

Interpreting basal sediments and plant fossils in kettle lakes: insights from Silver Lake, Michigan, USA

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Abstract: We report on pollen, plant macrofossils, and associated lithostratigraphy of a sediment core extracted from the base of Silver Lake, a kettle lake in northern Lower Michigan, USA, which reveal a complex deglacial scenario for ice block melting and lake formation, and subsequent plant colonization. Complementary multivariate statistical and squared chord distance analyses of the pollen data support these interpretations. The basal radiocarbon age from the core (17 540 cal years BP) is rejected as being anomalously old, based on biostratigraphic anomalies in the core and the date's incongruity with respect to the accepted regional deglaciation chronology. We reason that this erroneous age estimate resulted from the redeposition of middle-Wisconsin-age fossils by the ice sheet, mixed with the remains of plants that existed as the kettle lake formed at ca. 10 940 cal years BP by ice block ablation. Thereafter, the kettle lake became a reliable repository of Holocene-age fossils, documenting a mature boreal forest that existed until 10 640 cal years BP, followed by a pine-dominated mixed forest, an early variant of the mixed conifer-hardwood forest that persists to the present day. Our study demonstrates that researchers investigating kettle lakes, a common depositional archive for plant fossils in deglaciated landscapes, should exercise caution in interpreting the basal (Late Pleistocene/early Holocene-age) part of lake sediment cores.

Key words: deglaciation, Holocene, kettle lakes, Michigan, pollen, radiocarbon dating.

Résumé : Nous rendons compte des pollens, des macrofossiles de plantes et de la lithostratigraphie associée d'une carotte de sédiments extraite de la base du lac Silver, un lac de kettle situé dans le nord du bas Michigan (États-Unis), qui révèlent un scénario de déglaciation complexe pour la fonte de blocs de glace et la formation de lacs, et la colonisation subséquente par des plantes. Des analyses statistiques multivariées et du carré de la distance de cordes complémentaires des données sur le pollen appuient ces interprétations. L'âge au carbone radioactif basal obtenu pour la carotte (17 540 a étal. BP) est rejeté parce qu'il est anormalement vieux, à la lumière d'anomalies biostratigraphiques dans la carotte et de l'incongruité de cet âge par rapport à la chronologie de déglaciation régionale acceptée. Nous interprétons cet âge estimé erroné comme étant le résultat du re-dépôt de fossiles d'âge wisconsinien moyen par l'inlandsis, mélangés aux restes de plantes qui existaient au moment de la formation du lac de kettle vers 10 940 a étal. BP par ablation de blocs de glace. Par la suite, le lac de kettle est devenu un centre de dépôt fiable de fossiles d'âge holocène, qui documentent la forêt boréale mature qui existait jusqu'à 10 640 a étal. BP, suivie d'une forêt mixte dominée par les pins, une variante précoce de la forêt mixte à conifères et feuillus qui persiste à ce jour. L'étude démontre que les chercheurs qui étudient les lacs de kettle, une archive répandue de fossiles de plantes dans des paysages de déglaciation, devraient faire preuve de prudence dans l'interprétation de la partie basale (d'âge pléistocène tardif à holocène précoce) de carottes de sédiments de lac. [Traduit par la Rédaction]

Mots-clés : déglaciation, Holocène, lacs de kettle, Michigan, pollen, datation au carbone radioactif.

Introduction

Researchers are becoming increasingly aware of the challenges and intricacies of reconstructing terminal Pleistocene environments, including elucidating the timing of deglaciation events and the stages of landscape evolution at the end of marine isotope stage 2 (e.g., Jiménez-Moreno et al. 2010; Carson et al. 2018). Much of this research has focused on the final recession of the Laurentide ice sheet of North America from its terminus in northern Ohio and adjacent states, revealing a more intricate sequence of biogeomorphic processes associated with deglaciation than had been originally assumed. One area with complex glacial geology is the Lower Peninsula of Michigan (i.e., Lower Michigan), USA; here, several ice lobes converged, depositing, in places, hundreds of metres of sediment (Schaetzl et al. 2017; Blewett et al. 2018). Con-

sidering the dynamic nature of the Laurentide ice sheet, establishing the chronology of its retreat is challenging.

Wood and other plant macrofossils dated using the radiocarbon (^{14}C) method often provide minimum-limiting ages for deglacial events; e.g., the deposition of moraines associated with ice-sheet recession or the final melt-out of ice blocks in kettles. Key to this procedure is the proper selection of organic materials for ^{14}C dating; they should be derived from terrestrial, not aquatic, plants, because the latter typically incorporate ancient (dead) carbon from ground water in their tissues, and, thus, provide anomalously old ages (Marty and Myrbo 2014). One also has to assume that the material being examined correlates to the geomorphic event that is under study. A few paleobotanical studies have considered the possibility of redeposited terrestrial organics derived from older deposits, as these would provide erroneous ages, usu-

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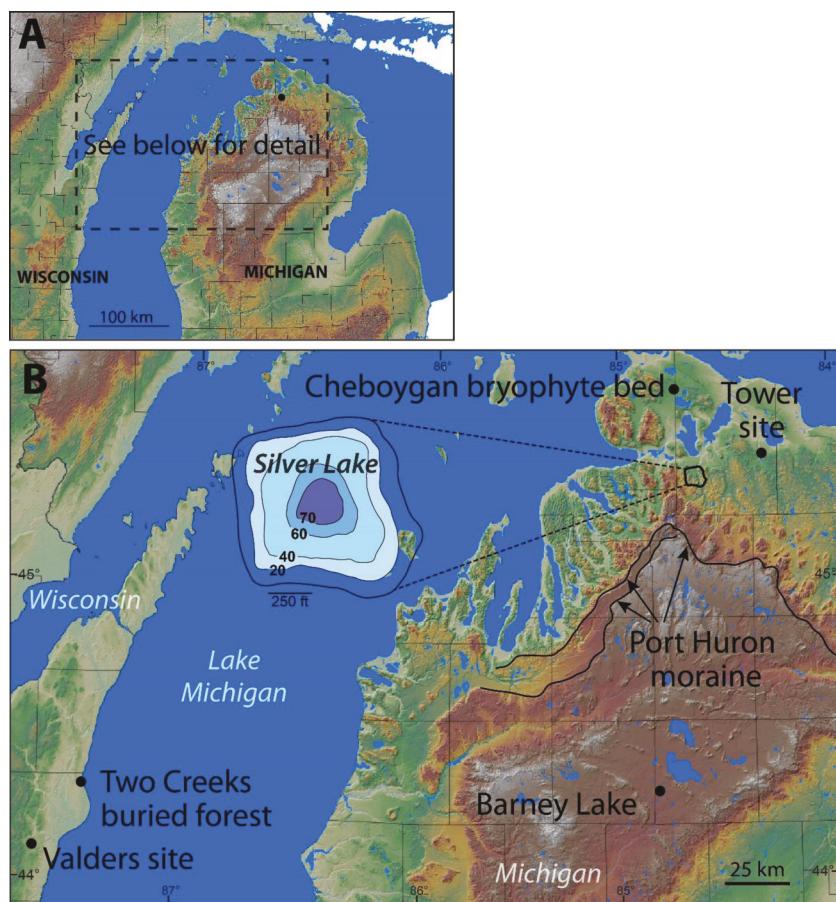
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Fig. 1. (A) Location of study area in northern Lower Michigan, USA. (B) Close-up of study area with location and bathymetry of Silver Lake, as well as the locations of other fossil sites and the Port Huron moraine in the region. [Color online.]



ally dates older than actuality for the timing of sediment (and fossil) deposition (Schirrmeyer et al. 2002; Work et al. 2005). However, none of these prior taphonomic-focused studies involved the paleobotanical analysis of fossils from kettle lakes, which form by topographic inversion as ice blocks melt out, capturing organics from nearby plants during deglaciation.

Numerous researchers have reported on the characteristic trash layer of plant fossils, primarily of *Picea* (spruce), found at the bottom of kettle lakes located in the glaciated portions of the Great Lakes region and adjacent area (e.g., Clayton 1967; Clayton et al. 2001; Watson et al. 2018). However, these studies have not adequately questioned the validity of basal ages obtained by ¹⁴C dating organics from those fossil assemblages, because they overlooked or underemphasized the role of taphonomic processes. This complex melt-out process, moreover, brings into question what the plant remains from trash layers found in the bottoms of kettle lakes are actually dating. Were the plants existing at the time when the kettle lakes finally took form? Or do they date to prior times, when plants grew in sediments overlying the stagnant ice, or even earlier if the glacier eroded plant fossils from buried organic deposits and reworked them during ice melting? Alternatively, do the organics in the trash layer come from a mix of these materials? Our study of the fossil and stratigraphic record of Silver Lake is the first to examine this issue.

