 and 18,000 cal yr BP (Liu et al., 2013). At Cupola Pond, the successive development of two distinct no-analog assemblages coincided with Bølling-Allerød warming and the Younger Dryas. Moreover, high levels of temperate pollen taxa indicate warm conditions during the Younger Dryas, similar to the findings at Lake Tulane (Jones et al., 2017), but in contrast to cold climates in the North Atlantic and north-central United States (Gonzales and Grimm, 2009; Gill et al., 2012; Watson et al., 2018). Additional well-dated fossil pollen records and independent paleoclimate data from the Southeast can help resolve and explain these apparent inconsistencies among sites.

A second area of recent research seeks to achieve a better understanding of possible interactions among climatic and vegetational changes, late Pleistocene megafaunal extinctions, and changing fire regimes. At sites in the central Great Lakes region, the development of no-analog pollen assemblages, featuring unique combinations of boreal conifer and hardwood taxa, has been linked to declines in megafaunal population densities and intensified fire regimes based on multiple-proxy analyses of fossil pollen, coprophilous spores (e.g., *Sporormiella*-type), and macroscopic charcoal (Gill et al., 2009, 2012). In the Southeast, recent work at the well-dated Page-Ladson site in the Florida Panhandle (41 AMS ^{14}C dates; Fig. 1) revealed declines in *Sporormiella* at 12,700 cal yr BP that may signal late Pleistocene megafaunal population declines (Halligan et al., 2016; Perrotti, 2018). *Sporormiella*-type spores have been scarce in other pollen sequences from the southeastern United States (Liu et al., 2013; Jones et al., 2017), however, and the few macroscopic charcoal records from the Southeast suggest very little biomass burning during the full and late glacial periods, in contrast to high fire activity during the Holocene (Hussey, 1993; Jones et al., 2017; Spencer et al., 2017). Fire plays a prominent role in shaping southeastern vegetation today, particularly in longleaf pine (*Pinus palustris*) ecosystems (Platt et al., 1988; Frost, 2006; Stambaugh et al., 2017), and additional macroscopic charcoal records are needed to accurately assess how fire regimes have changed through time.

To further understand the history and drivers of late Quaternary vegetation change in the southeastern United States, we developed a multi-proxy record of paleoenvironmental change from White Pond in central South Carolina that spans the last 30,000 yr (Fig. 1). White Pond is among the few sites between the Laurentide ice margin and the Florida Peninsula with continuous Holocene sedimentation, and therefore offers a rare uninterrupted record of late Quaternary ecological changes in the Southeast. We build on the pioneering work of Watts (1980b) at White Pond by producing robustly dated high-resolution fossil pollen, macroscopic charcoal, and coprophilous spore sequences, to reconstruct changes in vegetation, fire activity, and megafaunal populations. We also reconstruct deglacial temperature variations (21,000 to 4000 cal yr BP) using brGDGT analysis. Our new record

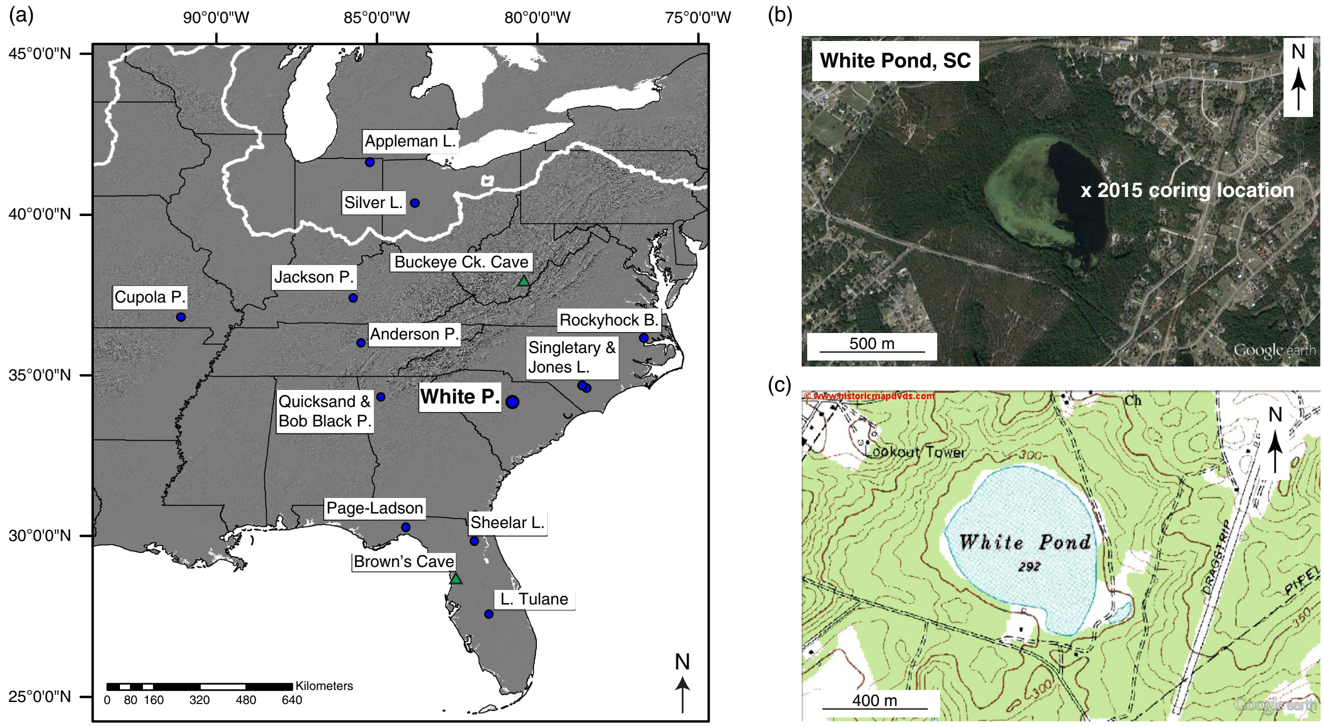

Figure 1. (a) Location of White Pond and other sites (blue circles, lacustrine records; green triangles, speleothem records) mentioned in the paper. Bold white line denotes the approximate LGM ice margin (ca. 21,000 yr BP; Dyke et al., 2003). (b) Google Earth image of the White Pond basin, including coring location. (c) Topographic map of White Pond and vicinity. Contour interval is 10 feet. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

from White Pond adds to the growing number of well-dated paleoenvironmental sites in the Southeast, and enables us to address the following questions: (1) how were millennial-scale climate events of the North Atlantic and Greenland expressed in vegetation records from the Southeast; (2) how strongly did no-analog plant communities manifest at White Pond and elsewhere in the Southeastern Coastal Plain, and were late-glacial vegetational changes linked to declining megaherbivore populations and changing fire regimes; and (3) how did interactions between climate, fire, and vegetation shape the development of Holocene southeastern forests?

STUDY SITE

White Pond is situated in a shallow groundwater-fed basin in the Carolina Sandhills region of the Inner Atlantic Coastal Plain in South Carolina (Fig. 1; 34°10′5″N, 80°46′36″W; 90 m elevation; <1.5 m water depth; 20 ha). The Carolina Sandhills, a region of late Quaternary aeolian sand sheets and dunes, occur just below the fall line, which marks the boundary between unconsolidated Cretaceous sands of the Coastal Plain and crystalline rocks of the Piedmont (Swezey et al., 2016). The Sandhills have been dated to the full-glacial period and are associated with increased aeolian activity, drier climatic conditions, and sparser vegetation (Swezey et al., 2013, 2016). White Pond likely originated as a wind-excavated depression in the Sandhills (Stone, P.A., personal communication, 2017), and the site is surrounded by sandy slopes and hills composed of typical Sandhills soils (i.e., Lakeland and Alpin sandy soils *sensu* Soil Survey Staff, 2018). Although Carolina Bays occur in the region, the White Pond basin lacks their diagnostic morphological features (e.g., elliptical shape with northwest-southeast orientation and a sand rim). Water levels fluctuate seasonally and annually; during a regional drought from 1998 to 2002, the pond experienced a severe drawdown, with most of the basin occupied by mudflats (Jackson, S.T., personal observation, 2002; Stone, P.A., personal communication, 2017). This drought was characterized by unusually large precipitation deficits during the normal groundwater recharge period of late winter and spring. Stream flows and lake levels declined dramatically throughout South Carolina during this period (Gellici et al., 2004).

The Atlantic Coastal Plain supports a species-rich flora and diverse communities that include grasslands and savannas, shrublands, needle- and broad-leaved sclerophyllous woodlands, and rich mesophytic forests (Christensen, 1988). Elevations are generally less than 150 m, and vegetation composition in the Inner Coastal Plain of South Carolina is largely shaped by soil moisture, ranging from xeric sandhill pine communities to pine-dominated flatwoods in moister areas (Christensen, 1988). *Pinus palustris* and *Aristida stricta* characterize sandhill pine forests and *Quercus laevis* is the dominant understory tree along dry sandy ridge tops. Further downslope, finer-textured soils support *Q. marilandica*, *Q. margaretta*, and *Q. incana* in the subcanopy, as well as *Nyssa sylvatica*, *Diospyros virginiana*, and *Liquidambar styraciflua*. With increasing moisture availability, sandhill pine forests grade into denser pine-dominated flatwoods, where *Pinus taeda* is often the dominant pine, although *P. palustris* occurs on sandier soils, and *P. serotina* on moister sites. The prevalence of *P. taeda* in such forests is a consequence of historical land use, whereby extensive plantings of the species has increased its seed rain, while fire exclusion from many areas has given it a competitive advantage over *P. palustris* (Wahlenberg, 1946; Snyder, 1980; Christensen, 1981, 1988). Closer to the fall line, vegetation begins to resemble that of the Piedmont, where elevations range from 150 to 500 m, and the vegetation is characterized by a mixture of *Quercus* and *Carya* species and *P. taeda* and *P. echinata* in secondary forests (Braun, 1950; Greller, 1988). Vegetation before Euro- and Afro-American land clearance across much of the Southeastern Coastal Plain, including the vicinity of White Pond, included extensive tracts of open longleaf pine (Sargent, 1884; Mohr, 1897; Wahlenberg, 1946).

White Pond is currently located in a commercially managed *Pinus taeda* forest, and the pond and surrounding property have been managed for at least seven decades as a private hunting and fishing reserve. *Pinus echinata* and *Pinus palustris* are also present near the site and, prior to land clearance in the eighteenth and nineteenth centuries, *P. palustris* was probably much more abundant, even dominant. On the low ground surrounding the pond, *Quercus falcata*, *Carya* sp., and *Liquidambar sytraciflua* grow, as do *Acer rubrum*, *Vaccinium* sp., and other mesic trees and shrubs. On exposed sandy soils on the east side of the lake, *Quercus laevis*, *Ceratiola ericoides*, *Selaginella arenicola*, *Opuntia* sp., and lichens (*Cladonia* sp.) grow under open *P. palustris* canopy. The shallow western half of the pond is vegetated by emergent graminoids (Poaceae and Cyperaceae), while the deeper eastern half is dominated by floating-leaved macrophytes (*Nymphaea odorata* and *Brasenia schreberi*).

The Inner Coastal Plain of South Carolina has a humid subtropical climate characterized by hot humid summers and mild winters. At White Pond, winter (December, January, February) temperatures range from 0.4 to 15.2°C (average = 8°C) and summer (June, July, August) temperatures vary from 19.3 to 33.1°C (average = 26°C; PRISM Climate Group, 2016). Precipitation varies seasonally, with the majority of precipitation falling during the summer months, averaging 119 mm (PRISM Climate Group, 2016), as the Bermuda high-pressure system draws moisture north and west from the Atlantic Ocean and the Gulf of Mexico (Kunkel et al., 2013). Winters are slightly drier, averaging 91 mm of precipitation (PRISM Climate Group, 2016); the southward shifting jet stream brings extratropical cyclones and associated fronts to the region (Kunkel et al., 2013).

METHODS

Field

We collected two parallel overlapping sediment cores, each approximately 5.85 m long, from White Pond in April 2015. The cores were obtained from a floating platform at a water depth of 1.47 m using a modified Livingstone square-rod piston sampler (5-cm diameter) (Wright et al., 1983). All core segments were extruded, measured, and described in the field. Cores were wrapped in plastic wrap and aluminum foil and shipped to the University of Arizona where they were stored at 4ºC.

Lithology and chronology

Core segments were cleaned to eliminate potential contaminants (i.e., ~ 1 mm of outer core surface was removed), imaged, and described lithologically. We measured the sediment magnetic susceptibility of the cleaned cores at contiguous 1-cm intervals using a Bartington MS2E logging sensor. Each core segment was subsequently sliced into 1-cm thick disks and sub-sampled at specified depths (see method section for each proxy below) for pollen (1 cm^3), charcoal (3 cm^3), and brGDGT analyses (4 cm^3). Remaining sediment (> 4 cm^3) was archived.

Samples of plant macrofossils and/or charcoal, all of confirmed terrestrial origin to avoid inaccuracies due to hardwater effects (Grimm et al., 2009), were submitted for AMS radiocarbon dating (Table 1). Fifteen AMS ^{14}C age estimates were converted to calendar ages using the IntCal13 calibration curve (Reimer et al., 2013), and an age-depth model with uncertainty estimates was constructed using Bacon software for Bayesian modeling in R (Blaauw and Christen, 2011). Ages of individual sediment horizons (1-cm intervals) were based on the weighted mean age estimates from the Bacon analysis.

brGDGT-based paleotemperature reconstruction

brGDGTs are membrane-spanning lipids produced by Acidobacteria (Weijers et al., 2006; Sinninghe Damsté et al., 2011) that are present in many sedimentary environments, including soils, peats, marine sediments, and lakes (Weijers et al., 2006, 2007b; Tierney and Russell, 2009; Schouten et al., 2013; Sinninghe Damsté, 2016). The chemical structure of the alkyl chains in brGDGTs varies due to environmental conditions, most notably temperature and pH. Weijers et al. (2007b) investigated brGDGT distributions in a set of globally-distributed soil samples, and showed that the number of cyclopentyl moieties in the alkyl chains, characterized by the index of cyclization of branched tetraethers (CBT), responds primarily to pH, whereas the number of methyl branches, characterized by the index of methylation of branched tetraethers (MBT), varies according to mean annual temperature and pH. Weijers et al. (2007b) used these relationships to develop inference models for temperature based

Table 1. Accelerator mass spectrometry (AMS) radiocarbon dates from White Pond.

