

Vegetation history in central Kentucky and Tennessee (USA) during the last glacial and deglacial periods

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ABSTRACT

Knowledge about vegetation dynamics during the last glacial and deglacial periods in southeastern North America is under-constrained owing to low site density and problematic chronologies. New pollen records from two classic sites, Anderson Pond, TN, and Jackson Pond, KY, supported by AMS ¹⁴C age models, span 25.2–13.7 ka and 31.0–15.4 ka, respectively. A transition from *Pinus* dominance to *Picea* dominance is recorded at Jackson Pond ca. 26.2 ka, ~coincident with Heinrich Event H2. Anderson and Jackson Ponds record a transition from conifer to deciduous-tree dominance ~15.9 and 15.4 ka, respectively, marking the development of no-analog vegetation characterized by moderate to high abundances of *Picea*, *Quercus*, *Carya*, *Ulmus*, *Fraxinus*, *Ostrya/Carpinus*, Cyperaceae, and Poaceae, and preceding by ~2000 yr the advent of similar no-analog vegetation in glaciated terrain to the north. No-analog vegetation developed as a time-transgressive, south-to-north pattern, mediated by climatic warming. *Sporormiella* abundances are consistently low throughout the Jackson and Anderson Pond records, suggesting that megafaunal abundances and effects on vegetation varied regionally or possibly that the *Sporormiella* signal was not well-expressed at these sites. Additional records with well-constrained chronologies are necessary to assess patterns and mechanisms of vegetation dynamics during the last glacial and deglacial periods.

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Introduction

Vegetation changes during the last deglaciation in eastern North America are of considerable interest because they comprise rapid transitions from conifer-dominated vegetation to deciduous forests (Williams et al., 2004), successive emergence and disappearance of vegetation lacking modern analogs (Overpeck et al., 1992; Williams et al., 2001), and are linked in some regions to interactions between megafaunal collapse, shifts in fire regime, and climate change (Gill et al., 2009, 2012). Pollen sequences from the unglaciated southeastern United States are particularly critical in understanding late-glacial vegetational responses to climate changes and other factors. Most sites show transitions from boreal conifers to temperate hardwoods (Watts, 1970; Delcourt, 1979; Watts, 1980; Whitehead, 1981; Hussey, 1993), and many have no-analog pollen assemblages that differ strongly from modern assemblages and also differ somewhat in composition from each other and from late-glacial sites to the north (Jackson and Williams, 2004).

Precise and accurate pollen chronologies are needed from glacial-age and late-glacial sites in eastern North America to support delineation of spatiotemporal patterns of vegetation change, to correlate event

chronologies with paleoenvironmental records from other continental sites, marine records, and ice cores, and to assess the causes underlying vegetational transitions. However, the age-models of most existing pollen records in the southeastern US are based on bulk-sediment ¹⁴C dates, often obtained at low density in the stratigraphic column. Most sites outside peninsular Florida are shallow solution basins formed in limestone or dolomite bedrock, with carbonate-rich surface water. Carbonate errors (Olsson, 1986; MacDonald et al., 1991; Grimm et al., 2009), root intrusions (Whitehead and Sheehan, 1985), and hiatuses owing to shallow and fluctuating water levels (Webb and Webb, 1988; Jackson and Whitehead, 1993) impose large and unquantifiable uncertainties upon existing age models and age estimation of events. Blois et al. (2011) recently assessed late Pleistocene pollen records from eastern North America with the aim of identifying “benchmark” sites with high-quality chronologies capable of comparison among sites and with events recorded in marine and ice cores. Of the 22 benchmark sites, only three were from unglaciated terrain (Lake Tulane (FL), Clear Pond (SC), Browns Pond (VA)), and the latter site did not meet all criteria for high-quality chronologies.

In recent years, paleoecologists have devoted a growing effort to revisit classic pollen sites, with the goals of obtaining more precise and accurate chronologies, developing high-resolution pollen sequences, and reassessing causes and consequences of past ecological changes by linking events in the pollen records to signals from other paleoecological

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records and paleoenvironmental proxies. These reexaminations have been motivated by emergence of new questions with requirements for high chronological precision, together with development of analytical tools for increasing chronological precision (particularly accelerator mass spectrometry (AMS) ^{14}C dating of terrestrial plant macrofossils) and for quantifying and reducing uncertainties in age estimation of sediments. Such studies have identified and corrected substantial dating errors in earlier studies, revealed the role of such forcing mechanisms as climate change and megafaunal decline, and enabled detailed comparisons to ice-core, speleothem, and marine-sediment paleoenvironmental chronologies (Grimm et al., 2006; Nelson et al., 2006; Grimm et al., 2009; Gill et al., 2012).

Many of these studies have focused on the last deglaciation, and have generated important insights. The temporal and spatial patterns of the late-glacial no-analog assemblages are being increasingly well-characterized in the central Great Lakes region (Nelson et al., 2006; Gonzales and Grimm, 2009; Gonzales et al., 2009; Grimm et al., 2009; Gill et al., 2012). Recent application of *Sporormiella* dung-fungus spores as a biomarker for megafaunal populations suggests an important role for megafaunal browsing in late-glacial vegetation dynamics

in the central Great Lakes region (Gill et al., 2009, 2012). Further understanding of the patterns and controls of vegetation dynamics during the last glacial maximum and deglaciation requires reexamination of sites south of the Laurentide ice margin.

Here we focus on the Interior Low Plateaus region (Fenneman, 1938) south of the Ohio River valley, where knowledge concerning glacial-age vegetation history is based on records from two sites. Anderson Pond in central Tennessee (Fig. 1) was discovered and cored by Hazel Delcourt, who developed a detailed pollen and macrofossil record (Delcourt, 1978, 1979). Using eight bulk-sediment ^{14}C dates, Delcourt developed and applied an age model for the site that spanned the past 19,000 ^{14}C yr (ca. 22,500 calendar yr). Jackson Pond in central Kentucky (Fig. 1), 160 km north of Anderson Pond, was the subject of a later study (Wilkins, 1985; Wilkins et al., 1991). A pollen and plant macrofossil chronology spanning the past 20,000 ^{14}C yr (ca. 24,000 cal yr) was developed using six bulk-sediment ^{14}C dates (Wilkins, 1985; Wilkins et al., 1991).

Unfortunately, the sediment chronology at both sites is problematic. Low sedimentation rates estimated for the Holocene, apparent persistence of *Picea* into the Holocene, and abrupt transitions in the pollen



Figure 1. Map showing locations of Anderson Pond and Jackson Pond (purple circles) and other sites discussed in the paper (green squares). Hachured line denotes the approximate margin of the Laurentide Ice Sheet at its maximum (ca. 21 ka) (Dyke et al., 2003).

sequences suggest cessation of sediment deposition starting in the late-glacial or early Holocene (Webb and Webb, 1988; Jackson and Whitehead, 1993; Jackson et al., 1997). Both sites are solution basins in limestone or dolomite bedrock, and hence bulk-sediment ^{14}C chronologies may be offset by carbonate errors (Grimm et al., 2009). Because these sites appeared to have continuous records from before the last glacial maximum through much of the late-glacial period, we initiated a new study aimed at (1) developing robust age-models and well-dated pollen chronologies from both sites, (2) comparing vegetational changes at the sites with well-dated pollen and paleoclimate records from eastern North America and the North Atlantic region, and (3) identifying whether the sites contain reliable records of the late-glacial/Holocene transition and Holocene vegetational changes. Our study is aimed particularly at assessing the spatial and temporal patterns of no-analog vegetation in eastern North America, and evaluating underlying mechanisms.