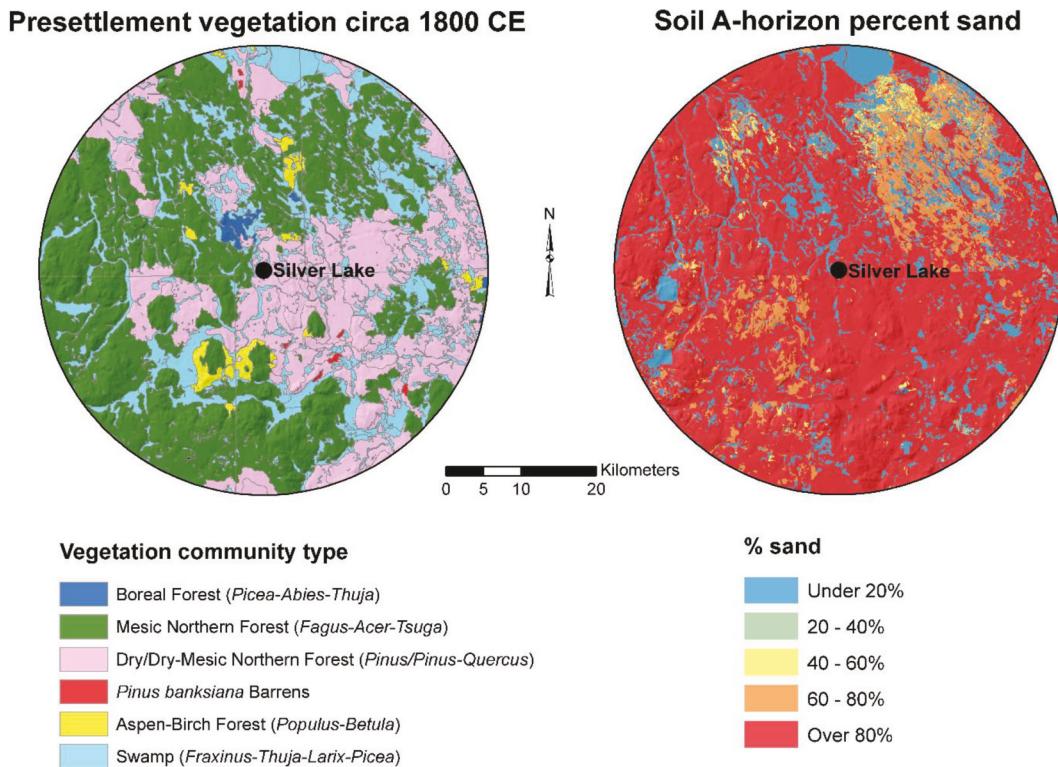
In this paper, we offer a detailed chronostratigraphic and paleobotanical examination of the basal, post-glacial sediments and plant fossils of Silver Lake in northern Lower Michigan with the goals of (1) improving understanding of the depositional processes associated with kettle lake formation and (2) assessing the accuracy of paleobotanical assemblages identified from the basal part

of a kettle lake's record (i.e., the trash layer). Our work documents the complexities of interpreting environmental events from post-glacial deposits in kettle lakes. We also report on multivariate statistical analyses of the Silver Lake pollen data set, non-metric multidimensional scaling (NMS), agglomerative hierarchical clustering (AHC), and squared chord distance (SCD) analysis, which strengthen our paleoecological interpretations. The results are then situated within the context of local and regional deglacial chronologies and paleovegetation records. Because kettle lakes are common fossil repositories in the formerly glaciated areas of the northern USA, Canada, and northern Europe (sites within Neotoma Paleoecological Database 2018), the findings we present provide insights into the interpretation of other paleoenvironmental records archived in the sediments of kettle lakes.

Study area

Silver Lake (45°16.3'N, 84°38.1'W) is a 30-hectare kettle lake in Cheboygan County, 2 km west of the town of Wolverine, in northern Lower Michigan (Fig. 1). It has a surface elevation of 251 m a.s.l. Although it has neither an inlet nor an outlet, it is part of the West Branch Sturgeon River watershed, which drains eastward towards Lake Huron (Godby 2012). Local soils are predominantly sandy, having formed in morainic and other stagnation deposits of coarse-textured sandy tills and glacial outwash (Godby 2012; Fig. 2). The current model of Late Pleistocene deglaciation for the region has the Silver Lake area being deglaciated shortly after the Port Huron re-advance at ca. 15 500 cal years BP (Blewett et al. 1993). Silver Lake is one of several kettle lakes within this interlobate region. Besides kettle lakes, there are several other land-

Fig. 2. Pre-Euro-American settlement vegetation (left) and soil texture (right) within a 30 km radius of Silver Lake. Data source for presettlement vegetation shapefiles: State of Michigan GIS Open Data, “Land Cover Circa 1800”: http://gis-michigan.opendata.arcgis.com/datasets/3269b9e0d086429c8472c508fe5ad6bb_2 (accessed 15 September 2018). Data source for soils shapefiles: United States Department of Agriculture, Natural Resources Conservation Service, Web Soil Survey homepage: <https://websoilsurvey.sc.egov.usda.gov/App/WebSoilSurvey.aspx> (accessed 15 September 2018). Geographic projection for both maps: NAD 1983 Michigan GeoRef (metres). [Color online.]



forms indicating collapse and stagnation topography in this area, as well as thick sequences of glaciofluvial sediments in the form of fans and kame deltas (Blewett et al. 2009; Schaetzl et al. 2017).

Today, Silver Lake is situated within the lake-effect climate belt, induced by lakes Michigan and Huron. This climatic modification accounts for the high annual snowfall (2000–2200 mm) totals found here (Scott and Huff 1996; Henne and Hu 2010). For this latitude, modern summertime precipitation is low compared with elsewhere in the Great Lakes region, with the annual total for precipitation being 750–800 mm (NOAA n.d.; Schaetzl et al. 2018). Temperatures are cool in summer (July mean of 19 °C) and cold during winter (January mean of –8 °C) (NOAA n.d.).

We used Public Land Survey notes and maps to determine vegetation in the Silver Lake area at the time of initial settlement by Euro-Americans. These data (Comer et al. 1995) indicate that a great diversity of forest types existed within a 30 km radius of the lake at ca. 1800 CE (Fig. 2). The most common plant communities at this time were (1) northern mixed conifer-hardwood (deciduous) forests, specifically forests of *Fagus grandifolia* – *Acer saccharum* – *Tsuga canadensis* (beech – sugar maple – hemlock), *Pinus strobus* – *Tsuga canadensis* (white pine – hemlock), as well as *Betula alleghaniensis* – *Tsuga canadensis* (yellow birch – hemlock); and (2) pine forests, specifically *Pinus banksiana* – *Pinus resinosa* (jack pine – red pine), *Pinus strobus* – *Pinus resinosa* (white pine – red pine), and *Pinus strobus*-mixed hardwoods. There was also a stand of *Picea mariana* – *Abies balsamea* – *Thuja occidentalis* (black spruce – balsam fir – northern white cedar) situated ~5 km north of Silver Lake. There were several other small areas of swamp forest as well, specifically scattered communities of *Fraxinus nigra* (black ash), *Thuja occidentalis*, mixed hardwood, and mixed conifer swamp. These same species exist today in this area, although the population and age structure of each species have been altered by 19th

century logging and subsequent forest regrowth (Comer et al. 1995).

Materials and methods

In June 1999, a 575 cm long sediment core was extracted from the bottom of Silver Lake through a 27 m deep water column (Fig. 1) by Chad Wittkop. The core was photographed and archived (MIVS-SL99-1-1K) in cold storage at the Limnological Research Center (LacCore), at the University of Minnesota, Minneapolis, USA, until it was made available for this study. One of us (Catherine Yansa) described the lithology, sampled the core for pollen and plant macrofossil analysis, and stored the samples in refrigeration until analyzed at Michigan State University, East Lansing, USA. This paper reports on plant fossil analysis from 528 to 438 cm in the sediment core; with the sediments below (575 to 528 cm) lacking fossils (Fig. 3). We studied the early postglacial interval of deposition, and not the entire Holocene biostratigraphic record, because our goal was to differentiate allochthonous deposition, i.e., taphonomic processes associated with stagnant ice ablation, from autochthonous (*in situ*) deposition of organic remains of the local vegetation once the lake basin stabilized.

A total of 24 samples (each 50 cm³) were sieved and searched for plant macrofossils, following the protocol of Birk and Birk (1980). Recovery of seeds and other subfossil plant remains was low and sporadic (in reference to sample depth), so they were not plotted, but instead are described in the text. Four strata contained sufficient plant remains to provide a radiocarbon (¹⁴C) chronology (Table 1), although the amount of carbon available for the basal age was near the lower limit so it could not be subdivided based on identified plant remains. All four dated samples were calibrated using CALIB 7.04 (Reimer et al. 2013). We excluded

Fig. 3. Correlation of lithology, lithological units, core photography, and pollen zones (last from Fig. 4). (A) Close-up photograph of the basal sediments showing rip-up clay pieces. (B) Close-up photograph of the 518–510 cm strata that produced the 17 540 cal years BP date. (C) Box-and-whisker plots of the calibrated ages associated with the Bacon age-depth model (Blaauw and Christen 2011) for the Silver Lake core. (D) Age-depth modeling (grey shading) with calibrated ^{14}C dates (see Table 1), represented as probability distributions for individual age estimates (in purple); darker grey = more robust age estimates; stippling = 95% confidence interval; and red = best-fit line. (E) Markov Chain Monte Carlo iterations. (F) Accumulation rates. (G) Memory (autocorrelation strength; green curves = prior distributions; grey histograms = posterior distributions). [Color online.]