Depth (cm)[a]	Uncalibrated ^{14}C age (^{14}C yr BP)	Calibrated age (cal yr BP; 2-sigma range)[b]	Material dated	Lab number/reference[c]
56.5	2035 ± 15	(1933–2040)	Charcoal	UCIAMS-180319
112.0	4150 ± 15	(4586–4821)	Charcoal	UCIAMS-180320
134.5	5065 ± 20	(5747–5898)	Charcoal	UCIAMS-180321
183.5	7040 ± 15	(7844–7933)	Charcoal	UCIAMS-180322
240.5	7880 ± 30	(8591–8854)	Wood	UGAMS-21713
260.5	9140 ± 35	(10,230–10,400)	Wood	UCIAMS-16591
300.5	11,390 ± 340	(12,657–14,011)	Wood	UCIAMS-16592
350.5	14,040 ± 130	(16,615–17,460)	Wood	UCIAMS-16593
389.5	16,185 ± 35	(19,385–19,703)	Wood	UCIAMS-182464
433.5	18,730 ± 60	(22,413–22,789)	Charcoal	UCIAMS-182465
443.5	19,700 ± 60	(23,499–23,966)	Wood	UCIAMS-182466
490.5	21,990 ± 300	(25,727–27,021)	Charcoal	UCIAMS-182467
503.5	23,300 ± 80	(27,365–27,714)	Charcoal	UCIAMS-182468
540.5	26,260 ± 60	(30,362–30,850)	Charcoal	UGAMS-21714
550.5	28,020 ± 200	(31,330–32,150)	Wood	UCIAMS-16954

[a] Depth below mud surface.

[b] Calibrated ages derived from CALIB 7.1 (Stuiver et al., 2017).

[c] UCIAMS, Keck Carbon Cycle AMS Lab, University of California, Irvine; UGAMS, Center for Applied Isotope Studies, University of Georgia.

on MBT and CBT. Subsequent studies have developed variants of these calibrations using both soil and lake sediments. Although questions remain concerning whether brGDGTs in lakes derive primarily from allochthonous sources (e.g., watershed soils) or autochthonous production (e.g., Tierney and Russell, 2009; Buckles et al., 2014; Loomis et al., 2014a), all studies to date show strong correlations between brGDGT distributions and mean annual temperatures (Peterse et al., 2009; Loomis et al., 2014a, 2014b). Although brGDGTs are just beginning to be used as a paleotemperature proxy in eastern North America (see Watson et al., 2018), they have been used to reconstruct regional late Pleistocene to early Holocene temperatures in New Zealand (Zink et al., 2010), Australia (Woltering et al., 2014), Europe (Niemann et al., 2012), the southwestern United States (Fawcett et al., 2011), and Africa (Loomis et al., 2012, 2015, 2017). Furthermore, brGDGTs from modern North American lacustrine sediments and soils have been used in several brGDGT temperature calibration indices (Weijers et al., 2007b; Blaga et al., 2010; Peterse et al., 2012).

We measured the relative abundances of brGDGTs in sediment samples from White Pond every ~200 yr between 21,000 and 4000 cal yr BP and in a modern surface sample to estimate changes in mean annual temperature during the deglacial transition. While a brGDGT-based temperature reconstruction spanning the entire 30,000-yr record would have been ideal, analytical and time constraints led us to focus on the deglacial period. Sample preparation followed Loomis et al. (2012). Briefly, lipids were extracted from freeze-dried and homogenized sediment using a Dionex™ 350 Accelerated Solvent Extraction system using a 9:1 dichloromethane:methanol (DCM, MeOH) solution. The lipid extracts were separated into apolar and polar fractions using alumina columns with 9:1 hexane:DCM and 1:1 DCM: MeOH, respectively, as eluents. The polar fraction was dried under N_2, dissolved, and passed through a 0.45-μm filter. brGDGTs were analyzed using atmospheric pressure chemical ionization/high performance liquid chromatography-mass spectrometry (APCI/HPLC-MS) at Brown University using selective ion monitoring mode on an Agilent/Hewlett Packard 1100 series LC/MSD with an Alltech Prevail Cyano column (150 × 2.1 mm, 3 μm). Relative abundances of the brGDGTs were quantified by manually integrating the areas of the protonated molecular ions of each compound, monitoring *m/z* 1302, 1300, 1298, 1296, 1050, 1048, 1046, 4036, 1034, 1032, 1022, 1020, and 1018. These methods did not separate the 5- and 6-methyl isomers of brGDGTs (e.g., de Jonge et al., 2014; Russell et al., 2018), but allow us to calculate the degree of cyclization (CBT) and methylation (MBT) of the brGDGTs using the equations from Weijers et al. (2007b), as well as to calculate MBT using the equation of Peterse et al. (2009).

Different calibration functions for brGDGTs typically produce qualitatively similar temperature reconstructions and trends for late Quaternary sediments but often differ in their absolute values and magnitude (Loomis et al., 2012; Watson et al., 2018). brGDGTs are produced in both soils and lake sediments (Weijers et al., 2007b; Tierney and Russell, 2009; Weber et al., 2015), and the relative abundances of brGDGTs in soils can differ from those in lake sediments under the same temperature (Tierney et al., 2010; Loomis et al., 2011, 2014a). Lake-specific calibrations have shown promise when applied to sediment cores from tropical lakes (e.g., Loomis et al., 2012, 2015, 2017); however, soil-based calibrations have produced credible temperature reconstructions in temperate-zone lakes (e.g., Fawcett et al., 2011; Niemann et al., 2012; Watson et al., 2018). We calculated the ratio of branched to isoprenoidal GDGTs (the BIT index) to assess the variability of GDGT contributions from bacterial and archaeal sources to the lake sediment (Hopmans et al., 2004), which has been shown to inform the applicability of GDGTs to temperature reconstructions. We tested several brGDGT calibrations, including those developed for brGDGTs in soils by Weijers et al. (2007b) and Peterse et al. (2012), as well as lake-specific calibrations by Pearson et al. (2011) and Sun et al. (2011), to evaluate which calibration most accurately reflects modern temperatures at our site. We also used the CBT index (Weijers et al., 2007b) to estimate pH and evaluate the relationship between BIT, pH, and temperature reconstructions from the brGDGTs.

Pollen analysis

Sediment samples were analyzed for pollen at 2- to 8-cm intervals and prepared using standard methods described by Jackson (1999), including treatments with hot 10% KOH, 10% HCl, and 48% HF, sieving (180 µm), and acetolysis for two minutes. We added one *Lycopodium* tracer tablet (batch 3862, Lund University; 1 tablet = 9666 ± 671 spores) to the samples to calculate pollen concentrations (grains/cm^3) and pollen accumulation rates (grains/cm^2/yr), using the Bacon age model for the latter. A minimum of 300 terrestrial pollen grains were identified per sample at 400 × magnification. Identifications were made to the lowest taxonomic level possible using reference collections and atlases (e.g., McAndrews et al., 1973; Kapp et al., 2000). Pollen grains that could not be identified using available reference material were classified as “unknown,” while deteriorated or hidden pollen grains were classified as “indeterminate.” Terrestrial pollen percentages were calculated based on the total pollen sum of upland trees, shrubs, herbs (including Poaceae and Cyperaceae), and pteridophytes; aquatic pollen percentages were based on the total terrestrial and aquatic pollen sums. The pollen percentage record was divided into zones based on visual inspection and constrained cluster analysis (CONISS; Grimm, 1987). We carefully examined the pollen samples for coprophilous *Sporormiella*-type spores using reference material and illustrated guides (e.g., Bell, 1983; van Geel et al., 2003; Cugny et al., 2010). A subset of pollen samples spanning the entire record were counted for *Sporormiella* by both the Jackson and Williams labs to account for possible inter-lab biases and to confirm our findings.

We calculated the minimum dissimilarity of each fossil pollen sample from White Pond to 2594 modern pollen samples from eastern North America (east of 105°W; Whitmore et al., 2005) using the squared-chord distance (SCD) metric (Overpeck et al., 1985). SCD was calculated using the analogue program in R (Simpson, 2007) and incorporated 25 common eastern North American pollen taxa (see Williams et al., 2001 for list). Consistent with Jones et al. (2017), we considered samples with a minimum SCD ≥ 0.237 to have no modern analog. This threshold is based on receiver operating characteristic analysis and an analysis of paired modern assemblages from eastern North America (east of 105°W; Whitmore et al., 2005) from the same versus different vegetation formations (Gavin et al., 2003; Wahl, 2004).

Macroscopic charcoal analysis

Charcoal particles > 125 µm were extracted at contiguous 1-cm intervals using standard sieving methods (Whitlock and Larsen, 2001). We dispersed sediments in a solution of 10% sodium hexametaphosphate, $(NaPO_3)_6$, and 5% sodium hypochlorite (bleach), NaClO, for 24 hours and sieved (125-µm mesh). The sieved fraction was counted on a gridded platform using a stereomicroscope, and charcoal attributable to graminoids (i.e. Poaceae and other monocots) was distinguished from other types of charcoal (wood, conifer needles, and dicot leaves) based on morphology (Jensen et al., 2007; Mustaphi and Pisaric, 2014). Large charcoal particles (> 125 µm) are assumed to record high-severity fires within a few kilometers of the study site (Higuera et al., 2010). Our analysis focused on long-term trends in total charcoal accumulation rates (CHAR; particles/cm^2/yr), as well as changes in the percentage of graminoid (“grass”) charcoal over time to better understand the nature of past fires (i.e., surface versus crown fires). CHAR was calculated by dividing charcoal concentration (particles/cm^3) by deposition time (yr/cm) obtained from the age-depth model.

RESULTS

Lithology and chronology

The core lithology consisted of five units with no evidence of depositional hiatuses (e.g., abrupt lithological transitions, mottling, oxidative coloration, and blocky or prismatic sediment structures; Fig. 2). The base of the core (584 cm depth) is estimated to have an age of 33,300 cal yr BP, and the age-depth model indicates constant sedimentation (average rate = 13 cm/1000 yr) through the late Pleistocene, with notable changes in average sedimentation rates during the early Holocene (Fig. 3). From 584 to 553 cm depth (33,300 to 31,500 cal yr BP), lithological unit 1 consisted of massive coarse white sand mixed with clay with high magnetic susceptibility (13 to 33 SI units), indicating relatively high mineral clastic content. Unit 2, 553 to 507 cm depth (31,500 to 27,800 cal yr BP), was characterized by massive white-gray clay and included a 4-cm wood layer at 548 cm depth; high magnetic susceptibility (7 to 34 SI units) indicates high clastic mineral content. From 507 to 276 cm depth (27,800 to 11,500 cal yr BP), unit 3 featured interbedded gray clay and silt layers with increasingly abundant organic matter towards the top of the unit; sediment magnetic susceptibility values gradually decreased (−1 to 46 SI units), indicating diminishing clastic content. Unit 4, 272 to 262 cm depth (11,500 to 10,400 cal yr BP), was a transitional unit from organic clays and silts to brown gyttja that featured low sediment magnetic susceptibility values (−1 to 2 SI units). Unit 5, the uppermost unit, < 262 cm depth

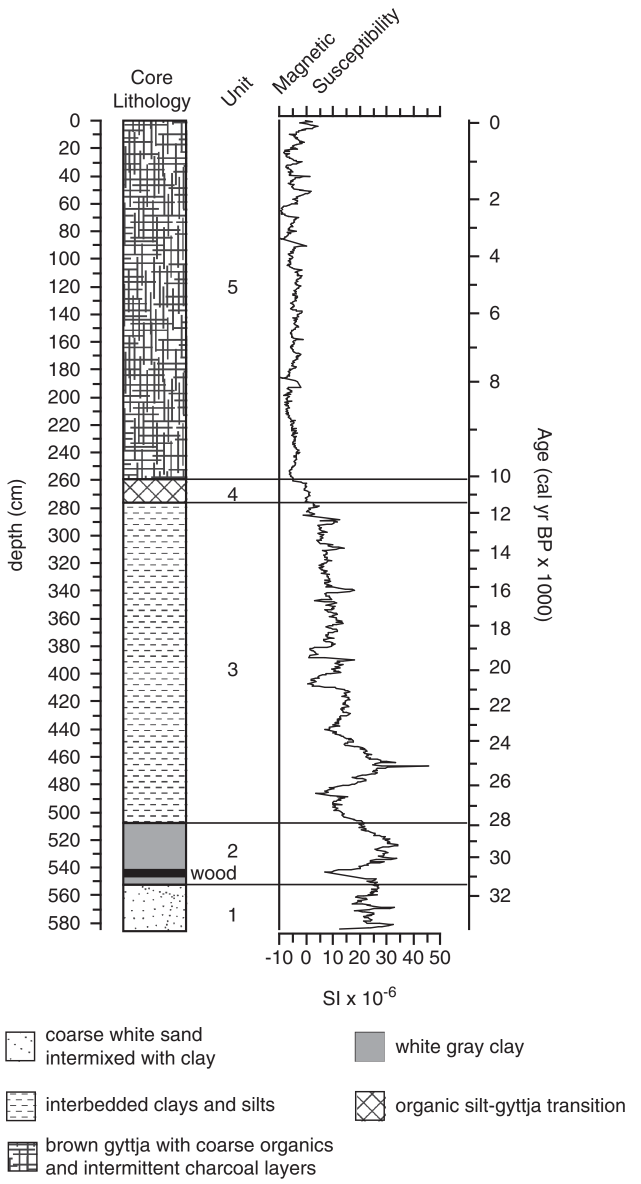

Figure 2. Lithologic and magnetic susceptibility data (SI units) from White Pond, including stratigraphic units. Timescale is based on Bacon age-depth model (Figure 3) and associated age controls (Table 1).

