Interacting effects of fire and hydroclimate on oak and beech community prevalence in the southern Great Lakes region

Abstract

1. Rising temperatures, increasing hydroclimate variability, and intensifying disturbance regimes increase the risk of rapid ecosystem conversions. We can leverage multi-proxy records of past ecosystem transformations to understand their causes and ecosystem vulnerability to rapid change.
2. Prior to Euro-American settlement, northern Indiana was a mosaic of prairie, oak-dominated forests/woodlands, and beech-dominated hardwood forests. This heterogeneity, combined with well-documented but poorly understood past beech population declines, make this region ideal for studying the drivers of ecosystem transformations.
3. Here we present a new record from Story Lake, IN, with proxies for vegetation composition (pollen), fire (charcoal), and beech intrinsic water use efficiency ($\delta^{13}C$ of beech pollen; $\delta^{13}C_{beech}$). Multiple proxies from the same core enable clear establishment of lead-lag relationships. Additionally, $\delta^{13}C_{beech}$ enables direct comparisons between beech population abundance and physiological responses to changing environments. We compare Story Lake to a nearby lake-level reconstruction and to pollen records from nearby Pretty and Appleman Lakes and the distal Spicer Lake, to test hypotheses about synchrony and the spatial scale of governing processes.
4. The 11.7 ka sediment record from Story Lake indicates multiple conversions between beech-hardwood forest and oak forest/woodland. Beech pollen abundances rapidly increased between 7.5 and 7.1 ka, while oak declined. Oak abundances increased after 4.6 ka and remained high until 2.8 ka, indicating replacement of mesic forests by oak forest/woodland. At 2.8 ka, beech abundances rapidly increased, indicating mesic forest reestablishment. Beech and oak

abundances correlate with charcoal accumulation rates but beech abundance is not correlated with $\delta^{13}C_{beech}$.

5. Fluctuations in beech abundances are synchronous among Story, Appleman, and Pretty Lakes, but asynchronous between Story and Spicer Lakes, suggesting regulation by local-scale vegetation-fire-climate feedbacks and secondarily by regional-scale drivers.
6. Holocene forest composition and fire dynamics appear to be closely co-regulated and may be affected by local to regional climate variations. The importance of extrinsic drivers and positive/negative feedbacks changes over time, with higher ecoclimate sensitivity before 2.8 ka and greater resilience afterwards.
7. *Synthesis*: Overall, oak- and beech-dominated ecosystems were highly dynamic over the Holocene, with multiple ecosystem conversions driven by shifting interactions among vegetation, hydroclimate, and fire regime.

Key Words

Aridity, *Fagus grandifolia*, *Quercus*, Holocene, disturbance regime, fire, hydroclimate, drought, pollen, stable carbon isotopes, lake-level, palaeoecology, rapid ecological change

Introduction

Much of the current literature on forest transformations driven by rising temperatures, increasing hydroclimate variability, and changes disturbance regimes has focused on areas that experience frequent drought or fires, such as the western US (Westerling et al. 2011, Romme et al. 2011, Hartmann et al. 2018, Allen et. al 2015), or in high-latitude regions where species and ecosystem distributions are closely regulated by temperature (Payette 2021). Palaeoecological evidence can provide a deeper time perspective of these dynamics by helping further our understanding of rapid population fluctuations and corresponding ecosystem transitions, including in areas that are today seemingly resilient. In the Great Lakes region, mesic tree taxa have experienced multiple abrupt population declines during the Holocene and provide a rich study system for understanding past rapid vegetation changes (Shuman et al. 2009, Shuman 2012, Booth et al. 2012a, Booth et al. 2012b, Wang et al. 2016). For example, the range-wide population collapse of eastern hemlock (*Tsuga canadensis*) at 5.5 to 5.3 thousand years before present (ka BP) has been extensively studied and is often associated with one or more severe drought events suggesting high sensitivity to hydroclimatic variation (Shuman et al. 2009, Shuman 2012, Oswald and Foster 2012, Booth et al. 2012a). However, other causes of the eastern hemlock collapse have been suggested including regional temperature changes (Shuman et al. 2023) and outbreaks of hemlock looper or other pests or pathogens (Bhiry and Filion 1996).

American beech (*Fagus grandifolia*, herein beech), another common mesic tree species in the eastern US, has undergone rapid population fluctuations throughout the Holocene (Booth et al. 2012b, Wang et al. 2016), but the patterns and causes are less well studied. After the last glacial maximum, beech expanded northward from the southeastern US, reaching the Great Lakes region between 8.0 and 6.0 ka (Williams 1974, Bernabo and Webb 1977, Davis 1981, Webb et al. 1984, Bennett 1985, Bennett 1988). After establishment in the Great Lakes region, beech populations experienced repeated declines across sites in

Ohio, Indiana (IN), Michigan (MI), and Wisconsin (Wang et al. 2016). At Spicer Lake, IN, beech populations rapidly expanded at 6.8 ka and subsequently ranged from near 30% to <5% pollen abundance (Wang et al. 2016). Beech populations at Spicer Lake experienced five abrupt and well-dated declines (5.3 ka, 4.3-4.0 ka, 3.2–2.0 ka, 1.2 ka, 1 ka), all followed by abrupt increases, except for the decline at 1 ka, from which beech has not recovered (Wang et al. 2016).