Site descriptions

Anderson Pond

Anderson Pond is a large, irregularly shaped, shallow solution basin (ca. 35 ha) formed in Mississippian dolomite. Slopes surrounding the basin are moderately steep; hillcrests are 15–20 m above the basin, typically reached within 200 m of the basin edge. A few intermittent streams drain into the basin in small ravines. The basin is vegetated by a ring of swamp forest (*Liquidambar styraciflua*, *Acer rubrum*, *Ulmus rubra*, *Salix nigra*, *Nyssa sylvatica*, *Quercus phellos*), which surrounds a 28-ha complex of shallow marsh and shrub carr (*Itea virginica*, *Cephalanthus occidentalis*, *Alnus serrulata*) with scattered individuals of *A. rubrum* and *S. nigra*. Delcourt (1978, 1979) provides detailed descriptions of the surrounding landscape.

We visited Anderson Pond in October 2007, during a prolonged drought. No standing water was found anywhere in the basin. We used probe rods to locate the deepest sediments, which were in the south-central part of the basin (36°01'45"N, 85°30'04"W; 303 m elevation). Although we cannot determine with precision the proximity of our coring site to Delcourt's, we are confident that we were within 25 m of her coring sites based on her map, our probe-transects, and comparison of vegetation at our coring site with photos taken during Delcourt's coring trip. We obtained two parallel overlapping sediment cores using a 10-cm-diameter modified Livingstone piston corer (Wright et al., 1984). A chain hoist, tripod, and earth-anchors were required for all coring drives. The water table was ca. 30 cm below the sediment surface at the time of coring. Cores were described and measured in the field.

Jackson Pond

Jackson Pond is a circular, shallow sinkhole (3.5 ha) in a karst upland of gentle relief. Hillcrests are 10–15 m above the surface of the basin. Most of the surrounding area is in cropland or pasture, with scattered woodlots of *Quercus* and *Carya* spp. *Fagus grandifolia*, *Fraxinus americana*, *Acer saccharum*, and other mesic species occur in valley bottoms. The basin itself at the time of coring was vegetated by emergent *Nuphar*, graminoids (Cyperaceae and Poaceae), and scattered individuals of *C. occidentalis* and *A. rubrum*. Wilkins (1985) provides more detailed descriptions of the region.

Jackson Pond was also heavily drawn down by severe drought conditions at the time of coring (October 2007), with surface water in the basin restricted to a few small, shallow pools. Over most of the basin, the water surface was at or a few centimeters below the sediment surface, which was covered with *Nuphar* rhizomes and leaves, Cyperaceae corms and foliage, colonies of *Dulichium arundinaceum*, and scattered individuals of *C. occidentalis*. The soft sediment surface made it impossible to walk or float a raft to the center of the basin, so we chose a coring location as close to the center as we could safely walk. This site was on

the southeast side of the basin, approximately 40 m from shore and 40 m from the center of the basin (37°25'56"N, 85°43'27"W; 260 m elevation). Probing indicated at least 6 m of sediment, comparable to the sediment depth reported by Wilkins et al. (1991). We obtained two parallel overlapping sediment cores using the same equipment as at Anderson Pond. The water table at the coring site was 3 cm below the sediment surface at the time of coring.

Laboratory methods

Cores were split longitudinally into two halves, imaged at the National Lacustrine Core Facility at the University of Minnesota and scanned for magnetic susceptibility. Our laboratory analyses concentrated on one-half of the split cores. Both halves were kept in cold storage (ca. 4 °C). The working half of each core was sliced into 1 cm-thick half-disks. Each half-disk was trimmed on the outer surface to remove potential contaminants, and subsamples were obtained from the interior portion of each half-disk for pollen (1 cm³) and archive/backup (4 cm³). The remainder of each disk was used for plant macrofossil analysis.

Pollen samples were prepared using standard chemical digestion techniques for unconsolidated lake sediments (Jackson, 1999). Individual pollen samples were counted to a minimum sum of 300 arboreal grains. Pollen percentages were calculated using a total terrestrial pollen sum (aquatic or ambiguous types, including *Alnus*, *Cephalanthus*, *Salix*, Cyperaceae, *Nuphar*, *Brasenia*, and *Sagittaria* were excluded, as were spores), and informal pollen zones were demarcated with the aid of CONISS, a stratigraphically constrained cluster analysis (Grimm, 1987). Percentages of aquatic taxa were calculated based on a sum of terrestrial pollen plus aquatic pollen, and those of spores were based on a sum of terrestrial pollen plus spores. We cross-checked our identification of *Sporormiella* spores by examining pollen samples from Appleman and Silver Lakes (Gill et al., 2009, 2012). We further confirmed our *Sporormiella* findings in a double-blind trial, whereby five replicate pollen samples from our sites were assigned arbitrary codes by a third person, and submitted to Dr. Jacquelyn Gill for *Sporormiella* counting. We pooled *Fraxinus* pollen morphotypes in preparing pollen diagrams, but nearly all *Fraxinus* grains observed were assignable to or consistent with the *Fraxinus nigra* morphotype.

We used macrofossils analyses mainly to provide material of known provenance for AMS dating and for identification of coniferous trees. Sediment samples were measured volumetrically by water displacement, dispersed in water, and sieved (710- μm mesh). Sieve residues were scanned under a stereomicroscope. Selected, well-preserved conifer needles were dehydrated, embedded, and sectioned on a rotary microtome to support species identification.

We obtained 14 AMS ^{14}C age estimates from plant macrofossils of known terrestrial origin from Anderson Pond, and twelve from Jackson Pond (Table 1). AMS ^{14}C dates and associated uncertainties were converted to 95% calibrated-year ranges (cal yr BP) using the IntCal09 calibration curve (Reimer et al., 2009) in the CLAM program in R (Blaauw, 2010). We used the Bacon program in R (Blaauw and Christen, 2011) to develop age-models with uncertainty estimates for the sediment sequences. We applied linear interpolation of weighted-mean age-estimates from the Bacon analysis to sample depths at 1-cm intervals to determine ages of individual horizons in the sequence. All ages are expressed in 'calendar' years (cal yr) or thousands of calendar years (ka) before present (1950 CE datum).

We determined the minimum dissimilarities relative to modern pollen samples from eastern North America for all fossil pollen samples from Anderson Pond and Jackson Pond. The dissimilarity distance was measured and compared in squared-chord distance (SCD) scores, using the analog program in Matlab of Williams and Shuman (2008). For each fossil sample, the most similar modern sample was determined using SCD scores. The modern-sample dataset was obtained from the North America Modern Pollen Database (Whitmore et al., 2005). Both modern and fossil pollen data used in this analysis contain 25 common

Table 1
AMS ^{14}C dates obtained from Anderson Pond and Jackson Pond sediments.