(10,500 cal yr BP to present), was composed of brown gyttja with abundant coarse organics and intermittent charcoal layers, and magnetic susceptibility values reached their lowest levels of the record (–11 to 4.3 SI units). Within this lithologically uniform upper unit, the age model indicates that average sedimentation rates increased to 66 cm/1000 yr between 240 and 184 cm depth (8700 to 7900 cal yr BP), and subsequently decreased to 22 cm/1000 yr thereafter (Fig. 3). With the exception of this brief 800-yr period of elevated sedimentation, average Holocene sedimentation rates were lower than typical Holocene rates for lakes in eastern North America (Goring et al., 2012), but comparable to other continuous Holocene records from the Southeast (Jones et al., 2017).

brGDGT-based paleotemperature reconstruction

The BIT index varied between 0.93 and 1.0 in sediments from White Pond, indicating that the majority of the GDGTs were derived from bacteria. BIT values were originally interpreted to reflect the relative contribution of GDGTs derived from soils (brGDGTs) versus aquatic environments (isoprenoidal GDGTs), but subsequent work has shown that lake sediments can have abundant aquatically-derived brGDGTs (e.g., Tierney et al., 2010; Buckles et al., 2014; Loomis et al., 2014a; Weber et al., 2015). The high BIT values in White Pond sediments are compatible with an abundance of soil-derived GDGTs, assuming the brGDGTs are terrestrial, and the stability of the BIT index through time suggests little change in GDGT sources to the sediment that might impact our temperature reconstructions.

The five mean annual temperature (MAT) calibrations yielded similar trends in temperature over time, but with significant differences in average values (Fig. 4; Supplementary Fig. 1). The Peterse et al. (2012) and Weijers et al. (2007b) calibrations produced temperature estimates in the modern sediment that were closest to the instrumental mean annual air temperature at White Pond (17.1°C; PRISM Climate Group, 2016), which might suggest that the brGDGTs in White Pond were produced in soils (see also Watson et al., 2018). Soil pH values inferred from CBT (Peterse et al., 2012) average 5.9 and vary between 4.7 and 6.8. pH values were relatively high during the late glacial period, became gradually more acidic during the deglaciation, and average 5.2 in sediments deposited during the last 10 ka. The gradual decrease in pH during the last deglaciation is compatible with increasing vegetation cover and chemical weathering (e.g., Weijers et al., 2007a) as climate became warmer and wetter, and the relatively acidic values during the Holocene are compatible with pH values of sandy soils covered with pine forests, such as those surrounding White Pond today. Together, these lines of evidence all suggest a terrigenous source for the brGDGTs in White Pond.

The Peterse et al. (2012) modern calibration (16.9°C) is closest to the instrumental value, and we used this calibration in our downcore reconstructions. Neither reconstructed soil pH nor BIT values are correlated to reconstructed MAT values ($R^2 = 0.06$ and 0.00, respectively); soil chemistry and GDGT source had little impact on temperature reconstructions. The Peterse et al. (2012) calibration has a relatively large error (root-mean-square error) of 5.0°C, which could derived from many sources, including analytical error, uncertainty in the MAT values to which brGDGTs are calibrated, and/or inherent variability in the response of brGDGTs to changes in MAT. As such, our temperature reconstruction is primarily qualitative, and our interpretations focus primarily on trends rather than absolute values.

MATs according to the Peterse et al. (2012) calibration were low but gradually increasing between 21,000 and

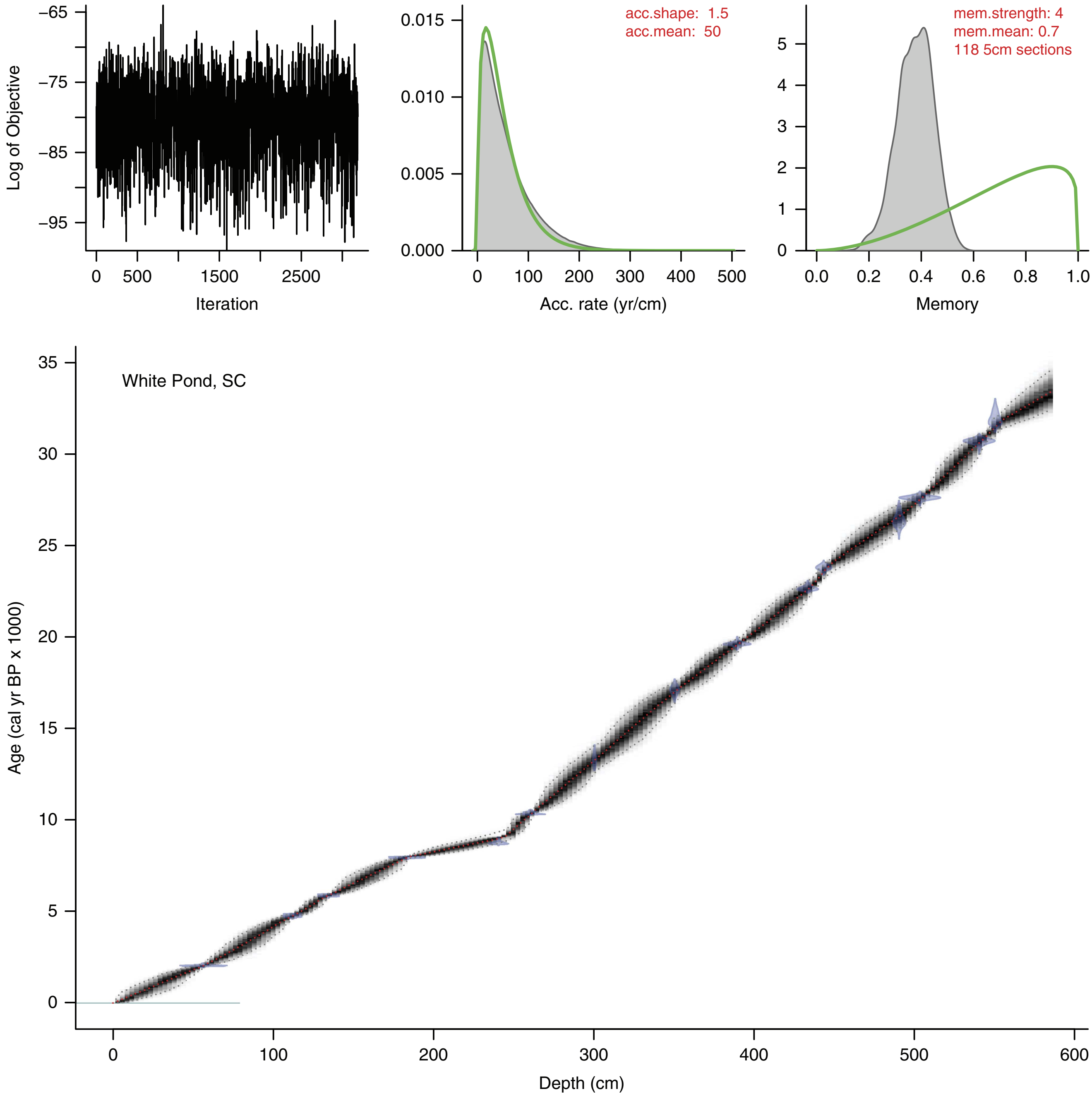

Figure 3. Bacon age-depth model for White Pond. In the main plot (bottom), blue violin plots show the probability-density function for each calibrated radiocarbon age estimate. Dotted red line indicates weighted averages of all fitted chronologies. Grayscale cloud represents age-model probability and is bounded by a dotted line representing the confidence interval (95%). Left top plot shows the Markov chain Monte Carlo (MCMC) iteration history, the middle top plot shows the prior (line) and posterior densities (area fill) for the mean accumulation rate, and the right top plot shows the prior (line) and posterior (area fill) of sediment memory (1-cm autocorrelation strength). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

16,500 cal yr BP. During this time, temperatures were highly variable and ranged from 11.7 to 18.1°C (average = 15.2°C). After 16,600 cal yr BP, inferred temperatures decreased slightly until 13,800 cal yr BP and varied between 14.7 and 16.9°C (average = 15.6°C). At 13,800 cal yr BP, MAT increased abruptly and reached the highest temperatures of the record until 10,500 cal yr BP; temperatures ranged from 18.6 to 20.4°C (average = 19.5°C) over this period and peaked at 12,200 cal yr BP. After 10,500 cal yr BP, inferred temperatures gradually decreased and varied between 15.5 and 18.6°C (average = 17.5°C), with the exception of an abrupt temperature excursion toward colder temperatures between 9000 and 8000 cal yr BP; MAT varied between 14.0 and 16.5°C (average = 15.2°C) during this cold period and

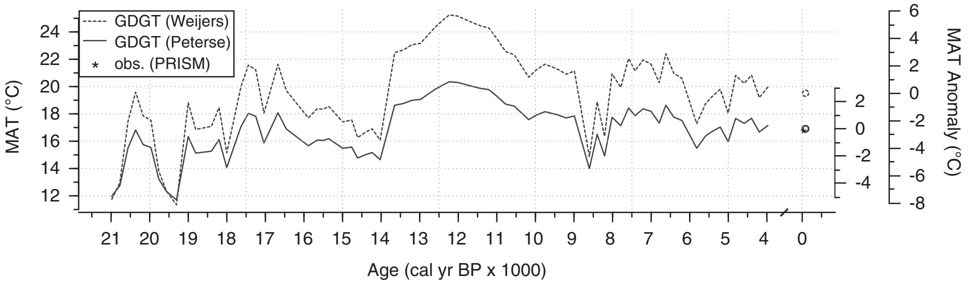

Figure 4. Reconstructed mean annual temperature at White Pond based on brGDGT data and the calibrations of Weijers et al. (2007b; dashed line) and Peterse et al. (2012; solid line).

were similar to temperatures recorded during the late glacial period.

Pollen sequence

The White Pond fossil pollen record featured three broad zones between 30,000 cal yr BP and present, based on CONISS and visual inspection (Fig. 5; Supplementary Fig. 2). These informal zones represent broad transitions between conifer and hardwood vegetation and are further divided into subzones based on changes in the abundance of specific taxa. Sediments older than 30,000 cal yr BP (below 540 cm depth) had very poor pollen preservation and were not counted as part of the analysis.

Basal subzone WHT-1a (30,400 to 19,700 cal yr BP; 540 to 391 cm depth) featured high levels of *Pinus* pollen (70 to 95%) and very low percentages of hardwood taxa, including *Quercus* (<7%), *Carya* (<1%), and *Ostrya/Carpinus* (<1%). *Picea* pollen occurred at low to moderate levels (1 to 7%), while *Abies* occurred sporadically and recorded low percentages (<1%). Total upland herbaceous pollen, including *Artemisia* (<2%), *Ambrosia*-type (<2%), Asteraceae (<3%), and Poaceae (<2%), occurred at sustained low to moderate levels (2 to 10%), as did percentages of *Polygonella polygama*-type and *P. fimbriata*-type pollen (<2%) and *Selaginella arenicola* spores (<1%). *Isoetes* (5 to 75%) dominated aquatic assemblages, often at very high levels.

Gradually increasing levels of *Quercus* pollen (5 to 14%) and to a lesser extent, *Carya* (1 to 2%), characterized subzone WHT-1b (19,700 to 16,300 cal yr BP; 391 to 341 cm depth); *Pinus* percentages decreased slightly (69 to 78%). *Picea* levels increased somewhat (3 to 8%), while *Abies* pollen was absent from the record. Pollen from upland herbaceous taxa increased slightly (5 to 13%), mostly due to elevated Asteraceae levels (<4%). *Isoetes* continued to dominate aquatic assemblages, although at substantially diminished levels (4 to 12%), and *Equisetum* spores occurred at low percentages (<2%).

Subzone WHT-2a (16,300 to 13,500 cal yr BP; 341 to 304 cm depth) featured decreasing *Pinus* pollen percentages (23 to 54%) and increasing levels of hardwood taxa, including *Quercus* (17 to 38%), *Carya* (5 to 14%), *Ostrya/Carpinus* (1 to 4%), and *Fagus* (<3%). Pollen from other hardwood taxa at low but consistent levels, including *Ulmus* (<1%), *Fraxinus pennsylvanica*-type (<2%), *Juglans nigra*-type (<1%), *Corylus* (<1%), and *Platanus* (<2%). *Picea* registered the highest percentages (1 to 15%) of the record in this subzone. Levels of upland herbaceous pollen slightly decreased (2 to 9%), while percentages of *Isoetes* spores increased (10 to 49%).

Pinus pollen percentages continued to decrease (6 to 24%) in subzone WHT-2b (13,500 to 12,000 cal yr BP; 304 to 284 cm depth), while *Picea* dropped to very low levels (<2%). Percentages of *Carya* reached their highest levels (8 to 19%) of the record, and *Quercus* (36 to 53%) and *Ostrya/Carpinus* (3 to 10%) continued to increase; percentages of *Fagus* (<3%), *Ulmus* (<3%), *Fraxinus pennsylvanica*-type (<2%) and other hardwood taxa (*Juglans nigra*-type, *Corylus*, and *Platanus*) and herbaceous pollen (5 to 8%) remained unchanged. *Juniperus* pollen increased slightly (1 to 6%) from the previous zone. Percentages of *Isoetes* decreased (5 to 19%) but continued to dominate the aquatic assemblage.

Subzone WHT-2c (12,000 to 10,400 cal yr BP; 284 to 262 cm depth) was characterized by very low *Pinus* levels (2 to 12%) and the highest percentages of *Fagus* (4 to 10%), *Ostrya/Carpinus* (4 to 9%), *Corylus* (<2%), and *Platanus* (<2%) of the record. Levels of *Quercus* continued to increase (47 to 59%), while *Carya* decreased slightly (9 to 16%). *Ulmus* (<3%), *Fraxinus pennsylvanica*-type (<2%), and *Juglans nigra*-type (<1%) percentages remained unchanged, and *Juniperus* pollen sustained high levels (2 to 7%). Upland herbaceous taxa reached their lowest levels (2 to 4%) of the record, and percentages of *Isoetes* continued to decrease (1 to 11%).