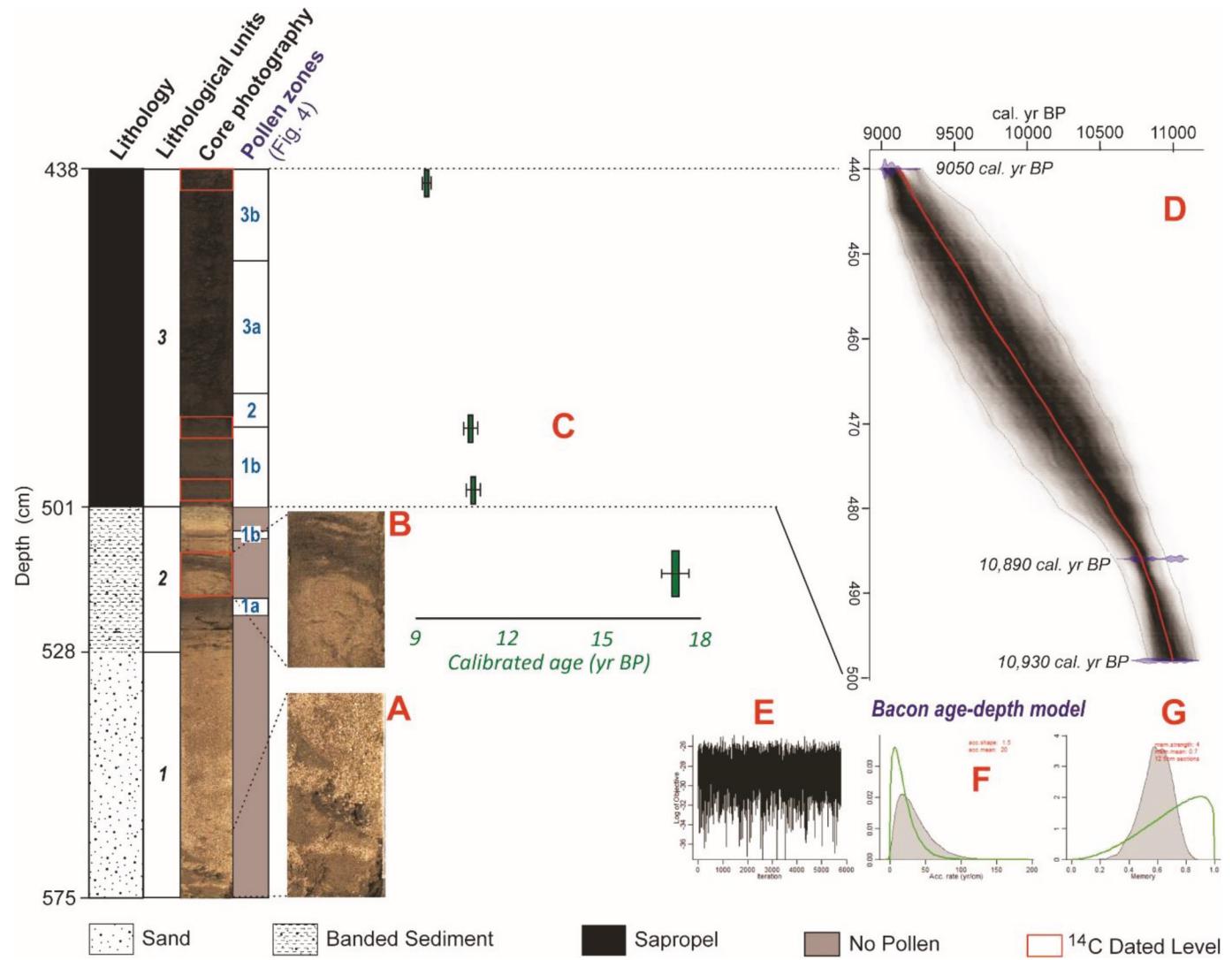


Table 1. Radiocarbon dates and their calibrated ages from the Silver Lake core samples.

Depth (cm)	Uncorrected ^{14}C year BP ^a	Calibrated 2-sigma age range ^b	Mean cal age BP	Lab No.	Plant materials used for dating (mg carbon, dried)
438–442	8120±25	9006–9095 (92%) ^c	9050	UGAMS 30952 ^d	1 <i>Abies balsamea</i> seed, small charcoal fragments (2.1)
484–488	9530±30	10 708–11 073 (100%) ^c	10 890	UGAMS 29168 ^d	1 <i>Picea glauca</i> seeds, 1 <i>Picea mariana</i> seed, 1 fragment of <i>Picea</i> seed, 1 charred <i>Picea</i> needle, wood fragments (2.9)
496–500	9590±30	10 763–11 106 (100%) ^c	10 930	UGAMS 30951 ^d	1 <i>Picea</i> needle, 3 <i>Potentilla</i> seeds, small wood fragments (1.8)
510–518	14 390±100	17 226–17 848 (100%)	17 540	CAMS 175419 ^e	2 <i>Dryas</i> leaves, 1 <i>Ranunculus</i> seed, 1 <i>Betula</i> fruit wing, 2 <i>Picea</i> twigs, 1 small charcoal fragment (0.7)

^aAll dated samples had a $\delta^{13}\text{C}$ of -25.

^bDates (^{14}C) for all four samples were calibrated using CALIB 7.04, with the ranges shown (92%–100%) have the highest likelihoods. CALIB 7.04 is based on the IntCal13 calibration curve (Reimer et al. 2013).

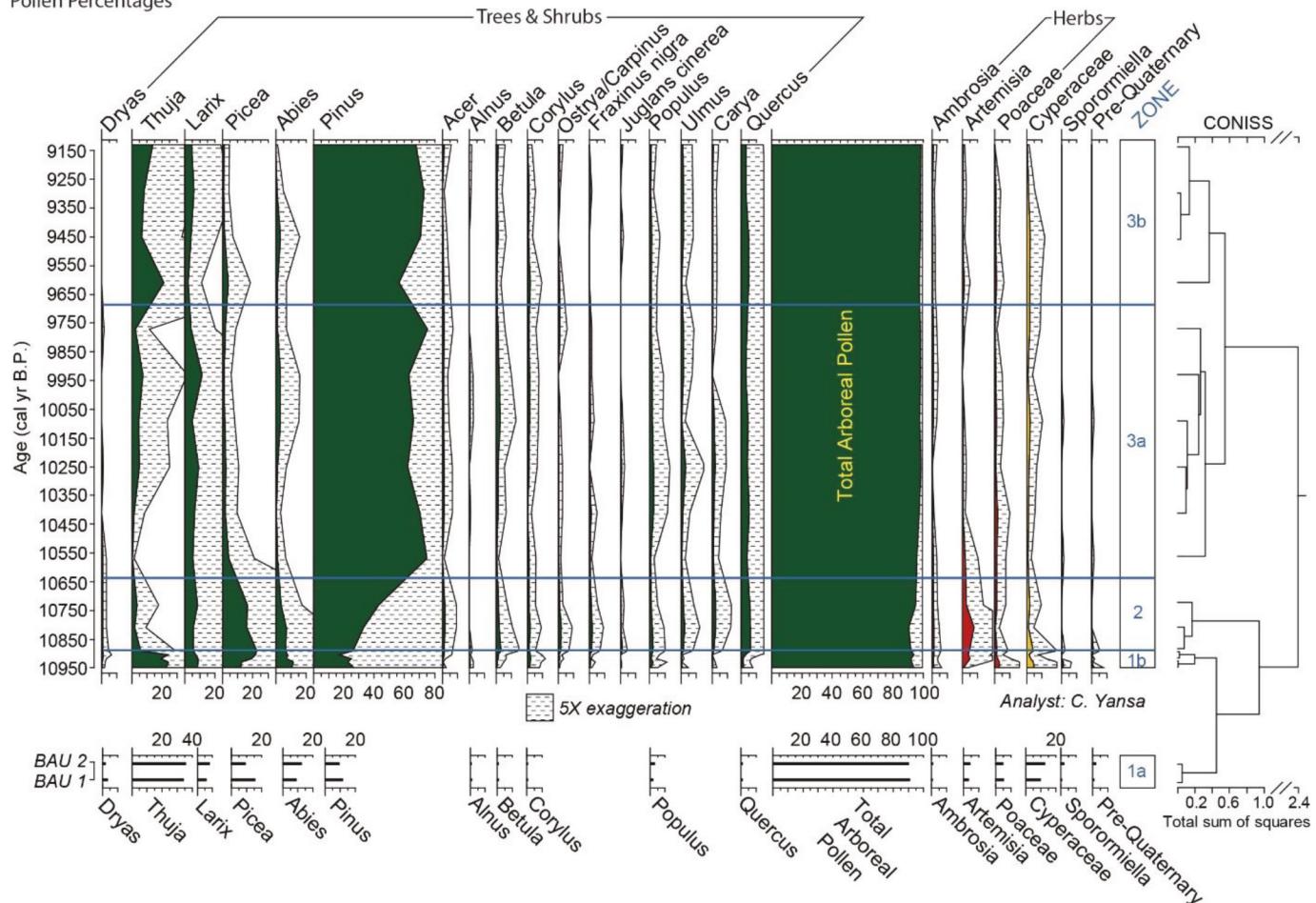
^cThe age model is based on these three calibrated ages. Bacon software was used to create this model, based on the IntCal13 calibration curve (Reimer et al. 2013).

^dUGAMS = Center for Applied Isotope Studies, University of Georgia AMS Laboratory, Athens, Georgia, USA.

^eCAMS = Center for Accelerator Mass Spectrometry, Lawrence Livermore National Laboratory, Livermore, California, USA.

Fig. 4. Pollen percentage diagram for the Silver Lake core. Bar graphs were used to plot the two pollen samples comprising Zone 1a, instead of silhouettes (Zones 1b, 2, and 3), to improve the readability of this basal zone in the diagram. Ages were not assigned to the Zone 1a samples; instead they are referred to as basal unknown age-estimate (BAU 1 at 520 cm depth) and BAU 2 (at 518 cm depth). [Color online.]

Silver Lake, Cheboygan Co., Michigan
Pollen Percentages



the basal age of $14\,390 \pm 100$ ^{14}C years BP from age-depth modeling, because we considered it erroneous (see below). This modeling, therefore, was performed on the three other dates using the Bacon 2.3.3 software package (Blaauw and Christen 2011). Bacon employs Bayesian statistics to divide a core into numerous small vertical segments and performs repeated Markov Chain Monte Carlo iterations to estimate sedimentation time ($\text{year}^{-1} \cdot \text{cm}^{-1}$) for each segment, which collectively form a core's age-depth model. For this study, default settings of 5 cm thickness and a mean accumulation rate of $20 \text{ year}^{-1} \cdot \text{cm}^{-1}$ were used.

The calibrated ages of the four samples (levels) obtained using CALIB 7.04 software, are comparable with the age estimates for strata between the dated levels acquired using Bacon software, because both programs are based on the same IntCal13 calibration curve (Reimer et al. 2013). Additionally, we propose that our use of two different AMS ^{14}C dating facilities, namely the Center for Accelerator Mass Spectrometry (CAMS; Lawrence Livermore National Laboratory, Livermore, California, USA) for the basal date ($14\,390 \pm 100$ ^{14}C years BP; 17 540 cal years BP) and the University of Georgia AMS Laboratory (UGAMS; Athens, Georgia, USA) for the three younger ^{14}C ages, does not account for any error. Our justification is that both laboratories have excellent reputations for producing accurate results that are periodically cross-validated with other AMS labs (Norton 2011). Additionally, the ^{13}C values of all four dates are the same (−25; Table 1), suggesting that the ^{14}C ages are directly comparable.