Site	Depth	Lab ID	^{14}C age $\pm 1\sigma$	Calibrated age	Material dated
	cm		^{14}C yr BP	cal yr BP, 2σ	
Anderson	67	OS-77549	115 \pm 35	11–270	<i>Scirpus</i> seed and trigonous Polygonaceae seed
Anderson	86	OS-82719	Less than modern		Polygonaceae seeds, and twig
Anderson	110	OS-82720	12,050 \pm 60	13,753–14,051	Cyperaceae seeds
Anderson	118	OS-77548	12,050 \pm 70	13,743–14,077	<i>Picea</i> needles and Cyperaceae achene
Anderson	174	OS-77356	12,550 \pm 150	14,082–15,217	<i>Picea</i> needle
Anderson	209	OS-79477	12,850 \pm 75	14,931–15,938	<i>Scirpus</i> achene, <i>Picea</i> seed, <i>Picea</i> needles
Anderson	314	OS-78370	14,250 \pm 170	16,933–17,826	<i>Pinus banksiana</i> needles
Anderson	346	OS-79439	14,500 \pm 110	17,207–17,958	<i>Abies</i> needle and <i>Picea</i> needle
Anderson	406	OS-79437	15,900 \pm 110	18,834–19,396	<i>Picea</i> seed coat, <i>Pinus resinosa</i> needle, <i>Picea</i> needle, charcoal
Anderson	478	OS-74779	16,550 \pm 120	19,430–20,062	Twig, and <i>Pinus banksiana</i> needles
Anderson	498	OS-79807	17,350 \pm 75	20,308–21,131	Charcoal, <i>Pinus resinosa</i> needle
Anderson	635	OS-67916	19,100 \pm 95	22,407–23,290	<i>Pinus</i> , <i>Picea</i> , and <i>Abies</i> needles
Anderson	681	OS-83176	17,300 \pm 120	20,230–21,147	<i>Pinus</i> needles
Anderson	732	UGAMS-11708	20,950 \pm 50	24,583–25,251	Wood
Jackson	120	UGAMS-6929	110 \pm 20	22–265	Wood
Jackson	120	OS-77620	1820 \pm 35	1629–1864	Charcoal, plant debris
Jackson	128–130	UGAMS-8271	660 \pm 25	561–670	Cyperaceae debris
Jackson	150	UGAMS-8272	8870 \pm 50	9771–10,177	Cyperaceae debris and small twigs
Jackson	170	OS-74777	14,000 \pm 55	16,815–17,406	Twigs
Jackson	229	UGAMS-6930	15,920 \pm 40	18,872–19,370	Cyperaceae stem and leaf fragments
Jackson	279	OS-86255	18,100 \pm 75	21,338–22,033	Cyperaceae debris and small twigs
Jackson	339.5–341.5	OS-86265	19,650 \pm 90	23,093–23,856	Cyperaceae debris
Jackson	407.5	OS-74914	21,600 \pm 85	25,457–26,234	Twigs
Jackson	457.5	OS-79476	14,800 \pm 80	17,671–18,505	Charcoal, plant debris
Jackson	547.5	OS-78371	22,400 \pm 410	25,983–28,025	Twig
Jackson	567.5	OS-67937	25,800 \pm 150	30,310–30,957	<i>Larix</i> , <i>Pinus</i> , and <i>Picea</i> needles

eastern North American pollen taxa (taxon list in Williams et al., 2001). Williams and Shuman (2008) suggested a no-analog threshold value of 0.2–0.3 for a 64-taxon list with some taxa split regionally. Since we used a smaller 25-taxon list, we considered samples with minimum SCD scores > 0.2 to have no modern analog, based on the suggested lower bound in Williams and Shuman (2008).

Results

Chronology

The bases of the Anderson Pond and Jackson Pond records are dated to ca. 25 ka and ca. 31 ka, respectively (Table 1, Fig. 2). Sedimentation rates at both sites were relatively constant (ca. 55 cm/ka and 29 cm/ka at Anderson and Jackson, respectively) until the late-glacial period, dropping dramatically at both sites thereafter (beginning ca. 14 ka at Anderson and after 17 ka at Jackson) (Fig. 2). Several lines of evidence indicate late-glacial and Holocene depositional hiatuses in the records. First, inferred sedimentation rates of the upper sediment sequences (top 110 cm at Anderson Pond; top 129–170 cm at Jackson Pond) are too slow to infer continuous deposition (Webb and Webb, 1988; Goring et al., 2012). Second, AMS dates from these upper sediments show date reversals and modern dates at both sites (Table 1), suggesting sediment mixing during drawdown periods (e.g., Jackson and Whitehead, 1993). Third, both sites are currently shallow-water basins subject to substantial drawdown (see site descriptions) and lake desiccation. Fourth, upper sediments are laden with roots and show evidence of oxidation penetrating at least 40–50 cm below the sediment surface (Supplementary Fig. 1). Fifth, pollen profiles (discussed below) show abrupt transitions at or near the points at which sediment accumulation rates decline, consistent with a loss of sediment record.

In modeling age-depth relationships, we initially included the sediment surface as a modern date (50 cal yr BP with a standard deviation of 20 yr). However, the posterior estimate of sedimentation rate by Bacon represents an overall sediment rate for the entire sequence, even when a hiatus is suggested. By including the “surface date” with its narrow uncertainty, the Bayesian age-depth models were strongly

forced to fit to this date, while treating the different depositional histories over the younger and older sections in generally similar fashion. As a result, the Bacon age models yielded large uncertainties in the upper portions of the age-depth models and poor fits to the AMS radiocarbon ages (Supplementary Fig. 2). Accordingly, we created and used here a Bacon age model that used only the AMS radiocarbon dates in the age-depth models and excluded the “surface date” (Fig. 2). Therefore, our age models were informed primarily by the pre-hiatus portions of the cores. In presenting results we focus on the time periods preceding the hiatuses.

For the final Anderson Pond age model (Fig. 2a), we also discarded an obviously erroneous date at 86 cm (Table 1), within the period of suspected hiatus. All other AMS dates were used. Below 110 cm, the age model is approximately linear with low associated uncertainties (Fig. 2a). The uncertainties increased moderately above 110 cm owing to a modern date at 67 cm, which suggests a hiatus and sediment mixing. In addition, a major pollen transition occurs at ca. 106 cm. Therefore, we regard the sediment stratigraphy and chronology above 106 cm depth (< 13.7 ka) as unreliable.

For Jackson Pond, we used all AMS dates to construct the age model. For the section below 130 cm, the age model shows a linear pattern and low associated uncertainties (Fig. 2b). Uncertainties increased rapidly above 130 cm, owing to modern dates and reversals at 120 cm and 129 cm. A major pollen-zone boundary occurs ca. 127 cm. We regard sediment stratigraphy and chronology above 130 cm depth (ca. 15.5 cal ka BP) as unreliable, and probably mixed (Supplementary Figs. 1, 2). Bacon-estimated uncertainties increase sharply above this horizon, but we also note that the interval between 170 cm and 130 cm depth effectively represents an extrapolation of the sedimentation rates above the topmost reliable ^{14}C date (Fig. 2b). This extrapolation is reasonable in view of the apparent continuity of the pollen sequence and absence of obvious lithological discontinuities. However, we also note that the chronology of the interval between 170 cm and 130 cm depth is most strongly informed by the AMS dates at and below 170 cm depth, and hence age estimates for samples younger than 17 ka may be less reliable than older samples.