A step-like increase in *Pinus* pollen to moderate amounts (25 to 45%) marked the transition to subzone WHT-3a (10,400 to 6400 cal yr BP; 262 to 149 cm depth). Levels of *Carya* (1 to 4%), *Ostrya/Carpinus* (<2%), *Corylus* (<1%), and *Fagus* (<1%) decreased, as did *Juniperus*-type percentages (<1%). *Quercus* levels remained high (40 to 60%), and percentages of *Ulmus* (<2%) and *Fraxinus pennsylvanica*-type (<1%) pollen were relatively unchanged. *Liquidambar* pollen registered consistent low levels (<3%). Percentages of Poaceae (1 to 5%) and Cyperaceae (<4%) increased, particularly towards the top of the subzone. *Brasenia* (1 to 15%) replaced *Isoetes* (<1%) as the dominant taxa in the aquatic assemblage; *Nymphaea* pollen percentages increased as well (<2%).

Subzone WHT-3b (6400 cal yr BP to present; 149 to 0 cm depth) featured decreased levels of *Quercus* (10 to 25%) and elevated *Pinus* pollen percentages (55 to 80%). Pollen from

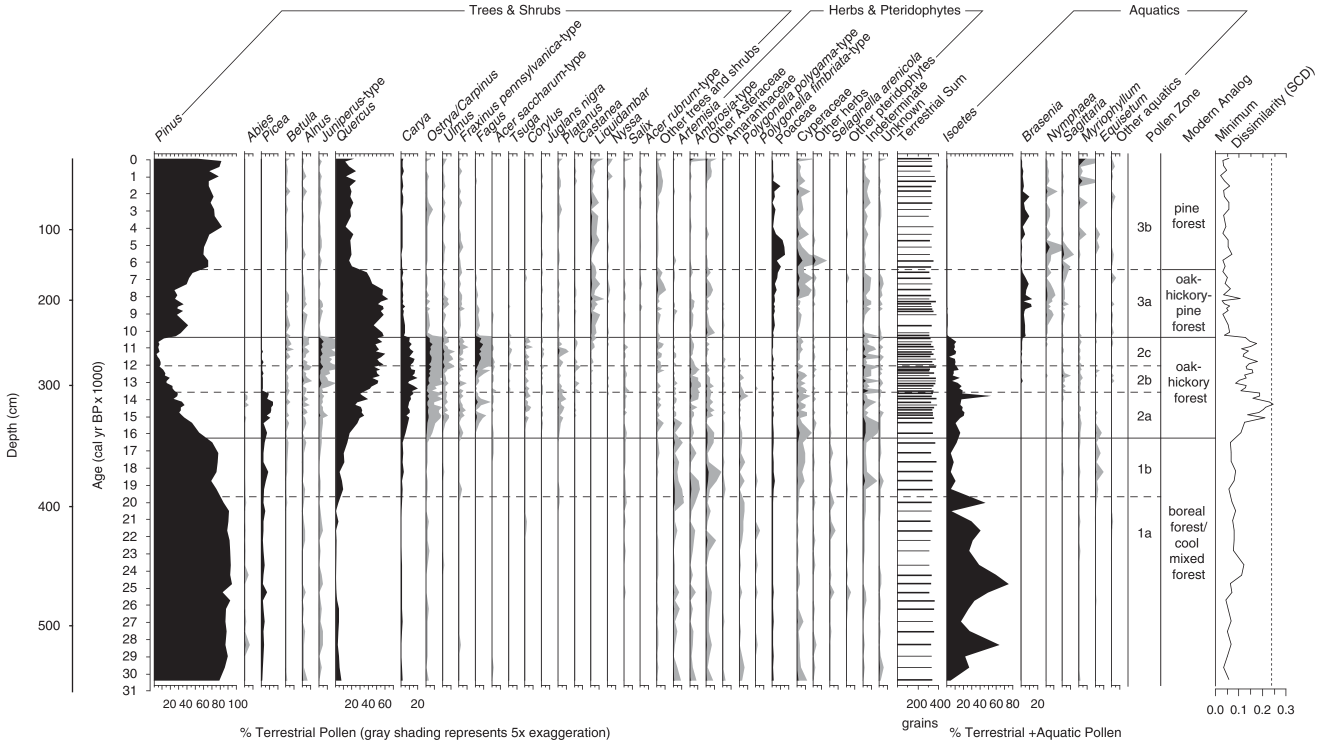

Figure 5. Pollen percentage profile for White Pond, showing selected taxa. Minimum vegetation dissimilarity to modern pollen assemblages (an index of novelty and no-analog communities) is represented as square-chord distance values (SCD). Pollen zonation based on CONISS (Grimm, 1987) and visual inspection. The no-analog threshold (SCD = 0.237; Jones et al., 2017) is shown as a vertical dashed line.

hardwood taxa were poorly represented, with the exception of *Liquidambar,* which maintained consistent low levels (<3%). Percentages of Poaceae pollen were elevated in at the bottom of the subzone and decreased (<15%) towards the present day. *Brasenia* pollen (<10%) continued to dominate the aquatic assemblage, which also included low to moderate amounts of *Nymphaea* (<5%) and *Myriophyllum* (<10%) pollen.

Sporormiella-type spores

With the exception of the modern surface sample, no *Sporormiella*-type spores were observed in pollen samples obtained from the White Pond sediments.

Analog analysis

Almost all fossil pollen assemblages had modern analogs (Fig. 5). Prior to 16,300 cal yr BP, fossil assemblages most resembled modern boreal forests and cool mixed forests of the Appalachian Mountains. Increasing hardwood taxa, including *Quercus*, *Carya*, *Fraxinus pennsylvanica*-type, and *Ostrya/Carpinus*, at 16,300 cal yr BP marks the onset of elevated minimum dissimilarities that last until 10,400 cal yr BP (pollen zone WHT-2), indicating a period of high ecological novelty in the southeastern United States relative to modern assemblages in North America. Except for the pollen assemblage at 14,300 cal yr BP, however, minimum dissimilarities never exceed the 0.237 no-analog threshold used in previous Southeast studies (Jones et al., 2017). Pollen assemblages between 16,300 and 10,400 cal yr BP had modern analogs in oak-hickory forests of the central Great Lakes region, while the no-analog assemblage at 14,300 cal yr BP featured particularly high levels of *Picea* and *Fagus* pollen. After 10,400 cal yr BP, *Carya*, *Ostrya/Carpinus*, *Fraxinus pennsylvanica*-type, and *Fagus* pollen sharply decrease and *Pinus* pollen abundance increases. Levels of *Quercus* pollen remain relatively unchanged until 6400 cal yr BP when they subsequently decreased. Assemblages from this high *Quercus* period (pollen subzone WHT-3a) generally match modern assemblages in oak-hickory-pine forests of the Appalachian Mountains. Following the decline in *Quercus*, assemblages after 6400 cal yr BP (pollen subzone WHT-3b) resemble samples from present-day pine forests in the Southeast.

Macroscopic charcoal data

Late Pleistocene and Holocene sediments from White Pond differed significantly in their abundance of macroscopic charcoal (Fig. 6). Total CHAR values were extremely low in late Pleistocene sediments and increased substantially at the start of the Holocene. Before 10,400 cal yr BP, CHAR ranged from 0–0.889 particles/cm^2/yr (average = 0.103 particles/cm^2/yr), and elevated periods of grass charcoal were recorded between 30,400 and 25,500 cal yr BP (average = 12.59%),

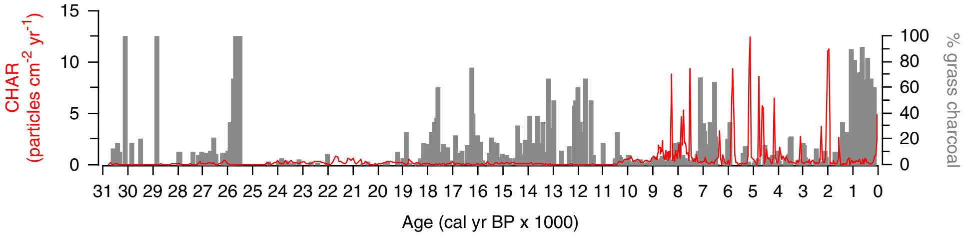

Figure 6. Macroscopic charcoal profile for White Pond. Solid red line denotes total charcoal accumulation rate (CHAR), and gray bars show relative contribution of grass charcoal to overall charcoal sum (% grass charcoal). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

and from 19,300 to 10,400 cal yr BP (average = 12.63%). After 10,400 cal yr BP, total CHAR increased tenfold and remained high throughout the Holocene (0.009–12.404 particles/cm^2/ yr, average = 1.101 particles/cm^2/yr). A number of very large charcoal peaks are recorded at 8300 cal yr BP (8.78 particles/cm^2/yr), 7500 cal yr BP (9.40 particles/cm^2/yr), 5800 cal yr BP (8.78 particles/cm^2/yr), 5100 cal yr BP (12.40 particles/cm^2/yr), 4800 cal yr BP (8.60 particles/cm^2/yr), and 2000 cal yr BP (11.26 particles/cm^2/yr), and likely represent high-severity fire events. Elevated levels of grass charcoal occurred between 7100 and 6500 cal yr BP (average = 24.70%), and from 1200 cal yr BP to present (average = 35.65%).

DISCUSSION

The paleorecord at White Pond covers the central portion of a network of well-dated fossil pollen records in the southeastern United States (Fig. 1), including Jackson and Anderson ponds in the Interior Low Plateaus region of Kentucky and Tennessee (Liu et al., 2013), Cupola Pond in the Ozark highlands of southern Missouri (Jones et al., 2017), and Lake Tulane in peninsular Florida (Grimm et al., 2006). These sites provide a point of comparison with the White Pond record to better understand spatiotemporal patterns and mechanisms of late Quaternary vegetation change in the southeastern United States. While additional records from the region (Fig. 1) still have substantial dating uncertainties owing to chronologies based on bulk-sediment ^{14}C dates and/ or low density of dates, some patterns can still be discerned.

How were millennial-scale climate events recorded in Greenland and the North Atlantic expressed in vegetation records from the Southeast?

During the last glacial period (65–21 cal yr BP), δ^{18}O profiles from Greenland ice cores record millennial-scale Dansgaard-Oeschger cycles, periods of short-term warming (ca. 60 yr) followed by slow cooling (up to 2000 yr; Dansgaard et al., 1984), and marine cores from the North Atlantic record ice-rafted debris deposits (Heinrich events) associated with cold stadials (Heinrich, 1988). The best continental evidence for Heinrich events in North America comes from Lake Tulane in peninsular Florida (Grimm et al., 2006), which records rapid millennial-scale alternations between cool, dry *Quercus*-scrub/prairie and warm, wet *Pinus* phases. These correspond respectively to the warm phases of Dansgaard-Oeschger cycles and the cold Heinrich events back to Heinrich (H) event H6, suggesting that temperature variations in central Florida were antiphased to those in the North Atlantic (Grimm et al., 2006). The Jackson Pond record from central Kentucky indicates a shift from *Pinus* to *Picea* dominance ca. 26,000 cal yr BP that is coeval with the onset of H2 and a warm, wet *Pinus* phase at Lake Tulane (Fig. 7). The transition to *Picea* at 26,000 cal yr BP suggests a shift to wetter and possibly cooler conditions in the Interior Low Plateaus region during H2, in partial contrast to warmer and wetter conditions at Lake Tulane. Moreover, the H2 *Pinus* phase is brief at Lake Tulane, reverting back to *Quercus*-scrub/prairie at 23,000 cal yr BP, while the *Picea*-dominated vegetation at Jackson Pond persists until 19,000 to 18,000 cal yr BP (Fig. 7; Liu et al., 2013).

Consistently high levels of *Pinus* and moderate amounts of upland herbaceous pollen between 30,000 and 20,000 cal yr BP at White Pond suggest generally cool, dry conditions. Unfortunately, because the brGDGT analyses were designed to address questions about deglacial climate and vegetation change, they do not extend before 21,000 cal yr BP. However, a decline of *Quercus* pollen from low to trace percentages ca. 26,000 cal yr BP coincides with onset of H2 and may indicate a transition to cooler conditions (Fig. 8). Records from the North Carolina Coastal Plain (Rockyhock Bay, NC; Whitehead, 1981) and Georgia highlands (Green Pond; Watts, 1973), Bob Black Pond (Watts, 1970) also show higher levels of *Quercus* and other deciduous taxa, and hence warmer conditions, before 26,000 cal yr BP, although these chronologies are not as well constrained by ^{14}C dates (all bulk sediment). A *Quercus-Betula-Alnus* maximum is recorded at Rockyhock Bay between 32,000 and 28,000 cal yr BP, and a *Pinus-Quercus-Carya* assemblage prevailed at Green and Bob Black ponds between ca. 33,000 and 27,000 cal yr BP; in all cases, these assemblages are succeeded by increases in *Pinus* and *Picea.* Not only is 26,000 cal yr BP associated with the onset of H2, but the interval of higher hardwoods prior to 26,000 cal yr BP also coincides with a period of extensive ice retreat indicated by glacial and non-glacial sediments in the Great Lakes region (Farmdalian Interstadial of Willman and Frye, 1970), probably equivalent