Additionally, 24 pollen samples (each 0.5 cm^3) were analyzed using a series of chemical treatments to remove sediment and debris and to concentrate the pollen and spores (Faegri and Iverson 1975). Per sample, a minimum of 300 (mean = 378) grains of upland tree and herb pollen (excluding Cyperaceae and other aquatics) were counted and identified, based on McAndrews et al. (1973) and the modern pollen collection in the Pollen Laboratory at Michigan State University. Pollen percentage data were plotted using Tilia 1.7.16 (Grimm 2011; Fig. 4), and the CONISS cluster-analysis application within Tilia identified the pollen zones. Plant taxonomy, ecology, and range distributions are based on Voss (1972), unless otherwise noted. Most pollen grains were identified to genus, with species-level taxonomic precision inferred where only one of the species lives in the Great Lakes region (*Larix laricina* (tamarack) and *Abies balsamea*), and where ecology identified the most likely candidate of related species (e.g., Cupressaceae pollen inferred as *Thuja occidentalis* (Parent and Richard 1990)). Where possible, some of the *Picea* pollen were differentiated between *Picea glauca* and *Picea mariana*, and the *Pinus* pollen were partitioned into *Pinus strobus* or *Pinus banksiana/Pinus resinosa*.

Raw pollen count data were analyzed using two complementary multivariate statistical methods commonly used in terrestrial plant ecology: (1) AHC (Peck 2016); and (2) NMS (Kent 2012), using the PC-ORD 6.19 statistical software package (McCune and Mefford 2011). The AHC analysis was conducted on pollen taxa to group them into discrete vegetation assemblages, irrespective of

chronology; these results were also used to verify the CONISS clustering of the dated pollen sampling units. The AHC analysis was accomplished using a Ward's Method sorting strategy on a matrix of Pearson product-moment correlation coefficients (r) between pollen taxa abundances and across stratigraphic levels. Terminology for vegetation community types identified in the Silver Lake pollen record and having a modern regional analog follows [Dickmann \(2004\)](#).

Biplots of NMS species scores, dated stratigraphic units, and AHC community types were generated to infer relationships between underlying paleoenvironmental gradients and major vegetation assemblages. NMS scores were plotted chronologically to ordinate pollen taxa along major paleoenvironmental gradients modulating Late Pleistocene–early Holocene forest dynamics. NMS uses rank-order information within a (dis)similarity matrix between taxa and sampling units to reduce data dimensionality to 1–6 synthetic axes (k -space) in which distances between taxa and sampling units have the same rank-order as in the original (dis)similarity matrix ([Kent 2012](#)). Goodness-of-fit between rank-orders in the k -space ordination and the (dis)similarity matrix is determined through a corresponding stress value (range 0–100), with values <20 generally indicating a stable, interpretable ordination ([Clarke 1993](#)). Pollen count data were relativized using a square-root (Hellinger) transformation prior to statistical analysis ([Legendre and Gallagher 2001](#)), to down-weight the overly common taxa while still preserving the proportional relationships among the taxa. To estimate the proportion of the total variance in the Silver Lake pollen data explained by each NMS axis, coefficients of determination (r^2) were calculated between the Relative Euclidean distance in the original, unreduced species space and Euclidean distance in the NMS ordination space. Finally, pollen frequencies from modern lake and wetland surface samples within the Great Lakes region and adjacent northeastern North America ($n = 1609$; [Whitmore et al. 2005](#)), obtained from the [Neotoma Paleoecological Database \(2018\)](#) were used to determine modern pollen analog sites for each stratigraphic unit of the Silver Lake pollen record. A SCD ([Gajewski 2015](#)) dissimilarity matrix was generated from the Hellinger-transformed pollen data using XLSTAT Version 2014.5.03 software ([Addinsoft 2014](#)). We selected and plotted the three modern pollen sites having the smallest SCD dissimilarity values as representing the closest analogs for each corresponding pollen sample, with associated calibrated dates derived from the core's age-depth model.

Results and interpretations

Core lithostratigraphy

[Figure 3](#) shows the core lithology and interpretation of three lithological units, which roughly correlate to the three major pollen zones ([Fig. 4](#)) described below. Unit 1 (575–528 cm) is coarse sand with isolated clay pieces (1–5 cm diameter) that appear “ripped up”. The clay was likely deposited in a pool overlying a sandy till-covered ice block, and upon ice ablation the clay pieces were re-bedded with sand at the bottom of Silver Lake. Unit 1 sediments lack plant fossils, and a gradual boundary separates this lithological unit from the overlying one. Unit 2 (528–501 cm) is banded, composed of several very thin organic lens within predominately coarse sand. This unit represents the final stage of ice ablation, culminating in the formation of Silver Lake, with the organics laid down between short pulses of sand deposition within the basin. This unit contained no pollen grains (as expected given that pollen is silt-sized), but did yield some plant macrofossils, enough to provide one ^{14}C dating sample at 518–510 cm ([Table 1](#)). The three pollen samples (520, 518, and 506 cm) analyzed from Unit 2 sediments came from two thin layers of clayey, silty sand containing fine plant fragments ([Fig. 3](#)). Unit 3 is a massive, black diatomaceous silty sapropel that extends from 501 cm (abrupt contact) to the top of the core. The lithology

of Unit 3 indicates that Silver Lake became a quiet deposition basin at 10 940 cal years BP (age estimate for 501 cm). To confirm this assumption, we analyzed plant fossils from 21 levels, up to 438 cm (dating to the early Holocene), to correlate to the pollen spectra of other sites in the Great Lakes region, where agreement indicates landscape stability and in situ fossil deposition at Silver Lake.

Pollen and plant macrofossil abundance data

Zones 1a (age?; 520–518 cm) and 1b (10 940–10 890 cal years BP; 506–486 cm)

Several lines of evidence suggest that the sediments and fossils of Zone 1a ([Figs. 3 and 4](#)) are a mixture of materials of different ages. The most probable explanation being that older plant remains originally incorporated into the glacier ice were later redeposited, along with those of the vegetation living at the time the kettle lake formed, by ca. 10 940 cal years BP. We assign this date, for the beginning of an intact fossil record in Silver Lake, based on an age model estimate for the onset of sapropel deposition at a core depth of 501 cm (base of Unit 3, [Fig. 3](#)). This age approximation seems reasonable given we obtained a ^{14}C date of 10 930 cal years BP for a depth immediately above (500–496 cm; [Table 1](#)). Silver Lake was probably established sometime before this time, but we were unable to ascertain when, and hence use 10 940 cal years BP as a minimum limiting age.

We reject the basal age of 17 540 cal years BP ($14\ 390 \pm 100\ ^{14}\text{C}$ years BP; core depth of 518–510 cm; [Table 1](#)) because (1) the date is >2000 years too old with respect to its geographic occurrence ([Blewett et al. 1993; Blewett and Winters 1995](#); see discussion below); and (2) the stratigraphic placement of this dated level is anomalous with respect to the three dates obtained for strata upcore ([Fig. 3](#)). Specifically, the mere ~ 18 cm of the core between the dated samples of 17 540 and 10 930 cal years BP (base of Zone 1b; [Table 1](#)) represent a short amount of time, definitely not 6660 cal years as suggested by the difference in these ^{14}C dates. We further reason that significantly more sediment (several metres) would have accumulated in the lake basin during six millennia, especially during the transition from a glacial to post-glacial environment. [Schaetzl \(2008\)](#) provided evidence of widespread landscape instability on sandy landforms across northern Lower Michigan, including the Silver Lake area, in the form of extensive permafrost melting, runoff, and gully development during immediate post-glacial times.

We attribute the late establishment of Silver Lake at 10 940 cal years BP to the prolonged melting of the ice block to create this lake. Geologic mapping and dating by [Attig and Rawling \(2018\)](#) indicate that ice block ablation in north-central Wisconsin, USA, took several millennia, given the considerable thickness (initially at least 35 m) of these ice blocks. The ice block that formed Silver Lake may have been of comparable thickness, given that its current water depth is 27 m, and >5 m of postglacial sediment were subsequently deposited into this closed basin. After factoring in the melting process, we interpret the study area as being deglaciated a few millennia before 10 940 cal years BP. This ablation was slowed by the ice blocks (including the one that created Silver Lake) being fully or partially covered by an insulating layer of till, which over time was colonized by plants. This reconstruction is well accepted by glacial geologists and paleoecologists (e.g., [Clayton 1967; Clayton et al. 2001; Yansa 2006; Curry et al. 2010](#)) and is backed by modern observations of vegetated glacier forelands ([Fickert et al. 2007; Walker et al. 2010](#)). These researchers also proposed that the remains of these plants, rooted in till overlying stagnant ice, were redeposited as trash layers at the bottom of kettle lakes during the topographic inversion that created knob-and-kettle, hummocky topography.

Additionally, the biostratigraphy of Zone 1a and the lower part of Zone 1b (Unit 2, [Fig. 3](#)) indicate allochthonous deposition during

formation of this lake, as evidenced by (1) the presence of organic stringers within sand, suggestive of rapid sedimentation and (2) the taxonomic composition of the fossils within these stringers (samples at 520, 518, and 506 cm; Fig. 4). These samples contain pre-Quaternary palynomorphs (as described by Nambudiri et al. (1980) and Yansa et al. (2007)), which were likely unearthed from Paleozoic carbonate bedrock and incorporated into the glacial sediment flooring the lake. Also, *Sporormiella* (dung spores; 0.4%–1.9%) indicate the inclusion of materials pre-dating 13 000 cal years BP, given that these spores drastically decline in lacustrine sediment core records after the megafaunal extinction that occurred in North America around that time (Feranec et al. 2011; Gill et al. 2012). Given that we were unable to assign accurate ages for these samples, we refer to them as “basal unknown age-estimates” (BAUs), with BAU 1 indicating the 520 cm pollen sample and BAU 2 representing the 518 cm sample with the erroneous ^{14}C date.