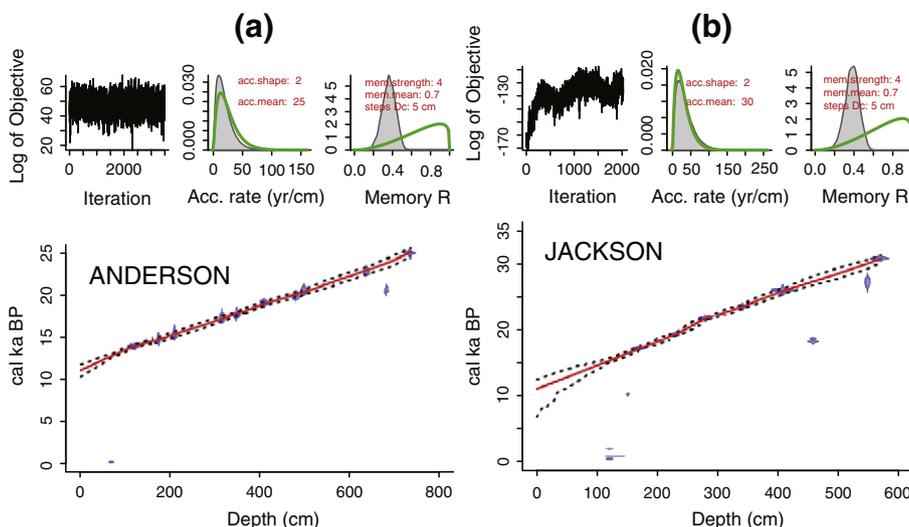


Figure 2. Bacon age-depth models (Blaauw and Christen, 2011) for Anderson Pond (a) and Jackson Pond (b). For each age model, insets in the upper panel show the iteration history and two parameters of the Bayesian age model. The left inset shows the iteration history, the middle inset shows the prior (green line) and posterior (gray area) of the sediment accumulation rate (yr/cm), and the right inset shows the prior (green line) and posterior (gray area) of the memory (1-cm autocorrelation strength). The bottom panels show the age-depth models with uncertainties. Solid red lines denote weighted averages of all possible chronologies. Associated uncertainties are represented by the gray-scale and confidence intervals (dashed black lines).

Anderson Pond pollen and macrofossil data

Zone AP-1a (741–510 cm; 25.2–20.8 ka)

Zone AP-1a is characterized by high *Pinus* (60–85%) and *Picea* percentages (10–30%; mostly >15%), with pollen from deciduous tree taxa absent or in trace percentages (Fig. 3). *Abies* pollen occurs consistently, but in trace amounts. Asteraceae and Poaceae occur consistently in low percentages (1–4%). Cyperaceae (excluded from the pollen sum) is abundant (5–30%) throughout the zone. Poorly preserved needles of *Picea* and *Pinus* occurred throughout the zone (Supplementary Table 1). *Pinus banksiana* was identified from a sample dating 22.6 ka. Poor preservation prevented species identification of other *Pinus* needles, but all were of the semicircular morphotype, consistent with *P. banksiana*. Needles of *Abies* and *Picea* cf. *mariana* also occurred in this zone.

Zone AP-1b (510–338 cm; 20.8–17.7 ka)

Zone AP-1b is similar in composition to Zone AP-1a, with a few key differences. *Pinus* pollen is overall higher in Zone AP-1b (70–85%), while *Picea* pollen is lower (5–20%). *Quercus* and *Fraxinus* pollen occur consistently in very low percentages (<3%) above 450 cm, and *Quercus* increases ca. 18 ka. Cyperaceae decreases to <5% at 455 cm depth. *Pinus* needles occurred throughout this period; all were of the semicircular morphotype and a few were identifiable to *P. banksiana* (Supplementary Table 1). *Picea* and *Abies* needles occurred in the uppermost samples.

Zone AP-2 (338–238 cm; 17.7–15.9 ka)

This period is characterized by declining *Pinus* and increasing *Picea* percentages, although both show fluctuations (Fig. 3). *Quercus* pollen fluctuates between 5 and 10%. *Abies* pollen and *Fraxinus* pollen occur

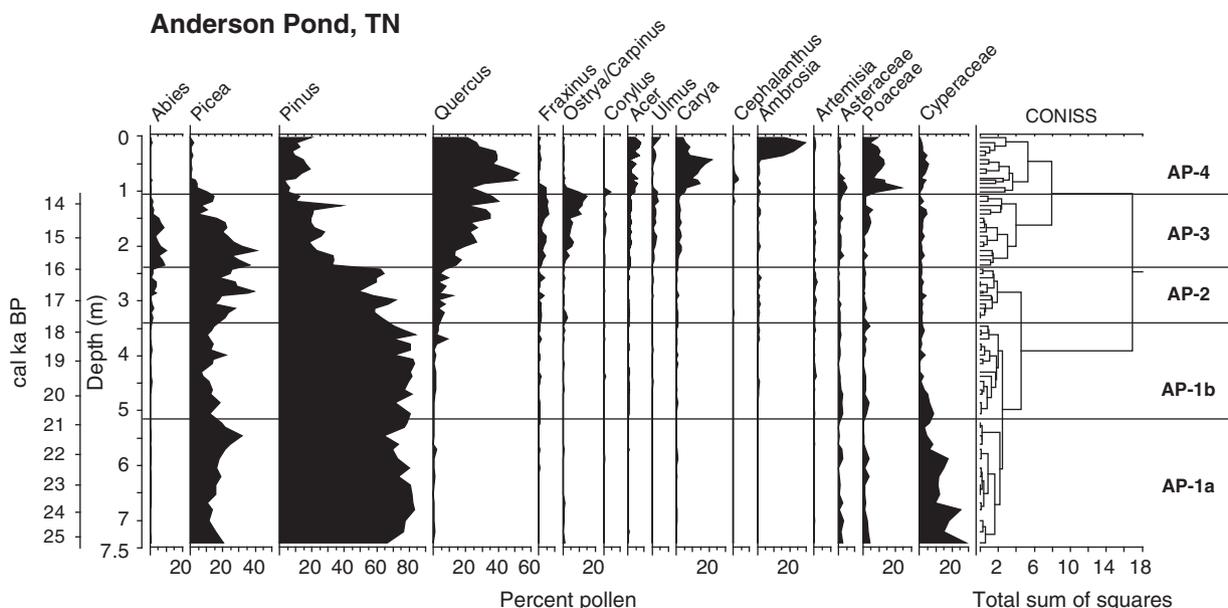


Figure 3. Pollen percentage diagram for Anderson Pond, TN, showing selected important taxa. Constrained incremental sum of squares (CONISS) analysis (Grimm, 1987) in TILIA v. 1.7.14 was used to guide delineation of pollen zones and subzones.

consistently at low percentages (<3%), and other deciduous taxa (*Acer*, *Carya*, *Ostrya* type) occur in trace amounts. *Ambrosia* also occurs, together with Asteraceae and Poaceae (each <2%). Needles of *Picea* and *Pinus* (semicircular morphotypes) occurred in some samples (Supplementary Table 1).