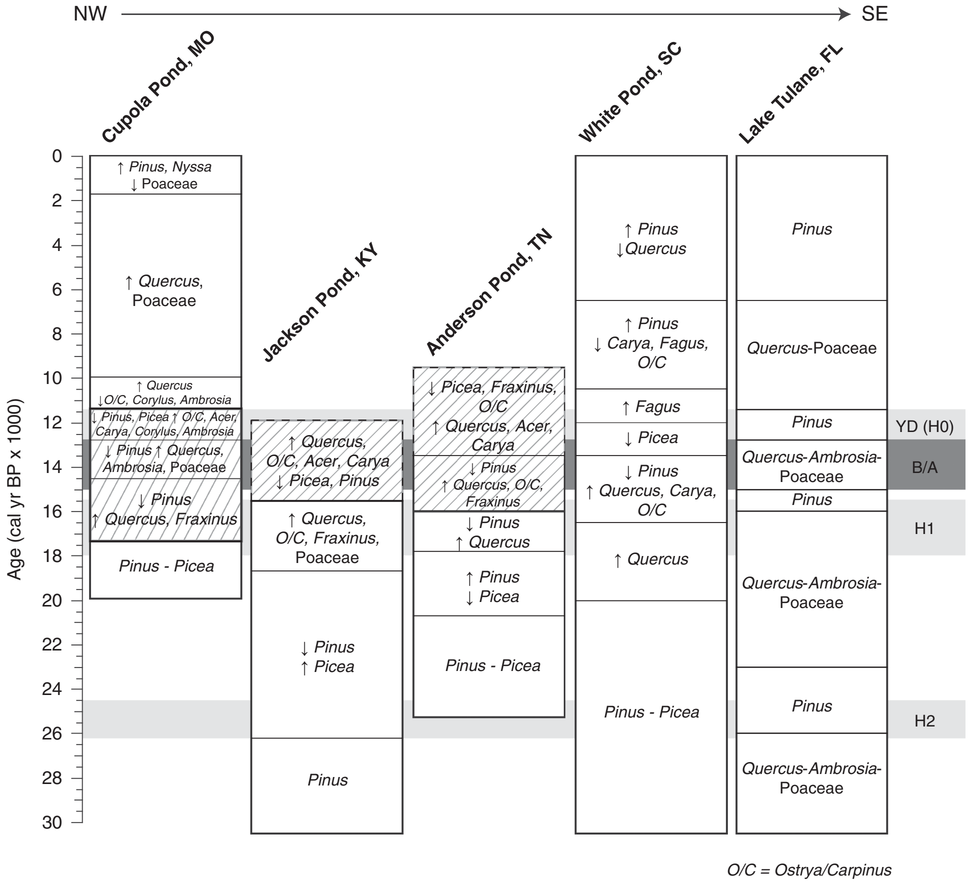

Figure 7. Comparison of late Quaternary vegetation changes from well-dated pollen records in the southeastern US, including Cupola Pond (Jones et al., 2017), Jackson Pond (Liu et al., 2012), Anderson Pond (Liu et al., 2013), White Pond (this study), and Lake Tulane (Grimm et al., 2006). Arrows indicate increasing or decreasing trends in pollen percentage data, and hatching represents assemblages lacking modern analogs (SCD ≥ 0.237; Jones et al., 2017). The ages and time spans of the Heinrich events (light gray bands) are based on GICC05 chronology (Svensson et al., 2008), while the timing of the Bølling-Allerød (B/A, dark gray band) is based on Rasmussen et al. (2006).

to the Plum Point Interstadial (Fullerton, 1980; Karrow et al., 2000) between 32,000 and 26,000 cal yr BP.

During the deglacial period (21,000 to 11,700 cal yr BP), global MATs increased by 3.5 to 5.5°C (Liu et al., 2009; Shakun and Carlson, 2010) and perhaps as much as 10°C in the north-central United States (Watson et al., 2018). Superimposed on this gradual warming trend were the Bølling-Allerød, a relatively warm and wet interstadial registered between 14,700 and 12,900 cal yr BP in the North Atlantic (Rasmussen et al., 2006) and the Younger Dryas, a subsequent cold stadial recorded between 12,900 and 11,700 cal yr BP (Rasmussen et al., 2006; Svensson et al., 2008; Shakun et al., 2012). At Lake Tulane in peninsular Florida, Bølling-Allerød warming was associated with a cool, dry *Quercus*-scrub/prairie phase, while the Younger Dryas was linked to a warm, wet *Pinus* phase, providing additional evidence that temperature variations in central Florida were antiphased to those in the North Atlantic (Grimm et al., 2006). At Cupola Pond in southern Missouri, the onset of the Bølling-Allerød and Younger Dryas was associated with the development of two distinct no-analog pollen assemblages (Jones et al., 2017). The first assemblage (Bølling-Allerød) included low amounts of *Pinus* and high percentages of *Picea*, *Quercus*, and *Fraxinus*, while the second (Younger Dryas) was associated with declines in *Pinus* and *Picea* and increases in *Ostrya/Carpinus*, *Carya*, and *Ambrosia* pollen, which suggest warming during the Younger Dryas (Jones et al., 2017).

Like Lake Tulane (Florida) and Cupola Pond (Ozark highlands), the fossil pollen and brGDGT-based temperature records from White Pond diverge from patterns of millennial-scale deglacial temperature variability recorded in the North Atlantic. Between 19,700 and 12,000 cal yr BP, *Pinus* and *Picea* decrease in the fossil pollen record and are replaced by hardwood taxa, first *Quercus* and *Carya* followed by *Ostrya/Carpinus, Ulmus, Fraxinus,* and *Fagus* under a generally warming but variable climate implied by the brGDGT data (Fig. 4 and 8). The Bølling-Allerød coincides with a period of cooling at White Pond between 16,500 and 13,800 cal yr BP, while the onset of the Younger Dryas postdates rapid increases in temperature at 13,800 cal yr BP by almost 1000 yr (Fig. 8). Furthermore, warm conditions persisted at White Pond after the termination of the Younger Dryas until 10,800 cal yr BP (Fig. 4). Similar to Lake Tulane and Cupola Pond, the White Pond record suggests that the Atlantic Coastal

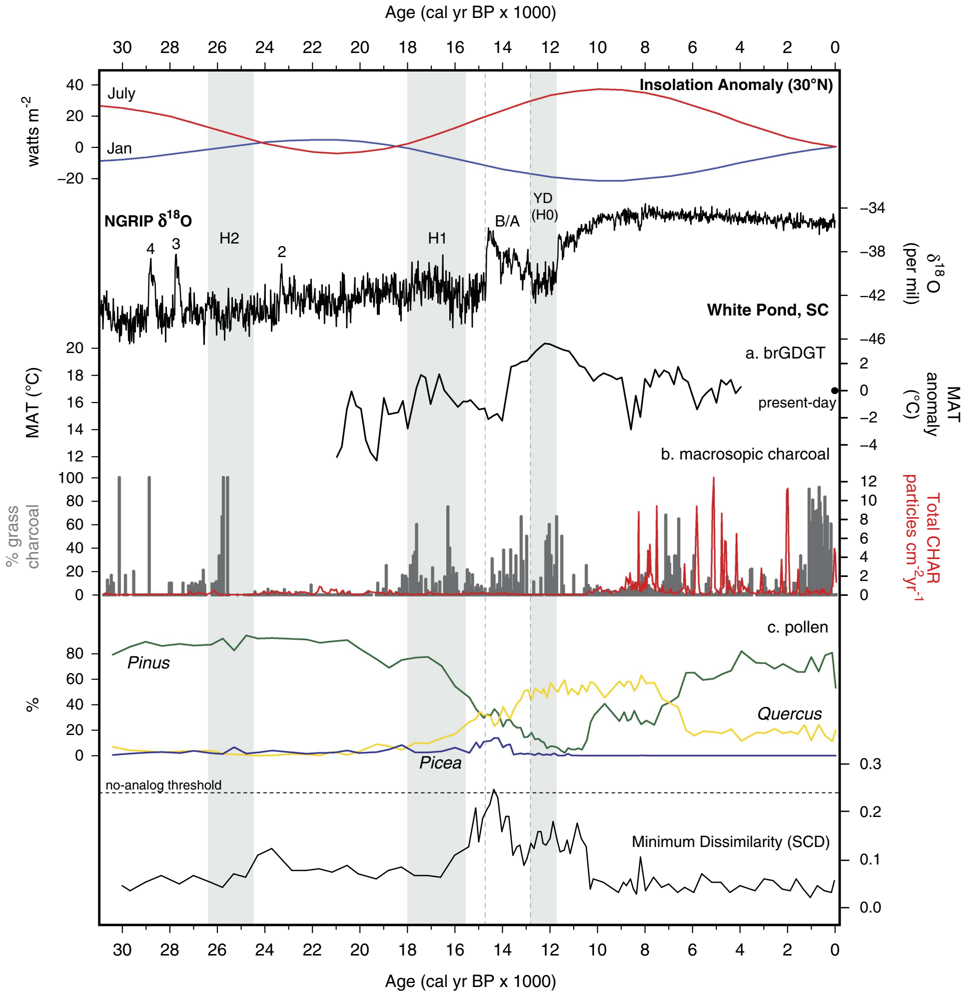

Figure 8. (color online) Summary of (a) paleotemperature (brGDGT), (b) macroscopic charcoal, and (c) pollen data from White Pond, compared with January and July insolation anomalies at 30°N (Berger and Loutre, 1991) and the NGRIP δ^{18}O curve (Rasmussen et al., 2006). The no-analog threshold (SCD = 0.237; Jones et al., 2017) is shown as a horizontal dashed line. The White Pond paleotemperature reconstruction is based on brGDGT data using the Peterse et al. (2012) calibration. The Greenland interstadials (i.e., Dansgaard-Oeschger interstadials) are numbered above the δ^{18}O graph. The ages and time spans of the Heinrich events (gray bands) are based on GICC05 chronology (Svensson et al., 2008). The timing of the Bølling-Allerød (B/A, gray vertical dashed lines) is based on Rasmussen et al. (2006).

Plain was warm during the Younger Dryas while the North Atlantic region cooled.

How strongly did no-analog plant communities manifest at White Pond and elsewhere in the Southeastern Coastal Plain? Were late-glacial vegetational changes linked to declining megaherbivore populations and changing fire regimes?

The last deglaciation in eastern North America was marked by the widespread development of pollen assemblages lacking modern analogs, indicating vegetation with no modern counterparts (Williams et al., 2001; Jackson and Williams, 2004; Williams and Jackson, 2007). Although these no-analog assemblages varied both spatially and temporally, all are characterized by a mixture of northern conifers (*Picea*, *Pinus*), temperate hardwoods (always *Quercus*, often *Carya*), mesic hardwoods (variously *Ostrya/Carpinus*, *Fraxinus pennsylvanica*-type, *Ulmus*, *Acer*, and *Fagus*), and sometimes herbaceous elements (Cyperaceae, *Artemisia*, *Ambrosia*). Regardless of location, all developed within a broader glacial to interglacial transition from coniferous to hardwood forests, inasmuch as they were preceded by pollen assemblages dominated by *Picea* and northern *Pinus*, and all developed while conifers (especially *Pinus*) declined and *Quercus* and other hardwoods increased (Jackson and Williams, 2004; Gill et al., 2009, 2012; Liu et al., 2013; Jones et al., 2017; Watson et al., 2018). White Pond records a similar transition starting at 16,300 cal yr BP, with gradually declining *Pinus* and increasing *Quercus* and *Carya* (Fig. 5). Percentages of *Ostrya/Carpinus*, *Ulmus*, and *Fraxinus pennsylvanica*-type also increased but remained at low

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levels. Unglaciated sites to the north and west, Anderson, Cupola, and Jackson ponds, also record conifer-to-deciduous transitions commencing at 15,900, 15,700, and 15,400 cal yr BP, respectively, consistent with a time-transgressive response to regional warming (Liu et al., 2013; Jones et al., 2017).

The White Pond pollen assemblages between 16,300 and 10,400 cal yr BP, representing three distinct pollen subzones (Fig. 5), resemble no-analog assemblages recorded at sites further north and west, but are more weakly expressed. Hence, dissimilarity scores are elevated but do not quite exceed the conservative dissimilarity threshold we applied (0.237). Critical differences are the higher percentages of *Quercus* and lower percentages of *Picea* and mesic hardwoods than sites in the unglaciated plateaus and glaciated central Great Lakes region. Hence, the White Pond assemblages appear to represent a dampened manifestation of the same general phenomenon: a unique mix of northern conifers (*Picea*, *Pinus*), temperate hardwoods (*Quercus*, *Carya*), and mesic hardwoods (in the case of White Pond, primarily *Ostrya/Carpinus* and *Fagus*). Similar to sites in the interior, White Pond shows evolution of vegetation composition during this no-analog period (Subzones 2a–2c in Fig. 5).

In formerly glaciated regions of the central Great Lakes region (Appleman Lake, Indiana and Silver lakes, Ohio; Fig. 1), the onset of no-analog pollen assemblages between 14,500 and 14,000 cal yr BP has been linked to declines in megafaunal populations and intensified fire regimes based on coprophilous fungal spore (e.g., *Sporormiella*) and macroscopic charcoal analyses (Gill et al., 2009, 2012). In contrast, *Sporormiella* spores were not found at White Pond, similar to findings at Jackson, Anderson, and Cupola ponds to the north and west (Liu et al., 2013; Jones et al., 2017). Furthermore, macroscopic charcoal abundance (total CHAR) remained low throughout the deglacial period (Fig. 6), similar to Cupola Pond (Jones et al., 2017), and it appears that fire did not play a role in shaping no-analog assemblages at White Pond.

The dearth of *Sporormiella* at the southeastern lakes is enigmatic, given the abundance of megafaunal remains uncovered in the Southeast (Voorhies, 1974; Webb, 1974; Hemmings, 1975; Roth and Laerm, 1980; Hoffman, 1983). The lack of spores may be due to differing intensities of megafaunal activity in depositional basins sited in open versus wooded landscapes, the ratio of grazers to browsers, taphonomic processes, or combination of these factors (Gill et al., 2013; Liu et al., 2013; Jones et al., 2017). Recent studies at the Page-Ladson archeological site in the Florida Panhandle, however, indicate a decline in *Sporormiella* abundance at 12,700 cal yr BP (Halligan et al., 2016; Perrotti, 2018). The Page-Ladson study used a different approach to *Sporormiella* counting that is better suited to low concentrations: they indexed spore counts to exotic marker grains added to their samples, rather than to fossil pollen grains. In our study, spores were tallied during routine counting of pollen grains to a minimum terrestrial-pollen sum of 300 to 400 grains, an approach that has worked well in much of the world (Davis, 1987; Burney et al., 2003; Robinson et al., 2005; Gill et al., 2009, 2012; Raczka et al., 2016). If spore influx is very low relative to pollen influx, however, low spore:pollen ratios will mask representation of coprophilous spores in routine pollen counts. For example, total pollen accumulation rates at White Pond were slightly higher than at Silver Lake (Gill et al., 2009), where there is a stronger spore signal, between 25,000 and 16,000 yr BP (Supplementary Fig. 2) (~11,000 grains/cm^2/yr versus 8000 grains/cm^2/yr). Search methods aimed at obtaining high spore counts (e.g., indexing to marker grains) may be more appropriate in low spore concentration settings.