We were unable to identify which of the plant fossils in the Zone 1a dating sample (518–510 cm; BAU 1) comprised the older component of the date. However, our observations point to a mingling of older tundra fossils with contemporaneous boreal forest plant remains when Silver Lake formed sometime before 10 940 cal years BP. Based on both fossil and modern ecological contexts (Curry and Yansa 2004; Blinnikov et al. 2011; Williams et al. 2011), we are suspicious of the *Dryas integrifolia* (arctic avens) fossils; the six leaves scattered from 518–500 cm, counting the two included in the 17 540 cal years BP dating sample (Table 1), and the pollen of this taxon in Zones 1a (1.9%–3.4%) and 1b (0.4%–0.8%) (Fig. 4). According to vegetation succession, *Dryas integrifolia*, being an arctic plant, would have existed in a tundra before the arrival of *Picea* trees; although, both *Dryas* and *Picea* can co-exist in forested tundra, a transitional vegetation phase between tundra and succeeding boreal forest. The fossil remains of *Dryas integrifolia*, however, are too few in number to indicate a forested tundra, which suggests that these fossils, and possibly some portion of the other non-arbooreal taxa (*Artemisia* (wormwood), *Ambrosia* (ragweed), and *Poaceae* (grass family) pollen grains), predate the tree fossils. A likely scenario is that *Dryas* and other arctic plants colonized the area during ice block ablation, with some of their materials preserved in shallow water created by melting ice, and later redeposited along with extant remains of the surrounding boreal forest into the newly created Silver Lake. Possibly, there was an additional source, of even older materials, in the amalgamation of carbon materials dated from the base (518–510 cm) of the core, which is discussed below, in the context of the regional fossil record.

Importantly, all of the conifers identified in Zones 1a and 1b (Fig. 4) exist in the study area, today (Dickmann 2004) and at the time of the ~1800 CE land surveys (Comer et al. 1995), within small, presumably remnant, patches consisting of low-lying areas within the hemlock – northern hardwood forest. The strong presence of *Thuja occidentalis* (~34% in Zone 1a, declining from 22.6% to 5.8% in Zone 1b) and *Abies balsamea* (~11% in Zone 1a, decreasing from 10.8% to 6.7% in Zone 1b), and the moderate pollen values of *Picea* (ranging from 9.2% to 22.6% in Zones 1a and 1b), indicate that a mature boreal forest existed during the early Holocene. *Picea mariana* likely inhabited lowland swamps along with *Thuja occidentalis* and *Larix laricina*, whereas upland mesic sites were probably dominated by *Picea glauca* (white spruce) and *Abies balsamea*, based on modern forest composition (Ritchie 1987; Dickmann 2004). *Picea* needles in both zones and a few seeds of *Abies balsamea* in Zone 1b confirm the local presence of these conifers, and a seed of *Lychnis* sp. (formerly called *Silene* sp., rose campion), also indicates a forested environment (Ritchie 1987). The closest modern analog for our interpretation of Zones 1a and 1b would be the southern/central boreal forest of southern Ontario and Quebec, Canada (described in Sirois 1997), and, by inference, the early Holocene climate of the study area would have been slightly colder than at present.

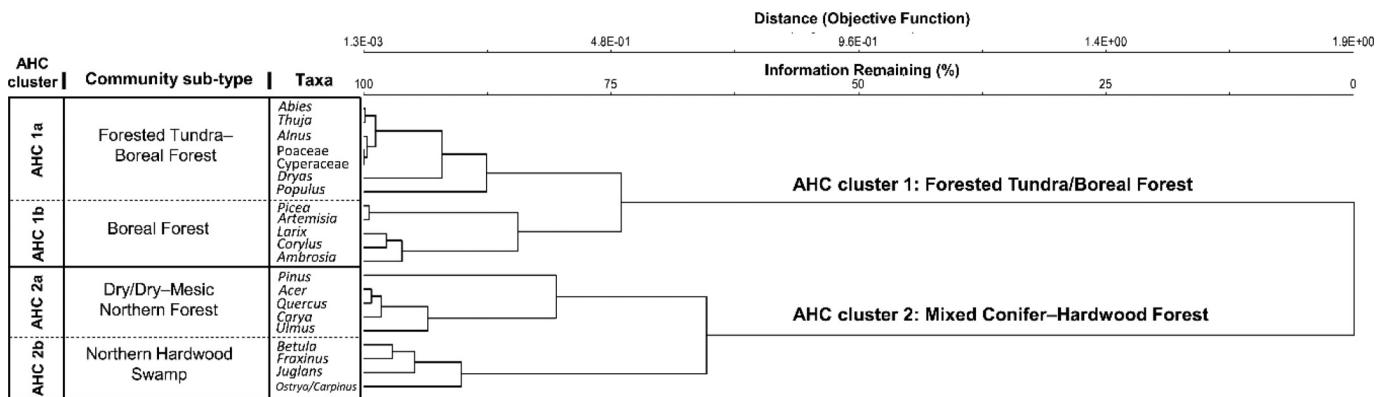
A caveat is our recognition that the vegetation reconstructed for Zones 1a and 1b (Fig. 4) was not an exact facsimile of the modern boreal forest, due to the absence of certain late-migrating trees. This provides another example of a novel plant community, lacking an exact modern counterpart, established during the Late Pleistocene and early Holocene in northern North America (first identified by Williams and Jackson 2007). For example, the values for *Pinus* (averaged 26% in Zone 1b) are considered low, after accounting for pine species substantially overproducing wind-dispersed pollen with respect to their actual abundance in a local flora (Birks and Birks 1980). Most of the pollen grains of *Pinus* and several deciduous arboreal taxa identified in Zones 1a and 1b were probably wind-transported to Silver Lake from trees living to the south. Research by Schaetzl et al. (2016) concluded that strong winds, particularly from the east and southeast, prevailed during the Late Pleistocene and earliest Holocene across the central (including the Silver Lake area) and northern Great Lakes region. One *Betula* (birch) wing found in Zone 1a (Table 1), and a few bracts of *Populus* (poplar/aspen) occur at 470 cm (10 250 cal years BP) and occasionally at levels upcore, do, however, confirm the local presence of these boreal hardwoods.

The local presence of open water and wetlands is also evident from fossil analysis of the basal sediments of Silver Lake, as expected for the landscape context. A fruit of *Stuckenia filiformis* subsp. *filiformis* (fineleaf pondweed), a submerged aquatic pioneer, was recovered from Zone 1a sediments. The existence of wetland/shoreline vegetation is verified by pollen of *Cyperaceae* (an aquatic-emergent plant family composed of sedges and bulrushes) in both Zones 1a (9.7%–12.7%) and 1b (1.5%–5.0%), and a seed of *Carex* sp. (sedge) found within the bottommost zone. The relatively low fossil abundances of these taxa suggest that the proportion of the Silver Lake area covered by wetland was likely low. Rather, the landscape at this time is best described as a closed-canopy boreal forest lacking pine and some of the temperate deciduous hardwood species, which arrived during the subsequent zone.

Zone 2 (10 890–10 640 cal years BP; 486–480 cm)

The rest of the Silver Lake pollen record bears no overt signs of taphonomic disturbance. Viewing Fig. 4 at face value, the boreal forest phase at Silver Lake began at 10 890 cal years BP, at the base of Zone 2. However, above we reasoned that this phase began earlier, before 10 940 cal years BP during Zone 1b. An earlier onset, and hence, longer duration of boreal forest at the study site seems more realistic, in terms of the timing of plant succession, than the duration of just 250 years implied by Zone 2. Overall, this zone is distinguished by the following: (1) a sharp decline in the pollen values for *Thuja occidentalis*, a drought-sensitive wetland tree (Housset et al. 2015); (2) a dramatic increase in pollen counts for the drought-tolerant *Pinus*, mainly of *Pinus banksiana*/*Pinus resinosa*, with some *Pinus strobus*; (3) a gradual decrease in *Cyperaceae* (sedge wetland taxa); and (4) the peak abundance of herbaceous pollen. Nonetheless, the vegetation at this time was still predominately arboreal. *Picea*, *Abies*, and *Larix* values remained high throughout Zone 2, as did pollen percentages indicating the local presence of *Ulmus* (elm), *Betula*, and other deciduous hardwoods adapted to mesic and hydric soils. Normally, these pollen spectra would indicate reduced precipitation from 10 890 to 10 640 cal years BP, compared with before. Instead, the strong representation of bog conifers and increased values of pine suggest that the local boreal forest was adjusting to the arrival of *Pinus*, which at this time became an important constituent of subsequent upland vegetation. This interpretation is supported by reconstruction of a cool and moist climate at this time, based on multi-proxy records from numerous other sites in the northern mid-latitudes (Voelker et al. 2015; Shuman and Marsicek 2016), which conflicts with the conventional interpretation of *Pinus* as a xeric taxon (Birks and Birks 1980; Ritchie 1987).

Fig. 5. Agglomerative hierarchical clustering (AHC) dendrogram of the Silver Lake pollen data partitioned into inferred modern plant communities (as defined by Dickmann 2004).



Zone 3 (10 640–9130 cal years BP; 480–442 cm)

The CONISS plot in Fig. 4 shows a major change in the pollen spectra from Zone 2 to Zone 3a at 10 640 cal years BP, which we interpret as the shift from boreal forest to a pine-dominated, mixed conifer-hardwood forest. Compared with older zones, the pollen values of *Pinus* are considerably higher (56.5%–75.2%) in Zone 3, concurrent with drastic declines of *Picea* and *Abies*; there are no significant percentage increases of the deciduous arboreal taxa. The decline of *Picea glauca* pollen in Zone 3 of Silver Lake suggests that the average summer temperature then probably exceeded 18 °C, because white spruce recruitment is inhibited above this temperature (Ritchie 1987). In contrast, *Picea mariana* can tolerate warmer summers, because it is thermally buffered by residing in the cooler microclimates of swamps (Dickmann 2004). Thus, we interpret the spruce pollen in Zone 3 as coming mainly from *Picea mariana*. A spike of *Thuja occidentalis* pollen at 9605 cal years BP is the most significant excursion in Zone 3, contributing to the differentiation of Zones 3a (10 640–9690 cal years BP, 480–456 cm) and 3b (9690–9130 cal years BP, 456–442 cm). This pollen peak of northern white cedar may indicate greater moisture, because it is a swamp tree, or, alternatively, water table lowering during droughts expanded the area of shallow wetland around lake margins.