Zone AP-3 (238–106 cm; 15.9–13.7 ka)

The lower zone boundary is marked by a dramatic decline of *Pinus* (65% to <40%) (Fig. 3). *Pinus* pollen fluctuates through the zone, but declines to <5% by the top of the zone. *Picea* undergoes fluctuating but declining values. *Abies* pollen attains a brief maximum (5–10%) in the lower part of the zone, declining to trace percentages above 145 cm. Both *Quercus* and *Ostrya* type increase steadily through the zone, attaining respective maxima of 45% and 15% near the top. Other deciduous-tree taxa (*Acer*, *Carya*, *Fraxinus*, *Ulmus*) occur consistently in low percentages. Herbs and graminoids are consistent at low percentages. *Picea* needles were present in most samples, with rare *Abies* and *Pinus* (semicircular morphotype).

Zone AP-4 (106–0 cm; undated Holocene)

The zone is characterized by high *Quercus* (30–60%), *Carya* (10–25%), and Poaceae (5–15%), moderate *Pinus* (5–20%), and low *Picea* and *Abies* (Fig. 3). *Ambrosia* pollen increases rapidly at 35 cm from ca. 1% to >20%. This zone represents Holocene deposition, but the low sedimentation rates, dating reversals, and lithology (discussed above) indicate that most of the Holocene record is absent or unreliable. Sediments above 35 cm depth (post-*Ambrosia* increase) postdate early 19th Century European land clearance, and the underlying 70 cm of sediment represents slow, perhaps intermittent, sediment accumulation over a period spanning more than 10,000 yr. Sporadic occurrence of *Picea* and *Abies* pollen throughout the zone indicates continued redeposition and sediment mixing (discussed in Jackson and Whitehead, 1993).

Jackson Pond pollen and macrofossil data

Zone JP-1 (582–421 cm; 31.0–26.2 ka)

The basal portion of the sequence is heavily dominated by *Pinus* (>80%), with moderate percentages of *Picea* (5–15%) and *Quercus* (2–5%) (Fig. 4). *Abies* and *Ostrya* type occur in very low amounts (<3%) in most samples. Cyperaceae pollen occurs consistently (2–5%),

and other non-arboreal types are scarce. *Pinus banksiana* needles occurred in the lower part of this zone (Supplementary Table 1); poorly preserved *Pinus* needles in the upper part are consistent with *P. banksiana*. Needles of *Picea* sp. occurred at several levels throughout this zone, and a *Larix* needle occurred in one sample.

Zone JP-2a (421–215 cm; 26.2–18.7 ka)

The lower zone boundary is marked by a rapid decline in *Pinus* (80% to <55% within 10 cm), mirrored by a *Picea* increase (10% to >35%) (Fig. 4). Other pollen taxa show little or no change across the zone boundary. *Pinus* and *Picea* pollen percentages show modest reciprocal fluctuations during the interval. Poaceae and *Ostrya* pollen increase near the top of the subzone. Needles of *Picea* were present.

Zone JP-2b (215–127 cm; 18.7–15.4 ka)

This subzone is characterized by increased pollen of *Quercus* (7–15%), *Ostrya* (2–5%), *Fraxinus* (trace, but consistently present), and Poaceae (5–10%). Cyperaceae pollen is particularly high (10–20%) during this interval, and the elevated Cyperaceae and Poaceae pollen may indicate emergent vegetation in shallow waters of the basin. Conifer macrofossils were absent from all sediments of this zone.

Zone JP-3 (127–0 cm; undated Holocene)

Both *Pinus* and *Picea* percentages plummet between 130 and 125 cm depth, accompanied by sharp increases in *Quercus* and other hardwoods (*Fraxinus*, *Acer*, *Carya*, *Fagus*), and in *Cephalanthus* and *Salix*. Excepting the topmost sample, *Ambrosia* pollen is low, suggesting that the sediments predate Euro-American land clearance. However, the young dates from 120 to 130 cm depth (Table 1; Fig. 4) indicate that most of the Holocene is absent from the record. Similar to Anderson Pond, the “smearing” of the *Picea* pollen profile suggests redeposition of Pleistocene sediments during Holocene drawdowns.

Discussion

Pollen stratigraphy and chronology: Comparison with previous studies

Our study provides revised and refined pollen chronologies for two key pre-Holocene sites in eastern North America. Overall, the pollen stratigraphy is similar between our study and the earlier studies

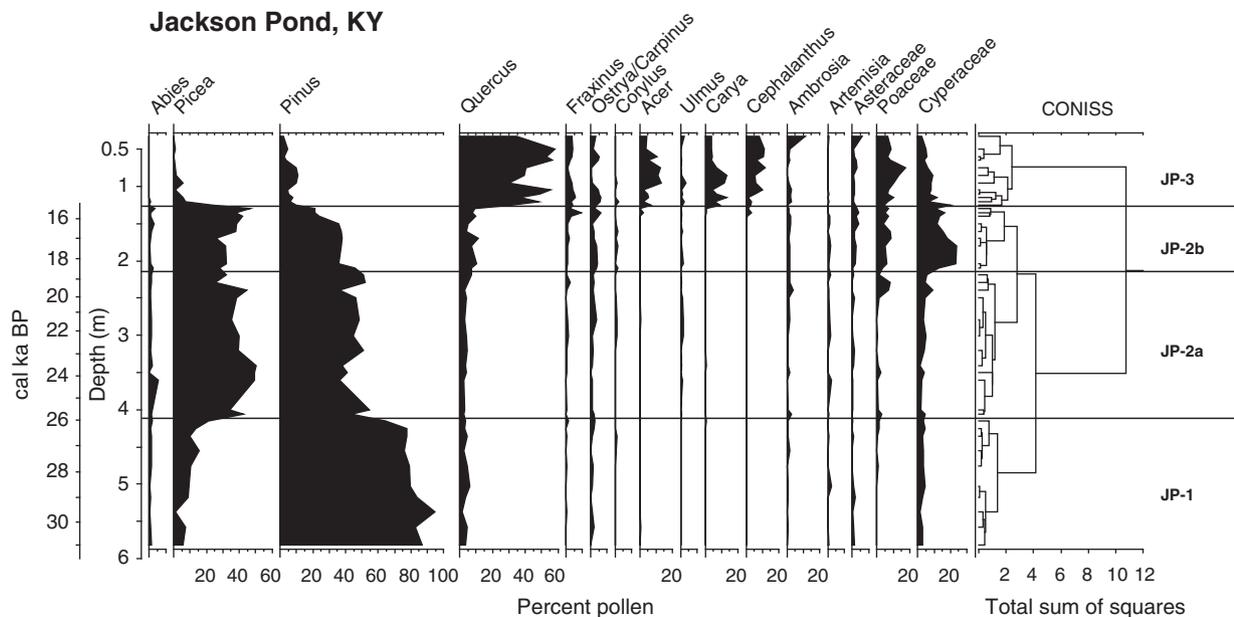


Figure 4. Pollen percentage diagram for Jackson Pond, KY, showing selected important taxa. Constrained incremental sum of squares (CONISS) analysis (Grimm, 1987) in TILIA v. 1.7.14 was used to guide delineation of pollen zones and subzones.