How did interactions between climate, fire, and vegetation shape the development of Holocene southeastern forests?

Rapid shifts in forest composition, changing hydrologic conditions, and increased fire activity marked the onset of the Holocene at White Pond. After 10,400 cal yr BP, mesic hardwood taxa, including *Fagus*, *Fraxinus*, *Ostrya/Carpinus*, and *Carya,* decrease rapidly in the fossil pollen record, while percentages of more drought-tolerant *Pinus* increase and *Quercus* maintain high values (Fig. 5 and 8). At the same time, the aquatic assemblage records a shift in the dominant taxon, from *Isoetes* to *Brasenia*, marking a shift to shallower, more eutrophic conditions (Fig. 5). Total macroscopic CHAR also increases tenfold, indicating increased fire activity (Fig. 6 and 8), with notable peaks in charcoal at 8300 and 7500 cal yr BP during the early Holocene and, while the brGDGT data suggest MATs decreased after 10,800 cal yr BP, they were still higher than the present day (Fig. 4). Given that the core chronology and lithology from White Pond provide no evidence of a sedimentation hiatus during this time, the rapidity of these changes appears to be genuine and could be a threshold response to gradually warmer summers associated with increasing summer insolation during the early Holocene (Bartlein et al., 1998; Alder and Hostetler, 2014). However, while warmer summers likely account for the increase in biomass burning, we cannot rule out anthropogenic influences. The Archaic Indian culture was well established by 10,000 to 8000 cal yr BP in the Coastal Plain, and Archaic Indians regularly used fire for hunting and clearing fields (Pyne, 1982; Fowler and Konopik, 2007).

brGDGT-based temperature reconstructions at White Pond suggest that MATs abruptly decreased between 9000 and 8000 cal yr BP, reaching temperatures up to 3°C colder than the present day, before rebounding to pre-9000 cal yr BP levels (Fig. 4). No changes in the terrestrial or aquatic communities are recorded during this time and either the temperature excursion was not sufficiently severe and/or did not last long enough to elicit a biotic response. Furthermore, without similar paleotemperature data from other sites in the Southeast, it is unclear if the inferred cooling at White Pond was site-specific or part of a widespread regional signal, possibly associated with the 8200 cal yr BP event in the North Atlantic (Alley et al., 1997; Thomas et al., 2007).

After 7500 cal yr BP, *Pinus* pollen percentages gradually increase in the fossil pollen record at White Pond at the expense of *Quercus*, and by 6400 cal yr BP, *Pinus* becomes the dominant taxa on the landscape. The well-dated fossil pollen record from Lake Tulane in peninsular Florida also shows an *Quercus*-to-*Pinus* transition at ca. 6000 cal yr BP (Fig. 7; Grimm et al., 2006) and, although not as well-dated, so do sites in southeastern North Carolina (Jones and Singletary lakes; Spencer et al., 2017), and could imply a possible widespread climatic forcing event in the southeastern United States during the mid-Holocene. The brGDGT data from White Pond indicate decreasing MATs after 6500 cal yr BP (Fig. 4 and 8), and it is plausible that cooling summers and warming winters associated with an amelioration in the seasonal cycle of insolation during the mid-Holocene (Bartlein et al., 1998; Alder and Hostetler, 2014) drove the regional *Quercus*-to-*Pinus* transition. Conditions were also likely drier in eastern North America during the mid-Holocene, as indicated by lake-level reconstructions from New England and $\delta^{18}O$ records from caves in West Virginia and Florida (Fig. 1), with the strongest declines between 4500 and 4000 cal yr BP (Shuman and Donnelly, 2006; Hardt et al., 2010; Pollock et al., 2016). Dry mid-Holocene conditions are also recorded at White Pond between 6400 and 4200 cal yr BP, inasmuch as elevated graminoid (Poaceae and Cyperaceae) percentages and diminished *Brasenia* levels in the fossil pollen record indicate decreasing water levels that favored sedges and aquatic grasses at the expense of floating-leaved or submerged aquatics like *Brasenia*. Mid-Holocene drought conditions could also account for the number of large charcoal peaks recorded at White Pond centered at 5800, 5100, 4800, and 4200 cal yr BP (Fig. 6 and 8).

After 4200 cal yr BP, *Pinus* percentages reach their highest levels of the Holocene and, except for *Quercus*, other hardwood taxa are poorly represented in the pollen record (Fig. 5). Water levels at White Pond also likely rebounded to their pre-6400 cal yr BP levels at this time, as indicated by rising *Brasenia* and decreasing graminoid percentages. After 1200 cal yr BP, elevated percentages of grass charcoal in combination with decreased total CHAR (Fig. 6 and 8) indicate a shift from an infrequent high-severity fire regime to one dominated by frequent low-severity surface fires, similar to fire regimes characteristic of southeastern longleaf pine forests today (Platt et al., 1988; Frost, 2006; Stambaugh et al., 2017). The mechanisms underlying this late Holocene shift in fire activity are unclear, and the fossil pollen record does not indicate any preceding changes in climate or fuel availability/biomass. While it is difficult to separate the influence of climate and vegetation from anthropogenic factors on fire activity, the establishment of the Mississippian culture in the Southeast ca. 1300 cal yr BP immediately precedes the shift in fire activity. The Mississippian culture, the most highly developed culture on the Coastal Plain before European conquest (Hudson, 1976), used fire extensively to modify tracts of land, to build political centers and villages, and to grow maize (Fowler and Konopik, 2007). Hence, an increase in surface burning at White Pond after 1200 cal yr BP could be the result of intensified land management using fire by Native Americans.

CONCLUSIONS

This multi-proxy paleoenvironmental reconstruction from White Pond revisits a classic record to contribute new information on the underlying drivers and causal mechanisms of late Quaternary vegetation dynamics in the southeastern United States. Growing evidence from well-dated sites in the interior Southeast, including White, Jackson, and Anderson ponds, indicate relatively stable *Pinus*- and *Picea*-dominated vegetation during the full-glacial period, although declining *Quercus* at 26,000 cal yr BP may mark the initiation of cooler conditions associated with the onset of H2 in the North Atlantic. Nonetheless, peninsular Florida (Lake Tulane) appears to have been particularly sensitive, compared with the adjacent continent, to changes in North Atlantic thermohaline circulation and Gulf of Mexico sea-surface temperatures during H2.

Vegetation turned over substantially during the last deglaciation at White Pond as mesic hardwood forest replaced the open *Pinus*- and *Picea*-dominated landscape in response to gradual warming. In the Southeast, sites significantly varied in their ecological responses to the Bølling-Allerød and Younger Dryas; however, vegetational changes at most sites seem to be consistent with warm conditions during the Younger Dryas, in contrast to cool conditions recorded nearer to the Laurentide Ice Sheet. While there was substantial turnover in the deglacial vegetation at White Pond and a rise in mesic hardwoods, the development of no-analog pollen assemblages was weakly expressed, likely due to the low abundance of *Picea* pollen compared with sites further north and west. *Sporormiella* was not recorded in the White Pond sediments, and charcoal abundance was extremely low during the late glacial period, similar to other records from the Southeast. Given that megafauna likely were present throughout the Southeast, the absence of *Sporormiella* spores could be attributed to differing intensities of megafaunal activity near depositional basins (open versus wooded landscapes), taphonomic processes, counting methods, or a combination of these factors. Fire apparently played a minimal role in shaping deglacial vegetation dynamics in the Southeast, in contrast to sites in the central Great Lakes region.

The Holocene at White Pond featured increasing *Pinus* dominance and a tenfold increase in CHAR due to elevated biomass burning associated with warmer summer conditions. *Pinus* expansion in the South Carolina Coastal Plain appears to have occurred in two phases, the first commencing at 10,400 cal yr BP and the second at 7500 cal yr BP; the latter was may have been due in part to increasing winter temperatures and/or drier conditions during the mid-Holocene. Low-intensity surface fires increased after 1200 cal yr BP near White Pond, as implied by increased percentages of grass charcoal and low CHAR, and suggests anthropogenic influence associated with the establishment of the Mississippian culture in the Atlantic Coastal Plain.

The southeastern United States is a critical region in North American biogeography, and well-dated multiple-proxy records remain scarce. Continued reexamination of existing paleoecological sites in the Southeast and the development of new chronologies and high-resolution multiple-proxy records are setting the foundation for a new generation of research into the spatiotemporal patterns of past vegetation, climate variability, and fire activity in the region. These new records strengthen our understanding of the underlying drivers and causal mechanisms of late Quaternary climate and vegetation dynamics in the southeastern United States.

SUPPLEMENTARY MATERIAL

To view supplementary material for this article, please visit https://doi.org/10.1017/qua.2018.95

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TRK, JMR, JWW, and STJ designed the research; TRK, JMR, RZ, and STJ collected and analyzed the data; and TRK, JMR, JWW, and STJ wrote the paper.

REFERENCES

Alder, J., Hostetler, S.W., 2014. Global climate simulations at 3000 year intervals for the last 21,000 years with the GENMOM coupled atmosphere-ocean model. *Climate of the Past* 10, 2925–2978.

Alley, R.B., Mayewski, P.A., Sowers, T., Stuiver, M., Taylor, K.C., Clark, P.U., 1997. Holocene climatic instability: a prominent, widespread event 8200 yr ago. *Geology* 25, 483–486.

Bartlein, P.J., Anderson, K.H., Anderson, P.M., Edwards, M.E., Mock, C.M., Thompson, R.S., Webb, R.S., Webb III, T., Whitlock, C., 1998. Paleoclimate simulations for North America over the past 21,000 years: features of the simulated climate and comparisons with paleoenvironmental data. *Quaternary Science Reviews* 17, 549–585.

Bell, A., 1983. *Dung Fungi: An Illustrated Guide to Coprophilous Fungi in New Zealand*. Victoria University Press, Wellington, New Zealand.

Bemmels, J.B, Dick, C.W., 2018. Genomic evidence of a widespread southern distribution during the Last Glacial Maximum for two eastern North American hickory species. *Journal of Biogeography* 45, 1739–1750.

Berger, A., Loutre, M., 1991. Insolation values for the climate of the last 10 million years. *Quaternary Science Reviews* 10, 297–317.

Blaauw, M., Christen, J.A., 2011. Flexible paleoclimate age-depth models using an autoregressive gamma process. *Bayesian Analysis* 6, 457–474.

Blaga, C.I., Reichart, G.-J., Schouten, S., Lotter, A.F., Werne, J.P., Kosten, S., Mazzeo, N., Lacerot, G., Sinninghe Damsté, J.S., 2010. Branched glycerol dialkyl glycerol tetraethers in lake sediments: can they be used as temperature and pH proxies? *Organic Geochemistry* 41, 1225–1234.

Blois, J.L., Williams, J.W., Fitzpatrick, M.C., Ferrier, S., Veloz, S., He, F., Liu, Z., Manion, G., Otto-Bliesner, B., 2013. Modeling the climatic drivers of spatial patterns in vegetation composition since the Last Glacial Maximum. *Ecography* 36, 460–473.

Bond, G., Broecker, W., Johnsen, S., McManus, J., Labeyrie, L., Jouzel, J., Bonani, G., 1993. Correlations between climate records from North Atlantic sediments and Greenland ice. *Nature* 365, 143–147.

Braun, E.L., 1950. *Deciduous Forests of Eastern North America*. MacMillan Publishing, New York.

Buckles, L.K., Weijers, J.W.H., Tran, X.-M. Waldron, S., Sinninghe Damsté, J.S., 2014. Provenance of tetraether membrane lipids in a large temperate lake (Loch Lomond, UK): implications for glycerol dialkyl glycerol tetraether (GDGT)-based palaeothermometry. *Biogeosciences* 11, 5539–5563.

Buizert, C., Gkinis, V., Severinghaus, J.P., He, F., Lecavalier, B.S., Kindler, P., Leuenberger, M., et al., 2014. Greenland temperature response to climate forcing during the last deglaciation. *Science* 345, 1177–1180.

Burney, D.A., Robinson, G.S., Burney, L.P., 2003. *Sporormiella* and the late Holocene extinctions in Madagascar. *Proceedings of the National Academy of Sciences of the United States of America* 100, 10800–10805.

Christensen, N.L., 1981. Fire regimes in southeastern ecosystems. In: Mooney, H.A., Bonnicksen, T.M., Christensen, N.L., Lotan, J. E., Reinsers, W.A. (Eds.), *Fire Regimes and Ecosystem Properties. USDA Forest Service General Technical Report WO-26*. USDA Forest Service, Washington, DC, pp. 112–136.

Christensen, N.L., 1988. Vegetation of Southeastern Coastal Plain. In: Barbour, M.G., Billings, W.D. (Eds.), *North American Terrestrial Vegetation*. Cambridge University Press, Cambridge, pp. 317–363.

Cugny, C., Mazier, F., Galop, D., 2010. Modern and fossil non-pollen palynomorphs from the Basque mountains (western Pyrenees, France): the use of coprophilous fungi to reconstruct pastoral activity. *Vegetation History and Archaeobotany* 19, 391–408.

Dansgaard, W., Johnsen, S.J., Clausen, H.B., Dahl-Jensen, D., Gundestrup, N., Hammer, C.U., Oeschger, H., 1984. North Atlantic climatic oscillations revealed by deep Greenland ice cores. In: Hansen, J., Takahashi, T. (Eds.), *Climate Processes and Climate Sensitivity*. American Geophysical Union, Washington, DC, pp. 288–298.

Davis, O.K., 1987. Spores of the dung fungus *Sporormiella*: increased abundance in historic sediments and before Pleistocene megafaunal extinction. *Quaternary Research* 28, 290–294.

de Jonge, C., Hopmans, E.C., Zell, C.I., Kim, J.-H., Schouten, S., Sinninghe Damsté, J.S., 2014. Occurrence and abundance of 6-methyl branched glycerol dialkyl glycerol tetraethers in soils:

implications for paleoclimate reconstruction. *Geochimica et Cosmochimica Acta* 141, 97–112.