The pollen data of these zones record shifts of *Pinus* (xeric soil indicator) vs. *Thuja*, *Larix*, *Picea*, and *Abies* (mesic/hydric taxa); however, these fluctuations were not pronounced enough to have altered the species composition of the pine-dominated mixed forest at this time during the early Holocene. These taxa, we reason, partitioned the landscape according to their soil moisture preferences to form distinct communities, as observed in the ~1800 CE public land surveys (Fig. 2) and today. Scant macrofossils confirm the local presence of *Larix* (a needle found at 450–446 cm), *Populus* (bracts at several levels), and *Picea* (seed wing fragments recovered in a few samples). Additionally, a few pollen grains and one seed of *Typha latifolia* (cattail) found in Zone 3 (not plotted) indicate the local presence of marsh vegetation, as seen today.

Zone 3 provides another interesting case of a non-analog vegetation, typical for other pollen records dating to this time throughout the region (Williams and Jackson 2007; Shuman and Marsicek 2016). Specifically, this zone represents a transitional stage in the development of a mixed conifer-hardwood forest. Compared with the modern version of this forest, Zone 3 pollen contained lesser numbers of *Acer saccharum* (sugar maple) and *Betula alleghaniensis* (yellow birch). Today, these mesophytic taxa are highly dependent upon heavy snowfall to offset living on well-drained sandy soils in the study area (Dickmann 2004). The lake effect snows also reduce spring-season fires, which are detrimental to *Acer* and *Betula* trees (Cleland et al. 2004; Schaetzl et al. 2018). However, the lake-effect climate was not in place until

sometime between 9500 and 5500 cal years BP in northern Lower Michigan, when the Great Lakes became large enough to impact the climate downwind (Rea et al. 1994; Lewis et al. 2007; Henne and Hu 2010; Lewis 2016), and thus could support greater populations of sugar maple, yellow birch, and other fire-intolerant, mesophytic arboreal species.

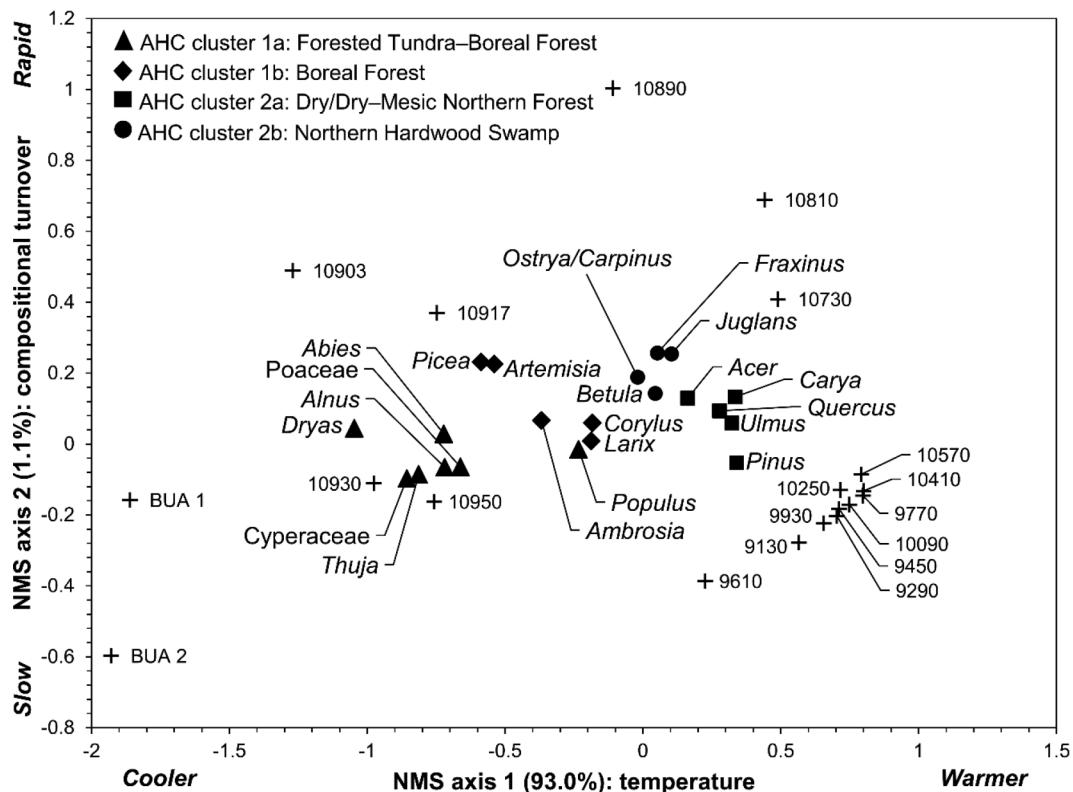
A more significant difference in the pollen interpretation of Zone 3 is the absence of two species that dominate the modern mixed conifer-hardwood forest, *Tsuga canadensis* (hemlock) and *Fagus grandifolia* (beech). These tree species did not arrive until later (9000–6800 cal years BP) in the Great Lakes region, although the exact timing varies by location and is explained by delays in developing a suitable microclimate for hemlock, and the slow dispersal rate of beech seeds (Davis et al. 1986; Calcote 2003). We interpret the occasional pollen grains of *Tsuga* and *Fagus* in Zone 3 as long-distance dispersal from populations, as these species were migrating northwards towards Silver Lake, but had not yet arrived. We further reason that the pine species (*Pinus strobus*, *Pinus banksiana*, and *Pinus resinosa*) occupied not just the sandy upland sites, but also mesic sites where later they would be outcompeted by shade-tolerant, late-successional species, including hemlock, beech, sugar maple, and yellow birch. Additionally, a reduction of precipitation at this time, as reconstructed from other paleoenvironmental records in the region (Booth et al. 2004; Henne and Hu 2010; Shuman and Marsicek 2016), also likely contributed to *Pinus* dominating the pollen spectra of Zone 3 at Silver Lake.

Statistical analysis of raw pollen data

AHC (Fig. 5) partitioned the Silver Lake pollen data into two primary vegetation assemblages: (1) forested tundra-boreal forest (AHC cluster 1); and (2) mixed conifer-hardwood forest (AHC cluster 2). AHC cluster 1 was further subdivided into two minor vegetation types: AHC cluster 1a of *Abies*–*Thuja*–*Alnus*–*Poaceae*–*Cyperaceae*–*Dryas* interpreted as forested tundra-boreal forest; and AHC cluster 1b composed of *Populus*–*Picea*–*Artemesia*–*Larix*–*Corylus*–*Ambrosia* classified as boreal forest. AHC cluster 2 was similarly subdivided into two secondary vegetation community types: AHC cluster 2a of *Pinus*–*Acer*–*Quercus*–*Carya*–*Ulmus* considered indicative of a dry/dry-mesic northern forest; and AHC cluster 2b of *Betula*–*Fraxinus*–*Juglans*–*Ostrya*/*Carpinus* interpreted as northern hardwood swamp.

NMS (Fig. 6) arrived at a two-dimensional solution with a final stress value of 1.1, well below Clarke's (1993) suggested upper limit of 20, indicating an extremely robust ordination. NMS axis 1 explained 93.0% of the total variance in the Silver Lake pollen data, separating pollen taxa indicative of a forested tundra environment including *Dryas* (−1.047), *Cyperaceae* (−0.856), *Thuja* (−0.813), and *Abies* (−0.723), from those associated with warmer/drier envi-

Fig. 6. Non-metric multi-dimensional scaling (NMS) of the Silver Lake pollen data. Symbols indicate those taxa clustered within each of the four agglomerative hierarchical clustering (AHC) cluster subtypes, and crosses show the placement of calibrated ages for pollen samples. Note: Zone 1a samples basal unknown age-estimate (BAU 1 at 520 cm depth) and BAU 2 (at 518 cm depth, with the erroneous age of 17 540 cal years BP) are outliers with regard to other dated pollen samples.



ronmental conditions, such as *Pinus* (0.341), *Carya* (0.335), *Ulmus* (0.323), and *Quercus* (0.279). NMS axis 2 explained an additional 1.1% of the total variance in the pollen data, with high scores on *Fraxinus* (0.257), *Juglans* (0.254), *Picea* (0.232), and *Artemisia* (0.225). Figure 5 also shows these taxa arranged into the four AHC cluster subtypes.

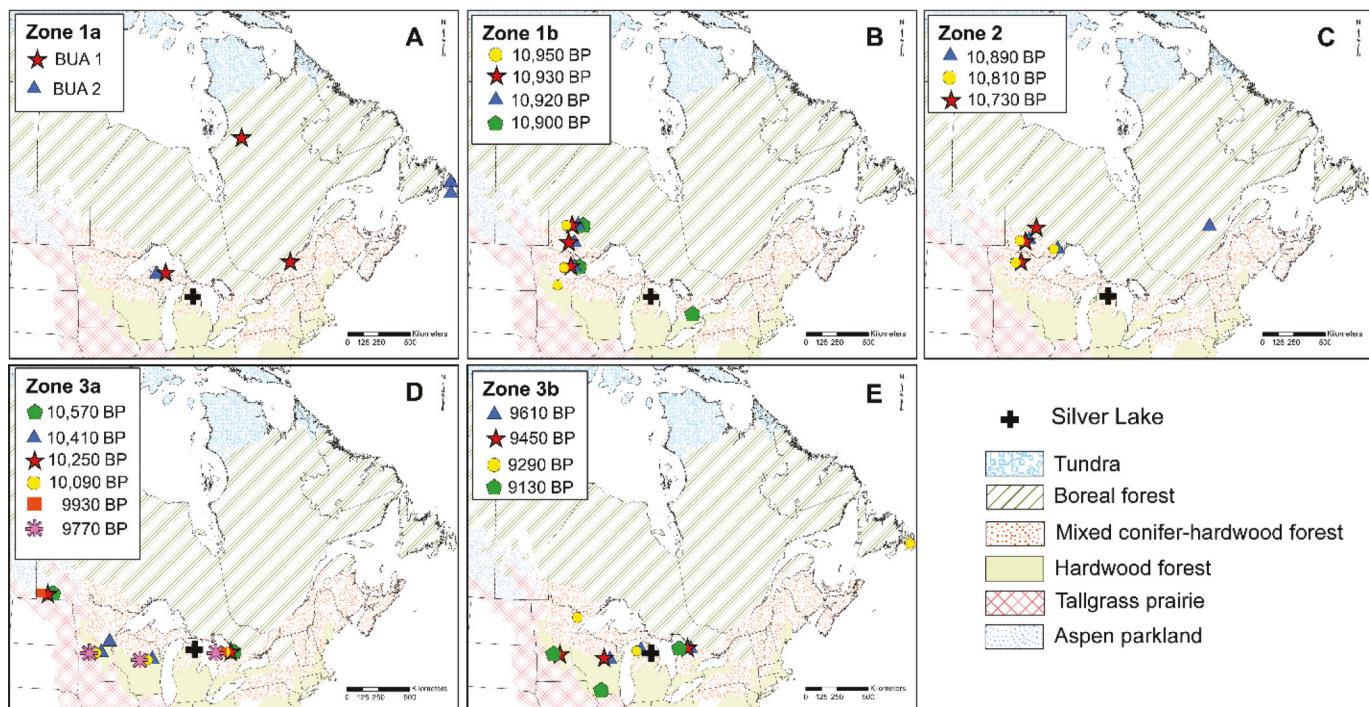
Comparison of pollen percentage zonation with AHC/NMS results