(Delcourt, 1979; Wilkins, 1985; Wilkins et al., 1991). Differences arise in part from the higher stratigraphic density of our sampling, which reveals high-frequency variation masked in earlier studies, and imparts greater sensitivity and precision to identification and age-estimation of transitions (e.g., Liu et al., 2012). A second difference emerges in age-estimation of events, resulting in part from differences in sampling density and in part from different dating methods employed in the two studies. At Anderson Pond, features of our pollen sequence are closely similar to those of Delcourt (1979), but age estimates for specific transitions appear to be approximately 1 ka older or more in our sequence.

A greater contrast in pollen stratigraphy is apparent at Jackson Pond, where our study shows an extended period of *Pinus* dominance (Zone JP-1) that is almost entirely missing from the earlier study. Only the lowest two pollen samples from the earlier study show similarly high *Pinus* percentages (Wilkins, 1985; Wilkins et al., 1991). Hence, the basal sediments were apparently older at our coring site than at Wilkins' site. On the other hand, the successive late-glacial maxima in *Fraxinus* and *Ostrya/Carpinus* pollen recorded by Wilkins (1985) are entirely absent from our sequence. Late-glacial or Holocene decomposition truncated the record at our coring site at an older horizon than at Wilkins' site. Although precise comparison of pollen sequences between the Jackson Pond records is difficult owing to differences in sampling density, some changes (e.g., those corresponding to our JP-1/2a and JP-2a/2b pollen-zone boundaries) appear to be ca. 1 ka earlier in Wilkins' record.

The stratigraphic similarities among pollen sequences within sites are unsurprising in view of the theory underlying pollen analysis, previous replication studies, and the technical standardization in palynology of the past several decades. However, the chronological offsets between the records are non-trivial, and underscore the need for improved chronologies supported by AMS-dating of terrestrial plant materials at sites with carbonate-rich groundwater and sediment (e.g., Grimm et al., 2009; Blois et al., 2011). Our results from Anderson Pond contrast with those of earlier comparative studies (e.g., Grimm et al., 2009), in that our AMS-based chronology appears older than the bulk-sediment chronology of the previous study. At other sites, mainly in glaciated terrain, carbonate-rich groundwater reservoirs contain “dead” carbon from bedrock and surficial sediments, causing bulk-sediment dates to be too old (e.g., Grimm et al., 2009). Anderson Pond, situated in karst terrain, is potentially subject to old-carbon effects, but instead our age model based on AMS dates of terrestrial plant macrofossils is about 1000 years younger than age estimates based on bulk sediments. The reason for this age offset is unclear, but could result from the lower number of ^{14}C dates constraining the previous age model, contamination of bulk sediments by younger materials (e.g., drag-down or root penetration), or other sources of error. Our results suggest that it should not be taken for granted that temporal offset of chronologies is necessarily unidirectional.

Our findings provide strong evidence for depositional hiatuses at both sites spanning most of the Holocene and a substantial part of the late-glacial period. The shallow nature of the basins, with high susceptibility to drawdown and even desiccation, has resulted in poorly resolved Holocene profiles that are highly mixed, episodically deposited, or both. Erasure of the pollen record at both our sites may have occurred in the late-glacial as well as the Holocene; in either case the erasure extended well into the late-glacial portion of the sediment sequence. Similar truncations or smearings are evident at other sites in terrain south of the Laurentide ice margin (e.g., Watts, 1970; Jackson and Whitehead, 1993). To date, complete, unambiguous records of the late-glacial/Holocene transition are lacking north of the Florida peninsula, except for Clear Pond (SC) (Hussey, 1993) and Cupola Pond (MO) (Smith, 1984; Jones, 2011). Better age estimates of the hiatuses at existing sites are needed to assess glacial-age and late-glacial vegetation dynamics of the region, and new sites should be sought to fill in temporal gaps. The age of the hiatus differs within sites (e.g., Jackson Pond) and among adjacent sites (e.g., Watts, 1970). Multiple cores from multiple sites may help extend pollen chronologies to cover more of the late-glacial/Holocene transition. In the meantime, synoptic

studies of late-glacial and Holocene vegetation should include careful filtering of these and other records in the region.

Glacial-age vegetation patterns south of the ice sheet in the interior low plateaus

Anderson and Jackson Ponds comprise the central portion of a latitudinal transect of fossil pollen records from the Laurentide ice margin south to the Florida Peninsula (Fig. 1). The transect is anchored to the north by well-dated pollen records from Appleman and Silver Lakes in formerly glaciated terrain (Gill et al., 2009, 2012), and to the south by a well-dated record from Lake Tulane, FL (Grimm et al., 2006). Three sites between Anderson and Tulane (Sheelar Lake, FL (Watts and Stuiver, 1980; Watts and Hansen, 1994), Bob Black and Quicksand Ponds, GA (Watts, 1970; Jackson et al., 2000; S.T. Jackson, unpublished)) still have substantial dating uncertainties owing to chronologies based on bulk-sediment ^{14}C dates and low density of dates. Despite these uncertainties, some patterns can be discerned.

At Lake Tulane in the Florida Peninsula, the period preceding the last glacial maximum was characterized by rapid, millennial-scale alternations between vegetation types, with timing of phases corresponding to Dansgaard–Oeschger intervals and Heinrich events (Grimm et al., 2006). The Tulane record shows major changes at ca. 29.5 ka, 26 ka, and 22 ka. Conversely, Jackson Pond shows little change between 31 and 26 ka, when *Picea* increases and *Pinus* decreases rapidly (Fig. 4). The transition at 26 ka appears to coincide with inception of a *Pinus*-dominated phase at Lake Tulane, which is linked to the Heinrich Event H2 (Grimm et al., 2006). However, at Tulane, the period of high *Pinus* abundance is relatively brief, persisting until 23 ka, when *Quercus* and forbs increase again. In contrast, pollen records at both Jackson and Anderson Ponds change relatively little between 25 and 18–19 ka. The apparent quiescence at Jackson Pond before 26 ka and both sites between 25 and 18 ka may result from absence of substantial climate change and variability in this region; peninsular Florida may have been more sensitive to variations in Atlantic thermohaline circulation and Gulf of Mexico sea-surface temperatures than the continental interior (Grimm et al., 2006). However, regional vegetational insensitivity to climate changes that occurred, masking of changes in some taxa by high pollen productivity of *Pinus*, or species-level changes masked by taxonomic smoothing in the pollen record (particularly *Picea*, *Pinus* and *Quercus*) (Jackson and Williams, 2004) may have contributed to the lack of variation at our sites.