Delcourt, H.R., 1979. Late Quaternary vegetation history of the Eastern Highland Rim and adjacent Cumberland Plateau of Tennessee. *Ecological Monographs* 49, 255–280.

Delcourt, H.R., Delcourt, P.A., 1994. Postglacial rise and decline of *Ostrya virginiana* (Mill.) K. Koch and *Carpinus caroliniana* Walt. in eastern North America: predictable responses of forest species to cyclic changes in seasonality of climates. *Journal of Biogeography* 21, 137–150.

Dyke, A.S., Moore, A., Robertson, L., 2003. Deglaciation of North America. Geological Survey of Canada, Ottawa, Ontario, Open File 1574. http://dx.doi.org/10.4095/214399.

Fawcett, P.J., Werne, J.P., Anderson, R.S., Heikoop, J.M., Brown, E.T., Berke, M.A., Smith, S.J., et al., 2011. Extended megadroughts in the southwestern United States during Pleistocene interglacials. *Nature* 470, 518–521.

Fowler, C., Konopik, E., 2007. The history of fire in the southern United States. *Human Ecology Review* 14, 165–176.

Frost, C., 2006. History and future of the longleaf pine ecosystem. In: Jose, S., Jokela, E.J., Miller, D.L. (Eds.), *The Longleaf Pine Ecosystem: Ecology, Silviculture, and Restoration*. Springer New York, New York, pp. 9–48.

Fullerton, D.S., 1980. Preliminary correlation of post-Erie interstadial events: (16,000–10,000 radiocarbon years before present), central and eastern Great Lakes region, and Hudson, Champlain, and St. Lawrence Lowlands, United States and Canada, US Geological Survey Professional Paper 1089. US Geological Survey, Washington DC.

Gavin, D.G., Oswald, W.W., Wahl, E.R., Williams, J.W., 2003. A statistical approach to evaluating distance metrics and analog assignments for pollen records. *Quaternary Research* 60, 356–367.

Gellici, J., Harwell, S.L., Badr, A.W., Kiuchi, M., 2004. Hydrologic effects of the June 1998–August 2002 drought in South Carolina. State of South Carolina Department of Natural Resources Report. South Carolina Department of Natural Resources, Columbia, SC.

Gill, J.L., 2014. The ecological legacy of the late-Quaternary extinctions of megaherbivores. *New Phytologist* 201, 1163–1169.

Gill, J.L., McLauchlan, K.K., Skibbe, A.M., Goring, S.J., Zirbel, C., Williams, J.W., 2013. Linking abundances of the dung fungus *Sporormiella* to the density of bison: implications for assessing grazing by megaherbivores in paleorecords. *Journal of Ecology* 101, 1125–1136.

Gill, J.L., Williams, J.W., Jackson, S.T., Donnelly, J.P., Schellinger, G.C., 2012. Climatic and megaherbivory controls on late-glacial vegetation dynamics: a new, high-resolution, multi-proxy record from Silver Lake, Ohio. *Quaternary Science Reviews* 34, 66–80.

Gill, J.L., Williams, J.W., Jackson, S.T., Lininger, K.B., Robinson, G.S., 2009. Pleistocene megafaunal collapse, novel plant communities, and enhanced fire regimes in North America. *Science* 326, 1100–1103.

Gonzales, L.M., Grimm, E.C., 2009. Synchronization of late-glacial vegetation changes at Crystal Lake, Illinois, USA with the North Atlantic Event Stratigraphy. *Quaternary Research* 72, 234–245.

Goring, S., Williams, J.W., Blois, J.L., Jackson, S.T., Paciorek, C.J., Booth, R.K., Marlon, J.R., Blaauw, M., Christen, J.A., 2012. Deposition times in the northeastern United States during the Holocene: establishing valid priors for Bayesian age models. *Quaternary Science Reviews* 48, 54–60.

Greller, A.M., 1988. Deciduous Forest. In: Barbour, M.G., Billings, W.D. (Eds.), *North American Terrestrial Vegetation*. Cambridge University Press, Cambridge, pp. 287–316.

Grimm, E.C., 1987. CONISS: a Fortran 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. *Computers and Geosciences* 13, 13–35.

Grimm, E.C., Maher, L.J. Jr., Nelson, D.M., 2009. The magnitude of error in conventional bulk-sediment radiocarbon dates from central North America. *Quaternary Research* 72, 301–308.

Grimm, E.C., Watts, W.A., Jacobson, G.L. Jr., Hansen, B.C.S., Almquist, H.R., Dieffenbacher-Krall, A.C., 2006. Evidence for Heinrich events in Florida. *Quaternary Science Reviews* 25, 2197–2211.

Halligan, J.J., Waters, M.R., Perrotti, A., Owens, I.J., Feinberg, J. M., Bourne, M.D., Fenerty, B., et al., 2016. Pre-Clovis occupation 14,550 years ago at the Page-Ladson site, Florida, and the peopling of the Americas. *Science Advances* 2, e1600375. http://dx.doi.org/10.1126/sciadv.1600375.

Hardt, B., Rowe, H.D., Springer, G.S., Cheng, H., Edwards, R.L., 2010. The seasonality of east central North American precipitation based on three coeval Holocene speleothems from southern West Virginia. *Earth and Planetary Science Letters* 295, 342–348.

Heinrich, H., 1988. Origin and consequences of cyclic ice rafting in the Northeast Atlantic Ocean during the past 130,000 years. *Quaternary Research* 29, 142–152.

Hemmings, E.T., 1975. The Silver Springs site, prehistory in the Silver Springs Valley, Florida. *Florida Anthropologist* 28, 141–158.

Higuera, P.E., Brubaker, L.B., Anderson, P.M., Hu, F.S., Brown, T., 2009. Vegetation mediated the impacts of postglacial climate change on fire regimes in the south-central Brooks Range, Alaska. *Ecological Monographs* 79, 201–219.

Higuera, P.E., Gavin, D.G., Bartlein, P.J., Hallett, D.J., 2010. Peak detection in sediment–charcoal records: impacts of alternative data analysis methods on fire-history interpretations. *International Journal of Wildland Fire* 19, 996–1014.

Hoffman, C.A., 1983. A mammoth kill site in the Silver Springs Run. *Florida Anthropologist* 36, 83–87.

Hopmans, E.C., Weijers, J.W.H., Schefuß, E., Herfort, L., Sinninghe Damsté, J.S., Schouten, S., 2004. A novel proxy for terrestrial organic matter in sediments based on branched and isoprenoid tetraether lipids. *Earth and Planetary Science Letters* 224, 107–116.

Hudson, C., 1976. The Southeastern Indians. The University of Tennessee Press. 573 p.

Hussey, T.C., 1993. A 20,000-year history of vegetation and climate at Clear Pond, northeastern South Carolina. Master's thesis, University of Maine, Orono.

Jackson, S.T., 1999. Techniques for analysing unconsolidated lake sediments. In: Jones, T., Rowe, N. (Eds.), *Fossil Plants and Spores: Modern Techniques*. Geological Society of London, Bath, pp. 274–278.

Jackson, S.T., Blois, J.L., 2015. Community ecology in a changing environment: Perspectives from the Quaternary. *Proceedings of the National Academy of Sciences of the United States of America* 112, 4915–4921.

Jackson, S.T., Williams, J.W., 2004. Modern analogs in Quaternary paleoecology: Here today, gone yesterday, gone tomorrow? *Annual Review of Earth and Planetary Sciences* 32, 495–537.

Jensen, K., Lynch, E.A., Calcote, R., Hotchkiss, S.C., 2007. Interpretation of charcoal morphotypes in sediments form Ferry Lake, Wisconsin, USA: do different plant fuel sources produce distinctive charcoal morphotypes? *The Holocene* 17, 907–915.

Jones, R.A., Williams, J.W., Jackson, S.T., 2017. Vegetation history since the last glacial maximum in the Ozark highlands (USA): a new record from Cupola Pond, Missouri. *Quaternary Science Reviews* 170, 174–187.

Kapp, R., King, J., Davis, O.K., 2000. *Ronald O. Kapp's Pollen and Spores*. American Association of Stratigraphic Palynologists Foundation Publication, Nottingham, UK.

Karrow, P.F., Dreimanis, A., Barnett, P.J., 2000. A proposed diachronic revision of late Quaternary time-stratigraphic classification in the eastern and northern Great Lakes Area. *Quaternary Research* 54, 1–12.

Koch, P.L., Barnosky, A.D., 2006. Late Quaternary extinctions: state of the debate. *Annual Review of Ecology, Evolution, and Systematics* 37, 215–250.

Kunkel, K., Stevens, L., Stevens, S., Sun, L., Janssen, E., Wuebbles, D., Konrad, C. II, et al., 2013. Regional Climate Trends and Scenarios for the US Climate Assessment: Part 2. Climate of the Southeast US. NOAA Technical Report 142-2. National Oceanic and Atmospheric Administration, Washington, DC.

Liu, Y., Andersen, J.J., Williams, J.W., Jackson, S.T., 2013. Vegetation history in central Kentucky and Tennessee (USA) during the last glacial and deglacial periods. *Quaternary Research* 79, 189–198.

Liu, Z., Otto-Bliesner, B.L., He, F., Brady, E.C., Tomas, R., Clark, P.U., Carlson, A.E., et al., 2009. Transient simulation of last deglaciation with a new mechanism for Bølling-Allerød warming. *Science* 325, 310–314.

Loomis, S.E., Russell, J.M., Eggermont, H., Verschuren, D., Sinninghe Damsté, J.S., 2014a. Effects of temperature, pH and nutrient concentration on branched GDGT distributions in East African lakes: implications for paleoenvironmental reconstruction. *Organic Geochemistry* 66, 25–37.

Loomis, S.E., Russell, J.M., Heureux, A.M., D'Andrea, W.J., Sinninghe Damsté, J.S., 2014b. Seasonal variability of branched glycerol dialkyl glycerol tetraethers (brGDGTs) in a temperate lake system. *Geochimica et Cosmochimica Acta* 144, 173–187.

Loomis, S.E., Russell, J.M., Ladd, B., Eggermont, H.R., Street-Perrott, F.A., Sinninghe Damsté, J.S., 2011. Distribution of branched GDGTs in soils and lake sediments from Western Uganda: implications for a lacustrine paleothermometer. *Organic Geochemistry* 42, 739–751.

Loomis, S.E., Russell, J.M., Ladd, B., Street-Perrott, F.A., Sinninghe Damsté, J.S., 2012. Calibration and application of the branched GDGT temperature proxy on East African lake sediments. *Earth and Planetary Science Letters* 357–358, 277–288.

Loomis, S.E., Russell, J.M., Lamb, H.F., 2015. Northeast African temperature variability since the Late Pleistocene. *Palaeogeography, Palaeoclimatology, Palaeoecology* 423, 80–90.

Loomis, S.E., Russell, J.M., Verschuren, D., Morrill, C., De Cort, G., Sinninghe Damsté, J.S., Olago, D., Eggermont, H., Street-Perrott, F.A., Kelly, M.A., 2017. The tropical lapse rate steepened during the Last Glacial Maximum. *Science Advances* 3, e1600815. http://dx.doi.org/10.1126/sciadv.1600815.

Lumibao, C.Y., Hoban, S.M., McLachlan, J., 2017. Ice ages leave genetic diversity 'hotspots' in Europe but not in Eastern North America. *Ecology Letters* 20, 1459–1468.

Marlon, J.R., Bartlein, P.J., Walsh, M.K., Harrison, S.P., Brown, K. J., Edwards, M.E., Higuera, P.E., et al., 2009. Wildfire responses to abrupt climate change in North America. *Proceedings of the National Academy of Sciences of the United States of America* 106, 2519–2524.

McAndrews, J., Berti, A., Norris, G., 1973. *Key to Quaternary Pollen and Spores of the Great Lakes Region*. Royal Ontario Museum Life Sciences Publishing, Toronto.

Mohr, C., 1897. *Timber Pines of the Southern United States*. United States Department of Agriculture, Washington, DC.

Mustaphi, C.J.C., Pisaric, M.F.J., 2014. A classification for macroscopic charcoal morphologies found in Holocene lacustrine sediments. *Progress in Physical Geography* 38, 734–754.

Niemann, H., Stadnitskaia, A., Wirth, S.B., Gilli, A., Anselmetti, F. S., Sinninghe Damsté, J.S., Schouten, S., Hopmans, E.C., Lehmann, M.F., 2012. Bacterial GDGTs in Holocene sediments and catchment soils of a high alpine lake: application of the MBT/CBT-paleothermometer. *Climate of the Past* 8, 889–906.

Ordonez, A., Williams, J.W., 2013. Climatic and biotic velocities for woody taxa distributions over the last 16,000 years in eastern North America. *Ecology Letters* 16, 773–781.

Overpeck, J.T., Webb, T., Prentice, I.C., 1985. Quantitative interpretation of fossil pollen spectra: dissimilarity coefficients and the method of modern analogs. *Quaternary Research* 23, 87–108.

Pearson, E.J., Juggins, S., Talbot, H.M., Weckström, J., Rosén, P., Ryves, D.B., Roberts, S.J., Schmidt, R., 2011. A lacustrine GDGT-temperature calibration from the Scandinavian Arctic to Antarctic: renewed potential for the application of GDGT-paleothermometry in lakes. *Geochimica et Cosmochimica Acta* 75, 6225–6238.

Perrotti, A.G., 2018. Pollen and *Sporormiella* evidence for terminal Pleistocene vegetation change and megafaunal extinction at Page-Ladson, Florida. *Quaternary International* 446, 256–268.

Peterse, F., Kim, J.-H., Schouten, S., Kristensen, D.K., Koç, N., Sinninghe Damsté, J.S., 2009. Constraints on the application of the MBT/CBT palaeothermometer at high latitude environments (Svalbard, Norway). *Organic Geochemistry* 40, 692–699.