The AHC analysis discerned nearly identical plant communities (Fig. 5) to those interpreted from CONISS (clustering) zonation of the pollen diagram (Fig. 4). Identical matches of these clades included the forested tundra (AHC 1a; pollen Zone 1a) and boreal forest (AHC 1b; Zones 1b and 2) assemblages. However, above we argued for *Dryas* and other arctic plant materials being redeposited and, thus, Zone 1a and 1b actually represent a boreal forest like that of Zone 2; by correlation, all of these zones are best represented by the AHC 1b cluster. In other words, AHC 1a (forested tundra) is considered an artifact of the mixed fossil assemblage, which supports our decision to not assign ages to the basal samples, denoted as BAU 1 (at 520 cm) and BAU 2 (at 518 cm) in Fig. 4. The AHC analysis also discerned two minor community types within AHC cluster 2, which compared favorably with the habitat partitioning inferred for Zone 3 using CONISS and modern ecological analogs (e.g., Dickmann 2004). The dry/dry-mesic northern forest (AHC 2a), particularly the dry aspect of this vegetation, correlated well with the upland pine-dominated forest interpreted for this zone, which is best expressed in Zone 3a. The northern hardwood swamp (AHC 2b) was similar to interpretation of a mixed conifer-hardwood forest that inhabited low-lying locales in the study area from 10 640 to 9130 cal years BP, and is most evident in Zone 3b due to the *Thuja occidentalis* pollen rise.

The chronology of NMS scores (Fig. 6) is also consistent with the CONISS-derived pollen zonation (Fig. 4) and inferred paleovegetation dynamics. NMS axis 1 scores are strongly negative ($\bar{x} = -1.895$) within basal Zone 1a, further substantiating our interpretation of this bottommost pollen zone (samples BAU 1 and BAU 2) being anomalous in its taxonomic composition, and best explained by older fossil redeposition. The NMS axis 1 scores rise abruptly during subsequent Zone 1b and Zone 2 to positive values within approximately a century, between 10 903 cal years BP (-1.270) and 10 810 cal years BP (0.441). This spike in NMS axis 1 scores indicates very rapid warming in the study area resulting in a major turnover of species composition in the local vegetation during the early Holocene, but also points to a shift from a taphonomically mixed Zone 1a to autochthonous Zones 1b (except for the basal sample, 506 cm) and 2. NMS axis 1 scores maintain positive values ($\bar{x} = 0.637$) from 10 810 to 9130 cal year (rest of Zone 2 as well as Zone 3). Given the trajectory of the NMS data, and that NMS axis 1 (Fig. 6) explained 93.0% of the total variance in the Silver Lake pollen data, we interpret NMS axis 1 scores as acceptable proxies for temperature during the early Holocene. Colder climates by age BAU 1, BAU 2, 10 950, 10 930, 10 917, and 10 903 cal years BP are positioned on the left and warmer climates associated with younger samples are on the right in Fig. 6.

NMS axis 2 scores (Fig. 6), explaining 1.1% of the total variance, identified rapid compositional changes in the local vegetation during the earliest Holocene. NMS axis 2 scores rise sharply from negative (-0.162) to positive (1.004) values between 10 950 and 10 890 cal years BP, nearly identical to the century-long interval (10 903–10 810 cal years BP) identified in the NMS axis 1 scores, and correlates well to Zone 1b (10 940–10 890 cal years BP). There are two possible causes for this step-function shift in the local vege-

Fig. 7. Geographic distribution of modern analog pollen sites for Silver Lake pollen Zones 1a–3b, shown in relationship to major biomes. Analog sites ($n = 3$) for each stratigraphic interval are shown as contrasting colored symbols, and were selected on the basis of having the lowest squared chord distance values. (A) Zone 1a trash zone. (B) Zone 1b (10 950–10 900 cal years BP). (C) Zone 2 (10 890–10 730 cal years BP). (D) Zone 3a (10 570–9770 cal years BP). (E) Zone 3b (9610–9130 cal years BP). [Color online.]



tation: (1) regional climate change, given that Shuman and Marsicek (2016) identified rate-of-change values from 40 paleo-ecological sites peaking at 10 900 cal years BP, and (2) the loss of *Dryas integrifolia* from the fossil record, and if this material was truly allochthonous this shift may have been due to local geomorphic processes associated with kettle lake formation. The subsequent decline in NMS axis 2 scores records the transient nature of the boreal forest and its subsequent replacement by pine-dominated mixed forest. Thereafter, the NMS axis 2 scores gradually decline to negative values (-0.085) by 10 570 cal years BP (within Zone 3a). NMS axis 2 scores also remain negative ($\bar{x} = -0.193$) through the rest of Zones 3a and 3b.

Modern pollen analogs

SCD analysis (Fig. 7) was able to situate modern analog sites, based upon Neotoma Paleoecological Database (2018) pollen data, for Silver Lake's terminal Pleistocene/early Holocene pollen record (Fig. 4) within the broader Great Lakes region. However, the two pollen samples comprising Zone 1a, BAU 1 (520 cm depth) and BAU 2 (518 cm depth), displayed noteworthy anomalies in SCD values and the geographic distribution of associated analog sites that contrasted sharply with the other CONISS-derived pollen zones. For example, analog sites possessing the highest SCD scores were associated with basal Zone 1a ($\bar{x} = 0.327$, $s = 0.032$, range = 0.297–0.372), whereas analog sites associated with overlying Zones 1b–3b had uniformly lower values ($\bar{x} = 0.188$, $s = 0.046$, range = 0.103–0.301). Additionally, the wide geographic spread of Zone 1a analog sites (~2500 km east–west, ~1300 km north–south; Fig. 7A), encompassing both boreal and mixed conifer-hardwood forest zones, is juxtaposed against the stronger spatial clustering of subsequent Zones 1b–3b (Figs. 7B–7E). These spatial patterns suggest an allochthonous, non-contemporaneous origin for Zone 1a, which agrees with our interpretation based on the pollen percentage data (Fig. 4).

The spatiotemporal sequence of analog sites within Zones 1b–3b (Fig. 7), however, reflects pronounced and coherent patterns of postglacial vegetation response. In general, there is an overall southeastward shift in the distribution of analog sites through time, supporting the interpretations for the upcore pollen sequence at Silver Lake. For example, analog sites associated with Zone 1b (10 950–10 900 cal years BP; Fig. 7B) and Zone 2 (10 890–10 730 cal years BP; Fig. 7C) are positioned near the current boundary between boreal forest and mixed conifer-hardwood forest in the far western Great Lakes region. In fact, eleven of the twelve analog sites for Zone 1b (91.7%) and eight of nine associated with Zone 2 (88.9%) are situated within a ~350 km, north–south axis centred upon northern Minnesota and adjacent Ontario. Silver Lake is currently located ~200 km south of the southern limit of boreal forest within the mixed conifer-hardwood forest zone, indicating that the local climate was slightly cooler (and possibly drier) than present from ~10 950–10 730 cal yr BP (Zones 1b and 2), substantiating our interpretations of the pollen data (Fig. 4).

In contrast, analog sites pertaining to Zones 3a and 3b are situated farther south and east than previous pollen zones, forming a distinctive east–west belt generally straddling the modern ecotone between the mixed conifer-hardwood forest and the hardwood forest biomes (Figs. 7D, 7E). Importantly, the majority of these analog sites lie at latitudinal positions comparable with that of Silver Lake (Fig. 7). Therefore, we infer that (1) by ~10 600 cal years BP temperature conditions at Silver Lake were roughly comparable with modern values, and (2) a mixed conifer-hardwood forest having relatively high *Pinus* values (in the absence of late-successional competitors that arrived later) had become established in the Silver Lake catchment during Zone 3.

Discussion

Timing and nature of kettle lake formation

Our study provides compelling evidence for a mixture of plant fossils of different ages in the trash layer (below 501 cm, Figs. 3–7)

of Silver Lake, including the carbon comprising the 17 540 cal years BP dating sample. We attribute this amalgamation to the topographic inversion inherent to kettle lake formation. Similarly, Maher et al. (1998) interpreted a glacial re-bedding of older tundra fossils with younger ones at the Valders site in eastern Wisconsin (Fig. 1), which produced ages ranging from 17 690 to 15 800 cal years BP thought to be too old for the site's deglacial history. In modern glacial environments, researchers have observed organics being transported considerable distances by glaciers before the plant remains are released upon melting (Fickert et al. 2007; Hood et al. 2009).

The allochthonous older carbon incorporated into the basal age sample from Silver Lake probably came from plant fossils dating to the middle Wisconsin (marine isotope stage 3), sometime between 50 000 and 30 000 ^{14}C years BP. If some of this older material had been combined with the organics of plants living in the vicinity of the newly formed Silver Lake (~10 940 cal years BP), the ensuing date would have reflected the mean age of all components, such as the 17 540 cal years BP date that we received from the radiocarbon lab. There are many sites containing buried peat/organic deposits of middle Wisconsin age in the region, in southern Michigan (Winters et al. 1986), southern Ontario (Warner et al. 1988; Bajc et al. 2015), and Cape Breton Island in Atlantic Canada (Fréchette and de Vernal 2013). These investigations indicate that the plant communities (arctic tundra and boreal forest) were the same during the middle Wisconsin as they were after the last glaciation (e.g., Webb et al. 2004; Yansa 2006; Hupy and Yansa 2009).