Latitudinal patterns of flora and vegetation during the last glacial maximum, and in fact during the entire late Wisconsinan glacial period, remain poorly resolved south of the maximum Laurentide ice margin (Jackson et al., 2000). Understanding of biogeographic and vegetational patterns is obscured not only by paucity of sites, but also by taxonomic smoothing in the pollen record of the three dominant arboreal pollen types: *Picea*, *Pinus*, and *Quercus*. *Picea* pollen shows a clear latitudinal gradient, from absence at Lake Tulane, to trace amounts in presumed glacial-age sediments of Sheelar Lake (Watts and Stuiver, 1980), to low percentages (2–6%) at Quicksand and Bob Black Ponds in NW Georgia (Watts, 1980; Jackson et al., 2000; S.T. Jackson, unpublished data). Well-preserved needles of both *Picea glauca*, a boreal species, and *P. critchfieldii*, a now-extinct species, occur in glacial-age sediments at Bob Black Pond (Jackson and Weng, 1999; Jackson et al., 2000). *Picea* pollen percentages continue to increase to the north (10–30% at Anderson, and 30–45% at Jackson Pond; Figs. 3–4). Needle preservation at the latter two sites was poor, and only *P. mariana* (another boreal species) could be documented. *Pinus* pollen is abundant at all sites, from peninsular Florida to our sites, although percentages taper off at the southernmost (Tulane) and northernmost (Jackson) sites. Macrofossil determinations are lacking at the Florida sites, but needles of *P. banksiana* occurred in glacial-age sediments at Bob Black Pond, as did a few needle fragments of *P. resinosa*, *P. strobus*, and *P. rigida* (Jackson et al., 2000; S.T. Jackson, unpublished data). Only *P. banksiana* was identifiable from Anderson and Jackson Ponds. Based on these data and on pollen-size analyses

(discussed in Jackson et al., 2000), a north–south *Pinus* species gradient occurred, with boreal *P. banksiana* at the northern sites, mixed with temperate and cool-temperate species (*P. resinosa*, *P. strobus*, *P. rigida*) species in NW Georgia, and Florida occupied by temperate, warm-temperate, and subtropical species.

Quercus pollen also shows a strong gradient at the last glacial maximum, from 10–40% at Lake Tulane (Grimm et al., 2006) and 10–25% at Sheelar Lake (Watts and Hansen, 1994) to 5–20% at Bob Black Pond (Jackson et al., 2000; S.T. Jackson, unpublished data) to trace amounts (before 18.5 ka) at Anderson Pond (Fig. 3). Pollen percentages of *Quercus* and other hardwood trees (*Ostrya/Carpinus*, *Fraxinus*, *Ulmus*) are higher at Jackson Pond than Anderson between 25 and 18.5 ka (Figs. 3,4). These elevated percentages of hardwood pollen at Jackson Pond may represent higher regional population abundances, unmasking of hardwood-pollen representation (from regional or distant sources) by lower regional *Pinus* populations, or more abundant local hardwood populations. These hypotheses are difficult to evaluate in the absence of a denser site network or site replication. A regional gradient of increasing deciduous-tree populations north of Anderson Pond seems implausible in view of the strong thermal gradients indicated immediately south of the Laurentide Ice Sheet at the last glacial maximum (Bromwich et al., 2004, 2005). This thermal gradient is consistent with the gradient of decreasing regional *Pinus* populations and increasing *Picea* populations from Anderson to Jackson indicated by our data. *Pinus* pollen productivity and dispersibility is sufficient to dampen pollen representation of other types (Jackson et al., 2000), and hence the elevated percentages of *Quercus* and other deciduous-tree types at Jackson may represent unmasking of pollen from distant sources (e.g., Aario, 1940; Jackson and Smith, 1994). However, *Quercus* pollen occurs consistently at Jackson Pond at ca. 5% between 31 and 19 ka, a period when *Pinus* pollen reached or exceeded 80%. This pattern suggests that the higher *Quercus* abundances at Jackson are not just an artifact of differential degrees of masking between Jackson and Anderson Ponds, and that the higher abundances of hardwood pollen types represent locally abundant populations near Jackson Pond. The occurrence of hardwood populations as far north as Jackson Pond is plausible in view of the occurrence of temperate-tree macrofossils at Nonconnah Creek, TN (discussed in Jackson et al., 2000) and molecular evidence for low-density populations of temperate trees within several hundred km of the ice margin (McLachlan et al., 2005). Small glacial-age populations of temperate deciduous trees have been documented from macrofossils and genetic data in Europe (e.g., Magri et al., 2006), and similar “cryptic refugia” (Stewart and Lister, 2001) likely also occurred in eastern North America.

The pollen records at Anderson and Jackson Ponds show increasing percentages of *Quercus*, *Fraxinus*, and *Ostrya/Carpinus* starting ca. 19 ka (Figs. 3, 4). Percentages of all three taxa increase rapidly at both sites some 3000–3500 yr later (15.9 ka at Anderson Pond; 15.4 ka at Jackson Pond), accompanied by sharp declines in *Pinus* and *Picea* pollen. The apparent earlier occurrence of this transition at Anderson Pond may indicate a time-transgressive pattern, but dating uncertainties near the hiatuses (particularly at Jackson Pond) render this inference tentative. *Acer*, *Ulmus*, and *Carya* increase at Anderson at 15.9 ka; increases in *Carya* and *Ulmus* are recorded in the Wilkins profile from Jackson Pond, but are truncated in our record. A similar pattern of declining conifers (primarily *Pinus*) and increasing hardwoods (especially *Quercus* and *Carya*) is recorded at Quicksand Pond (Watts, 1970) and Sheelar Lake (Watts and Hansen, 1994), but the timing is poorly constrained. Better-dated late-glacial pollen sequences from these sites should help determine whether the late-glacial conifer-to-hardwood transition was a time-transgressive, patchy, or regionally synchronous event.

Regional development of no-analog assemblages

The conifer decline and increase of *Quercus* and other deciduous trees at Anderson and Jackson Ponds at 15.9 to 15.4 ka marks the

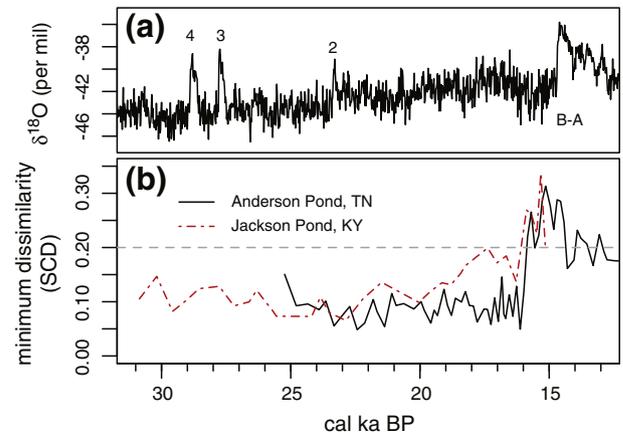


Figure 5. (a) The NGRIP oxygen isotope record (Rasmussen et al., 2006). B-A denotes the Bølling–Allerød interstadial; Dansgaard–Oeschger events 2, 3, and 4 are indicated by number. (b) Minimum vegetation dissimilarity represented as square-chord distance scores (SCD) for Anderson Pond and Jackson Pond. The no-analog threshold (SCD = 0.2, Williams and Shuman, 2008) is shown as the dashed gray line.

emergence of pollen assemblages lacking modern analogs (Fig. 5). The rapidity of the transition suggests that the underlying mechanism was either a rapid forcing event or an intrinsic threshold response to gradual forcing (e.g., Williams et al., 2011). Two kinds of abrupt changes have been identified as late-glacial forcing mechanisms for abrupt vegetational changes in eastern North America: rapid warming at onset of the Bølling–Allerød (Watts and Hansen, 1994), and regional megafaunal decline (Gill et al., 2009, 2012). However, gradual regional warming and northward expansion of hardwood taxa may have led to local non-linear responses. These alternative mechanisms for changes at our study sites can be evaluated by placing the changes in the broader context of climatic, megafaunal, and vegetational changes to the north and south, and to changes recorded in ice-core and marine records.