Peterse, F., van der Meer, J., Schouten, S., Weijers, J., Fierer, N., Jackson, R.B., Kim, J.-H., Sinninghe Damsté, J.S., 2012. Revised calibration of the MBT–CBT paleotemperature proxy based on branched tetraether membrane lipids in surface soils. *Geochimica et Cosmochimica Acta* 96, 215–229.

Platt, W.J., Evans, G.W., Rathbun, S.L., 1988. The population dynamics of a long-lived conifer (*Pinus palustris*). *The American Naturalist* 131, 491–525.

Pollock, A.L., Beynen, P.E. van, DeLong, K.L., Polyak, V., Asmerom, Y., 2016. A speleothem-based mid-Holocene precipitation reconstruction for West-Central Florida. *The Holocene* 27, 987–996.

PRISM Climate Group, 2016. PRISM Climate Data (accessed January 7, 2016). http://prism.oregonstate.edu.

Pyne, S.J., 1982. *Fire in America: A Cultural History of Wildland and Rural Fire*. Princeton University Press, Princeton.

Raczka, M.F., Bush, M.B., Folcik, A.M., McMichael, C.H., 2016. *Sporormiella* as a tool for detecting the presence of large herbivores in the Neotropics. *Biota Neotropica* 16, e20150090. http://dx.doi.org/10.1590/1676-0611-BN-2015-0090.

Rasmussen, S.O., Andersen, K.K., Svensson, A.M., Steffensen, J.P., Vinther, B.M., Clausen, H.B., Siggaard-Andersen, M.-L., et al., 2006. A new Greenland ice core chronology for the last glacial termination. *Journal of Geophysical Research: Atmospheres* 111, D06102. http://dx.doi.org/10.1029/2005JD006079.

Reimer, P.J., Bard, E., Bayliss, A., Warren, B.J., Blackwell, P.G., Bronk Ramsey, C., Buck, C.E., et al., 2013. IntCal13 and Marine13 Radiocarbon Age Calibration Curves 0–50,000 Years cal BP. *Radiocarbon* 55, 1869–1887.

Robinson, G.S., Pigott Burney, L., Burney, D.A., 2005. Landscape paleoecology and megafaunal extinction in southeastern New York State. *Ecological Monographs* 75, 295–315.

Roth, J.A., Laerm, J., 1980. A Late Pleistocene assemblaged from Edisto Island, South Carolina. *Brimleyana* 3, 1–19.

Royall, P.D., Delcourt, P.A., Delcourt, H.A., 1991. Late Quaternary paleoecology and paleoenvironments of the Central Mississippi Alluvial Valley. *Geological Society of America Bulletin* 103, 157–170.

Russell, J.M., Hopmans, E.C., Loomis, S.E., Liang, J., Sinninghe Damsté, J.S., 2018. Distributions of 5- and 6-methyl branched glycerol dialkyl glycerol tetraethers (brGDGTs) in East African lake sediment: effects of temperature, pH, and new lacustrine paleotemperature calibrations. *Organic Geochemistry* 117, 56–59.

Sargent, C.S., 1884. *Report on the Forests of North America (Exclusive of Mexico)*. United States Department of the Interior, Census Office, Washington, DC.

Schouten, S., Hopmans, E.C., Sinninghe Damsté, J.S., 2013. The organic geochemistry of glycerol dialkyl glycerol tetraether lipids: a review. *Organic Geochemistry* 54, 19–61.

Shakun, J.D., Carlson, A.E., 2010. A global perspective on Last Glacial Maximum to Holocene climate change. *Quaternary Science Reviews* 29, 1801–1816.

Shakun, J.D., Clark, P.U., He, F., Marcott, S.A., Mix, A.C., Liu, Z., Otto-Bliesner, B., Schmittner, A., Bard, E., 2012. Global warming preceded by increasing carbon dioxide concentrations during the last deglaciation. *Nature* 484, 49–54.

Shuman, B., Donnelly, J.P., 2006. The influence of seasonal precipitation and temperature regimes on lake levels in the northeastern United States during the Holocene. *Quaternary Research* 65, 44–56.

Simpson, G., 2007. Analogue methods in palaeoecology: using the analogue package. *Journal of Statistical Software* 22, 1–29.

Sinninghe Damsté, J.S., 2016. Spatial heterogeneity of sources of branched tetraethers in shelf systems: the geochemistry of tetraethers in the Berau River delta (Kalimantan, Indonesia). *Geochimica et Cosmochimica Acta* 186, 13–31.

Sinninghe Damsté, J.S., Rijpstra, W.I.C., Hopmans, E.C., Weijers, J.W.H., Foesel, B.U., Overmann, J., Dedysh, S.N., 2011. 13,16-Dimethyl Octacosanedioic Acid (iso-Diabolic Acid), a Common Membrane-Spanning Lipid of Acidobacteria Subdivisions 1 and 3. *Applied and Environmental Microbiology* 77, 4147–4154.

Snyder, J.R., 1980. Analysis of coastal plain vegetation, Croatan National Forest, North Carolina. *Veroffentlichongen des geobotanischen Institutes der eidgenoessiche technische Hochshule Stiftung Rubel in Zurich* 69, 40–113.

Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture. Official Soil Series Descriptions (accessed July 05, 2018). https://www.nrcs.usda.gov/wps/portal/nrcs/detail/soils/survey/geo/?cid=nrcs142p2_053587.

Soltis, D.E., Morris, A.B., McLachlan, J.S., Manos, P.S., Soltis, P. S., 2006. Comparative phylogeography of unglaciated eastern North America. *Molecular Ecology* 15, 4261–4293.

Spencer, J., Jones, K.B., Gamble, D.W., Benedetti, M.M., Taylor, A.K., Lane, C.S., 2017. Late-Quaternary records of vegetation and fire in southeastern North Carolina from Jones Lake and Singletary Lake. *Quaternary Science Reviews* 174, 33–53.

Stambaugh, M.C., Varner, J.M., Jackson, S.T., 2017. The biogeography of longleaf pine: an interweave of climate, fire, and humans. In: Kirkman, L.K., Jack, S. (Eds.), *Ecological Restoration of Longleaf Pine*. CRC Press, Boca Raton, pp. 17–38.

Stuiver, M., Reimer, P.J., Reimer, R.W., 2017. CALIB 7.1 (accessed January 09, 2017). http://calib.org.

Sun, Q., Chu, G., Liu, M., Xie, M., Li, S., Ling, Y., Wang, X., Shi, L., Jia, G., Lü, H., 2011. Distributions and temperature dependence of branched glycerol dialkyl glycerol tetraethers in recent lacustrine sediments from China and Nepal. *Journal of Geophysical Research: Biogeosciences* 116, G01008. http://dx.doi.org/10.1029/2010JG001365.

Svensson, A., Andersen, K.K., Bigler, M., Clausen, H.B., Dahl-Jensen, D., Davies, S.M., Johnsen, S.J., Muscheler, R., Parrenin, F., Rasmussen, S.O., Röthlisberger, R., Seierstad, I., Steffensen, J.P., Vinther, B.M., 2008. A 60 000 year Greenland stratigraphic ice core chronology. *Climate of the Past* 4, 47–57.

Swezey, C.S., Fitzwater, B.A., Whittecar, G.R., Mahan, S.A., Garrity, C.P., Alemán González, W.B., Dobbs, K.M., 2016. The Carolina Sandhills: Quaternary eolian sand sheets and dunes along the updip margin of the Atlantic Coastal Plain province, southeastern United States. *Quaternary Research* 86, 271–286.

Swezey, C.S., Schultz, A.P., González, W.A., Bernhardt, C.E., Doar, W.R., Garrity, C.P., Mahan, S.A., McGeehin, J.P., 2013. Quaternary eolian dunes in the Savannah River valley, Jasper County, South Carolina, USA. *Quaternary Research* 80, 250–264.

Thomas, E.R., Wolff, E.C., Mulvaney, R., Steffensen, J.P., Johnsen, S.J., Arrowsmith, C., White, J.W.C., Vaughn, B., Popp, T., 2007. The 8.2 ka event from Greenland ice cores. *Quaternary Science Reviews* 26, 70–81.

Tierney, J.E., Russell, J.M., 2009. Distributions of branched GDGTs in a tropical lake system: implications for lacustrine application of the MBT/CBT paleoproxy. *Organic Geochemistry* 40, 1032–1036.

Tierney, J.E., Russell, J.M., Eggermont, H.R., Hopmans, E.C., Verschuren, D., Sinninghe Damsté, J.S., 2010. Environmental controls on branched tetraether lipid distributions in tropical East African lake sediments. *Geochimica et Cosmochimica Acta* 74, 4902–4218.

van Geel, B., Buurman, J., Brinkkemper, O., Schelvis, J., Aptroot, A., van Reenen, G., Hakbijl, T., 2003. Environmental reconstruction of a Roman Period settlement site in Uitgeest (The Netherlands), with special reference to coprophilous fungi. *Journal of Archaeological Science* 30, 873–883.

Voorhies, M.R., 1974. Pleistocene vertebrates with boreal affinities in the Georgia Piedmont. *Quaternary Research* 4, 85–93.

Wahl, E.R., 2004. A general framework for determining cutoff values to select pollen analogs with dissimilarity metrics in the modern analog technique. *Review of Palaeobotany and Palynology* 128, 263–280.

Wahlenberg, W., 1946. *Longleaf Pine*. Charles Lathrop Pack Forest Foundation, Washington, DC.

Watson, B., Williams, J.W., Russell, J.M., Jackson, S.T., Shane, L., Lowell, T., 2018. Temperature variations in the southern Great Lakes during the last deglaciation: comparison between pollen and GDGT proxies. *Quaternary Science Reviews* 182, 78–92.

Watts, W.A., 1970. The full-glacial vegetation of northwestern Georgia. *Ecology* 51, 17–33.

Watts, W.A., 1973. The vegetation record of a mid-Wisconsin interstadial in northwest Georgia. *Quaternary Research* 3, 257–268.

Watts, W.A., 1980a. The Late Quaternary vegetation history of the southeastern United States. *Annual Review of Ecology and Systematics* 11, 387–409.

Watts, W.A., 1980b. Late-Quaternary vegetation history at White Pond on the Inner Coastal Plain of South Carolina. *Quaternary Research* 13, 187–199.

Webb, S.D., 1974. Chronology of Florida Pleistocene mammals. In: *Pleistocene Mammals of Florida*. University of Florida Press, Gainesville, pp. 5–31.

Weber, Y., de Jonge, C., Rijpstra, W.I.C., Hopmans, E.C., Stadnitskaia, A., Schubert, C.J., Lehmann, M.F., Sinninghe Damsté, J.S., Niemann, H., 2015. Identification and carbon isotope composition of a novel branched GDGT isomer in lake sediments: evidence for lacustrine branched GDGT production. *Geochimica et Cosmochimica Acta* 154, 118–129.

Weijers, J., Schefuß, E., Schouten, S., Damsté, J.S.S., 2007a. Coupled thermal and hydrological evolution of tropical Africa over the last deglaciation. *Science* 315, 1701–1704.

Weijers, J., Schouten, S., Donker, J. van den, Hopmans, E., Sinninghe Damsté, J.S., 2007b. Environmental controls on bacterial tetraether membrane lipid distribution in soils. *Geochimica et Cosmochimica Acta* 17, 703–713.

Weijers, J., Schouten, S., Hopmans, E.C., Geenevasen, J.A.J., David, O.R.P., Coleman, J.M., Pancost, R.D., Sinninghe Damsté, J.S., 2006. Membrane lipids of mesophilic anaerobic bacteria thriving in peats have typical archaeal traits. *Environmental Microbiology* 8, 648–657.

Whitehead, D.R., 1964. Fossil pine pollen and full-glacial vegetation in southeastern North Carolina. *Ecology* 45, 767–776.

Whitehead, D.R., 1965. Palynology and Pleistocene phytogeography of unglaciated eastern North America. In: Wright, H.E., Jr., Frey, D.G. (Eds.), *The Quaternary of the United States*. Princeton University Press, Princeton, pp. 417–432.

Whitehead, D.R., 1981. Late-Pleistocene vegetational changes in northeastern North Carolina. *Ecological Monographs* 51, 451–471.

Whitlock, C., Larsen, C.P.S., 2001. Charcoal as a fire proxy. In: Smol, J.P., Birks, H.J.B., Last, W.M. (Eds.), *Tracking Environmental Change Using Lake Sediments: Volume 3 Terrestrial, Algal, and Siliceous Indicators*. Springer, Dordrecht pp. 75–97.

Whitmore, J., Gajewski, K., Sawada, M., Williams, J.W., Shuman, B., Bartlein, P.J., Minckley, T., et al., 2005. Modern pollen data from North America and Greenland for multi-scale paleoenvironmental applications. *Quaternary Science Reviews* 24, 1828–1848.

Williams, J.W., Jackson, S.T., 2007. Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment* 5, 475–482.

Williams, J.W., Shuman, B.N., Webb, T. III, 2001. Dissimilarity analyses of late-Quaternary vegetation and climate in eastern North America. *Ecology* 82, 3346–3362.

Williams, J.W., Shuman, B.N., Webb, T. III, Bartlein, P.J., Leduc, P., 2004. Late Quaternary vegetation dynamics in North America: scaling from taxa to biomes. *Ecological Monographs* 74, 309–334.

Willman, H., Frye, J., 1970. Pleistocene stratigraphy of Illinois. Illinois State Geological Survey Bulletin 94. State of Illinois Department of Registration and Education, Urbana, Illinois.

Woltering, M., Atahan, P., Grice, K., Heijnis, H., Taffs, K., Dodson, J., 2014. Glacial and Holocene terrestrial temperature variability in subtropical east Australia as inferred from branched GDGT distributions in a sediment core from Lake McKenzie. *Quaternary Research* 82, 132–145.

Wright, H.E. Jr., Mann, D.H., Glaser, P.H., 1983. Piston corers for peat and lake sediments. *Ecology* 65, 657–659.

Zink, K.-G., Vandergoes, M.J., Mangelsdorf, K., Dieffenbacher-Krall, A.C., Schwark, L., 2010. Application of bacterial glycerol dialkyl glycerol tetraethers (GDGTs) to develop modern and past temperature estimates from New Zealand lakes. *Organic Geochemistry* 41, 1060–1066.