Therefore, we cannot conclusively ascertain which of the plant fossils that made up the 17 540 cal years BP dating sample were of middle Wisconsin age, but we suspect the *Dryas integrifolia* leaves for reasons described above. The implications of our study are that researchers should not assume that the ^{14}C ages obtained from trash layer fossils necessarily reflect the age of final melt-out and kettle lake formation, given the possibility of temporally mixed fossils deposits that can include considerably older materials. Consequently, we recommend that basal ^{14}C ages obtained from kettle trash layers be compared with those dates obtained from ice-contact depositional settings formed earlier, to better constrain the timing of deglaciation in a study area.

Regional assessment of deglaciation chronologies and onset of plant colonization

The strong and multifaceted evidence for rejection of the 17 540 cal years BP date for the final melt-out of ice in the Silver Lake basin, provided in this paper, is further validated by the currently accepted deglacial models, which place this area under ice of the Port Huron re-advance until at least 15 200 cal years BP (Blewett et al. 1993, 2009). That date is taken from the Inner Port Huron moraine in northwestern Lower Michigan (Fig. 1). Because Silver Lake is in the interlobate region of this advance, it could theoretically have been uncovered slightly earlier, but nonetheless, the basal age of 17 540 cal years BP appears to be too old for this landscape context. For comparison, Barney Lake (Fig. 1) has a basal date of 13 220 cal years BP ($11\,380 \pm 30$ ^{14}C years BP) obtained from conifer wood (R.J. Schaetzl and C.H. Yansa, unpublished data), and given that this kettle lake is located 120 km south of the study site it would have formed earlier than Silver Lake. Hence, Silver Lake likely formed sometime after 13 220 cal years BP, with deglaciation occurring at least a millennium beforehand.

Pollen and plant macrofossil analyses of two fossil sites situated north of Silver Lake also help to constrain the timeframe. The Tower buried forest site, located 27 km northeast of Silver Lake (Fig. 1), identified a forested tundra established on outwash from 11 720 to 11 460 cal years BP (Schaetzl et al. 2013). The Tower site's basal date thus provides a minimum age for vegetation establishment at Silver Lake, given their close proximity, and nearly identical floras. The Cheboygan bryophyte bed (Fig. 1), positioned

~32 km north-northwest of Silver Lake, contained an arctic tundra plant assemblage that included *Dryas integrifolia* (Miller and Benninghoff 1969), and was dated to 13 930 cal years BP ($12\,050 \pm 80$ ^{14}C years BP on *Salix* stems) by Larson et al. (1994). This moss bed in northern Lower Michigan, as well as the Two Creeks buried forest bed in Wisconsin (Fig. 1; dated between 14 500 and 13 900 cal years BP), are both overlain by glaciogenic sediments attributed to the Greatlakean re-advance of the Lake Michigan lobe, the last glacial advance to enter these areas between 13 790 and 13 400 cal years BP (Kaiser 1994; Larson et al. 1994; Rech et al. 2011). It remains debatable whether Greatlakean ice reached the Silver Lake and Tower site areas (Schaetzl 2001). If it did, the age for deglaciation of the Silver Lake area should postdate 13 400 cal years BP. The ages of these other locales in northern Lower Michigan, therefore, suggest that the deglaciation of the study area occurred sometime between ~15 000 and ~13 400 cal years BP, followed by formation of Silver Lake at least a millennium later.

Stabilized kettle lakes as reliable Holocene-age paleovegetation archives

Silver Lake began to accurately accumulate plant remains of the existing local vegetation starting at about 10 940 cal years BP and, based on reliable chronologies from other pollen sites, we interpret this to have occurred during the latter part of a boreal forest phase. The same *Picea*-dominated boreal vegetation existed at the nearby Tower site from 11 460 to 10 660 cal years BP (Schaetzl et al. 2013) and from 13 860 to 11 500 cal years BP at two pollen sites in southwestern Ontario (Yu 2000, 2003). North of our study area, this same or similar boreal vegetation inhabited the central Upper Peninsula of Michigan from 13 000 to 10 300 cal years BP (Woods and Davis 1989). The late appearance and short duration of the boreal phase at Silver Lake is thus an anomaly, providing additional evidence for the lag in kettle lake formation with respect to plant arrival and establishment, which began earlier by plant colonization of sediment on ablating ice blocks. This interpretation is reinforced by the mature nature of the boreal forest interpreted for Zones 1b and 2 (Fig. 4), which is verified by the highly clustered geographic placement of modern analog sites for these zones (Figs. 7B, 7C) at the ecotone between boreal forest and mixed conifer-hardwood forest.

Continuation of cool and moist conditions well into the early Holocene in the central Great Lakes region, as exemplified by the persistence of boreal forest at Silver Lake and the Tower site (Schaetzl et al. 2013) until ~10 640 cal years BP, was probably due to localized cooling downwind from glacial lake drainage at this time. Based on a seismostratigraphic, lithological, and pollen study of sediments in a bay of Lake Huron, Lewis and Anderson (2017) attributed a recurrence of *Picea* after the more temperate *Pinus* became common in the local vegetation to cold-water discharge from Glacial Lake Agassiz. This drainage occurred as downstream (eastward) outburst floods that caused the Mattawa high stands of Lake Huron between 10 800 and 10 600 cal years BP, which produced a climate that favored spruce. Silver Lake and the Tower site are close enough to Lake Huron to have been impacted by localized cooling resulting from these cold-water outbursts, which likely explains, at least in part, the late dominance of *Picea* in northern Lower Michigan until ~10 640 cal years BP. Additionally, strong, cold easterly and southeasterly winds off Lake Huron dominated the region at this time, further delaying warming (Schaetzl et al. 2016).

The most significant postglacial vegetation change in pollen records throughout the Great Lakes region is the rapid shift from *Picea*- to *Pinus*-dominated forest, which at Silver Lake is recorded by the transition from Zones 2 to 3 (Fig. 4), and by the prominent excursions of NMS axes 1 and 2 between 10 730 and 10 570 cal years BP (Fig. 6). The pronounced nature of this change is also clearly evident in the distribution pattern of modern analog sites during

this interval, shifting towards the south and east (Figs. 7C, 7D), indicating warming temperatures and possibly increasing precipitation. This floristic transition occurred in the Silver Lake area at 10 640 cal years BP (base of Zone 3a), essentially the same time (10 660 cal years BP) as at the Tower site (Schaetzl et al. 2013), but a few centuries after (10 900 cal years BP) this shift happened at two sites located to the southeast, in southern Ontario (Yu 2003). The pine-dominated vegetation of Zone 3 lacks a precise modern counterpart, which is typical of Late Pleistocene and early Holocene vegetation communities in glaciated North America due to a combination of novel climatic conditions, delays in soil development, and lagging migration rates of some tree species (Williams and Jackson 2007). Zone 3 at Silver Lake thus represents a transitional stage in the development of a mixed conifer-hardwood forest. Modern plant communities developed later in northern Lower Michigan, after the initiation of lake effect precipitation sometime between 9500 and 5500 cal years BP (Henne and Hu 2010), coincident with the late arrival of mesophytic forest taxa that came to dominate the local flora.

Conclusions

Proxy analysis of a sediment core from Silver Lake sheds light on the timing of deglaciation and subsequent landscape processes that led to kettle lake formation and plant colonization and succession in northern Lower Michigan. By reconstructing the core's biostratigraphy, and applying multivariate statistics and SCD analysis to the pollen data, we are able to reconstruct major plant communities, infer the geographic correlates of their modern pollen analogs, and identify environmental mechanisms that likely modulated paleovegetation changes. The paleovegetation data, when situated within the local glacial chronology, lead us to conclude that the basal plant fossils in Silver Lake are anomalously old for their depositional context, which we explain as likely due to a mixing of non-contemporaneous plant remains into the basal lacustrine sediments. In the case of Silver Lake, the amalgamation of ostensibly middle Wisconsinage (~50 000–30 000 ^{14}C years BP) plant macrofossils with those of the extant vegetation (boreal forest by ~10 940 cal years BP) probably occurred during ice block ablation.

Our research has two main implications. First, we cannot assume that ^{14}C dates based on terrestrial plant macrofossils from trash layers found at the base of kettles are accurate. Their use may result in significant errors in establishing the chronologies of lake formation. Our research thus highlights the importance of closely assessing the fossil and sediment deposits of kettle lakes, and looking to other depositional settings, such as proglacial and ice-walled lakes and outwash locales, to find the oldest fossils dating to the immediate recession of glacier ice lobes. By comparison with other dated fossil records from northern Lower Michigan, we estimate that the Silver Lake area was deglaciated sometime between 15 700 and 11 720 cal years BP, and not at 17 540 cal years BP, as indicated by the basal ^{14}C age sample of Silver Lake. Further, considering that many lake cores used for paleoecological reconstructions in the formerly glaciated areas of the United States, Canada, and Europe come from kettle lakes, we recommend that the basal sections of these cores be similarly evaluated for biostratigraphic integrity. We further suggest that whenever possible, two or more dates be obtained for each sample level by dating groupings of plant fossils according to plant community assemblages (e.g., tundra vs. boreal forest) in these basal core sections. Unfortunately, in the case of Silver Lake, there were insufficient organics in the basal dating sample to split and date separately. Second, the concurrence between the paleoecological patterns reconstructed for Silver Lake after 10 940 cal years BP (Unit 3; Zones 1b, 2, and 3) with those from several other proxy sites from the Great Lakes region, exemplify that kettle lakes, once formed and stabilized, do provide excellent archives of past

environmental changes. We interpret the reliable part of the Silver Lake record to capture (1) the presence of a mature boreal forest, which indicates that tundra plant colonization probably occurred at least a millennium before; and (2) by 10 640 cal years BP, the vegetation had shifted to a *Pinus*-dominated forest, an early Holocene variant of the mixed conifer-hardwood forest that exists in the study area today.

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