Development of no-analog vegetation at Anderson and Jackson Ponds occurred ca. 15.9–15.4 ka, clearly preceding the Bølling–Allerød (Fig. 5). Climatic patterns and timing may have been heterogeneous in the North Atlantic region during the last deglaciation (Grimm et al., 2006). Onset of the conifer-to-deciduous transition at Anderson Pond 15.9 ka coincides with a *Pinus* increase at Lake Tulane; the latter event indicates development of warm and wet conditions in peninsular Florida (Grimm et al., 2006). This pattern is consistent with contemporary changes at Anderson, where increases in *Quercus* and *Ostrya/Carpinus* indicate warming and increases in *Abies* and *Fraxinus* and decrease in *Pinus* suggest increasing moisture. These events coincide with Heinrich Event H1, associated with North Atlantic cooling (Stoner et al., 2000). The development of no-analog vegetation at Jackson Pond 15.4 ka also occurred during H1. At both our sites, vegetation did not rebound to a pre-transition state following termination of Heinrich Event H1, in contrast to the Tulane record. Similarly, as discussed earlier, a transition at 26 ka at Jackson Pond coincided approximately with H2. Conceivably, the Heinrich events triggered persistent state-shifts in vegetation deep in the North American continent, although the precise mechanisms remain obscure.

At Appleman and Silver Lakes, onset of no-analog vegetation coincided with a conifer-to-deciduous transition (Gill et al., 2009, 2012), similar to our study sites. However, the northern transitions postdated the transitions at Jackson and Anderson Ponds by nearly 2000 yr. The uppermost dated assemblages at Anderson Pond overlap with the earliest no-analog assemblages at Appleman and Silver Lakes. At approximately 14 ka, *Picea* percentages were higher at the northern sites (40–60%) than at Anderson (10–15%), while *Quercus* percentages were higher at Anderson (>30%, vs. <10% at the northern sites). Percentages of *Ostrya/Carpinus* were modestly higher, and *Fraxinus* lower,

at Anderson. Unfortunately, the evolution and duration of the no-analog assemblages, as well as the timing and pattern of their decline, cannot be assessed at our sites owing to sedimentation truncations.

Formation of no-analog assemblages at Appleman and Silver Lakes (Fig. 1) is associated with a decline in *Sporormiella* spores, a dung-fungus indicator of megafaunal activity (Gill et al., 2009, 2012). *Sporormiella* spores were absent or rare in all samples from our sites, in contrast to Appleman and Silver Lakes, where *Sporormiella* spores were abundant in the portions of the records that overlap with Jackson and Anderson (18.5 ka to 14.6 ka) (Gill et al., 2009, 2012). The near-absence of *Sporormiella* from our sites may indicate different patterns or intensity of megafaunal activity on landscapes in unglaciated terrain. Alternatively, *Sporormiella* representation may have been dampened by differences between the shallow solution-basins we study and the deeper glacial kettles to the north. *Sporormiella* abundance is apparently sensitive to taphonomic processes and depositional settings (Raper and Bush, 2009; Parker and Williams, 2011; Etienne et al., 2012).

Patterns and mechanisms of no-analog vegetation in interior eastern North America have received much attention (Overpeck et al., 1992; Williams et al., 2001; Jackson and Williams, 2004; Williams et al., 2004; Williams and Jackson, 2007; Gill et al., 2009, 2012), yet many questions remain. The 2000-yr difference between onset of no-analog vegetation at our sites and sites in glaciated regions indicates that development of no-analog vegetation was time-transgressive, from south to north, rather than synchronous across the region. Although the transition to no-analog vegetation at our sites coincided with Heinrich Event H1, development of no-analog vegetation was ultimately driven by progressive warming, and not by any particular millennial-scale oscillation. The transition at more northern sites occurred well after inception of the Bølling–Allerød warming; the transition may have been delayed by megafaunal herbivory (Gill et al., 2012). Megafaunal herbivory may have exerted differential effects on vegetation composition in different regions, with dampened influence to the south. Further delineation of spatiotemporal patterns of late-glacial vegetational change in the North American mid-continent, together with application of process-based vegetation models (e.g., Miller et al., 2008) will help assess the relative roles of climate change and megafauna in late-glacial vegetation dynamics.

Conclusions

A general outline of vegetational patterns and transitions during the last glacial period and the glacial-to-interglacial transition in eastern North America is available from existing data networks (Overpeck et al., 1992; Jackson et al., 1997, 2000; Williams et al., 2001, 2004). However, assessment of mechanisms, as well as detailed spatiotemporal patterns, is hampered by uncertainties in chronology of pollen sequences, prompting the collection of a new generation of well-dated records. Our study provides improved chronologies for two previously studied sites. Development of no-analog vegetation at these sites preceded development of no-analog vegetation at sites in formerly glaciated terrain by ca. 2000 yr. The near-absence of *Sporormiella* at our sites, and the coincident appearance of no-analog vegetation at our sites, a *Pinus maximum* in the Florida Peninsula, and onset of Heinrich Event H1, supports a cautious inference that no-analog vegetation was both ultimately and proximately under climatic control, in contrast to sites to the north, where megafaunal consumption may have exerted a proximal limit (Gill et al., 2012). Our study confirms that the late-glacial records at both our sites are truncated by a hiatus that spans not only the later portion of the late-glacial, but most of the Holocene as well. Uncertainty in the nature and timing of vegetational changes may be irreducible in the absence of sites with continuous records of the glacial-to-interglacial transition. Such sites may be scarce or absent from the region, but only a handful of sites have been intensively studied. Continued reexamination of existing sites in the region to develop improved chronologies and searches for new sites will provide a more solid basis for paleoecological inference. Spatiotemporal patterns in this region are currently on a thin foundation,

and conversion of existing sites to “benchmark” sites (Blois et al., 2011) and identification and study of new sites will further reduce uncertainties and strengthen studies aimed at applying lessons from the last glacial-to-interglacial transition to topical questions in ecology, biogeography, and conservation.

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STJ & JWW designed the research. YL, JJA, and STJ collected the data. YL analyzed data with assistance from JJA and STJ. STJ wrote the paper with contributions from YL and JWW.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.yqres.2012.12.005>.

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