Better constraints on the timing of the beech declines across sites is essential to testing causal hypotheses. The declines at Spicer Lake appear to be asynchronous with declines at other sites in the Great Lakes region (Wang et al. 2016). However, this apparent asynchrony could be caused by poor dating constraints, as many records were collected decades ago and rely on relatively few bulk-sediment radiocarbon dates, which are prone to biasing due to hardwater effects (Grimm et al. 2009). Synchronous beech declines across the region would suggest macro-scale extrinsic drivers, such as temperature variations or pest outbreaks, as has been invoked for eastern hemlock (Shuman et al. 2009, Booth et al. 2012a, Shuman et al. 2023). Asynchronous beech variations would suggest localized interactions between extrinsic, intrinsic, and disturbance processes, such as localized shifts in fire regime, local hydroclimate variability, or species interactions leading to shifts in the dominant taxon. Cross-scale interactions are also possible, e.g. local-scale feedbacks interacting with macro-scale extrinsic drivers, creating sub-regional temporal mosaics with clusters of synchronized declines (Williams et al. 2011). These intrinsic and extrinsic processes can further interact with disturbance regimes to amplify or mitigate rates of ecological change (Ratajczak et al. 2018) with transition zones between ecosystems being particularly susceptible to rapid changes in community composition (Nelson and Hu 2008, Williams et al. 2009, Hupy and Yansa 2009, Wiles 2023).

The thin bark of beech makes it vulnerable to damage by fire, while a shallow root system also makes it susceptible to changes in soil moisture (Tubbs and Houston 1990). During the Medieval Climate Anomaly (1.05 to 0.6 ka BP), beech declines were associated with increased fire frequency at some sites in northern Michigan (Booth et al. 2012b), but at Spicer Lake there was largely no consistent relationship between

beech abundance and fire (Wang et al. 2016). At some sites, fire regimes can stabilize vegetation composition. For example, in Minnesota's Big Woods the late-Holocene shift from oak woodland to mesic forest only occurred at the sites where fire was absent due to the presence of natural firebreaks (Calder 2016, Grimm 1984). Drought could also cause beech declines, but the Spicer Lake record lacks robust paleohydrology proxies (Wang et al., 2016). More independent paleohydrology proxies are needed, such as past lake level variations (Digerfeldt et al. 1993, Pribyl and Shuman 2014) or other indicators of the regional moisture balance to further evaluate the relationship between beech declines and hydroclimatic history (Booth 2008, Adams et al. 2015). Variations in beech abundances may also be affected by changes in temperature, which appear to have affected the region during the Holocene (Puleo et al., 2020; Shuman et al., 2023), and pathogen outbreaks, which are known from modern forests. For example, some studies attribute late-Holocene declines in beech in New England and the Great Lakes region to Little Ice Age cooling (Fuller et al., 1998; Gajewski, 1987), whereas the accidental introduction of beech bark disease to the US in the 1890s CE has devastated many beech forests, with mortality rates of 50% and infestation rates of 80 to 95% (Stephanson and Coe, 2017; Beckman et al. 2021).

Even with independent proxies of hydroclimate variation, the potential for different sensitivities and response times between lacustrine and terrestrial ecosystems remains a source of uncertainty. A relatively new approach that integrates the balance between carbon and water fluxes and thus shows promise for inferring shifts in the physiological sensitivity and response time of vegetation to climate forcing is stable carbon isotopic ($\delta^{13}C$) analyses of fossil pollen grains of C_3 plants (Jahren 2004; Loader and Hemming 2004; Griener et al. 2013, Nelson 2012). The $\delta^{13}C$ values provide a seasonally-integrated signal of intrinsic water use efficiency (iWUE), which is the ratio of photosynthesis and stomatal conductance of water (Farquhar et al., 1989). In terms of water-use strategies, plants that prioritize carbon gain relative to water loss have low iWUE and $\delta^{13}C$ values, whereas those that prioritize water conservation relative to carbon gain have high iWUE and $\delta^{13}C$ values (Bacon, 2009; Farquhar and Sharkey,

1982), and dry conditions tend to favor the latter (Sperry et al., 2017). Atmospheric CO_2, atmospheric pollution, and climate (temperature and precipitation) have been shown to affect plant iWUE during the historical record via their influences on photosynthesis and/or stomatal conductance (Mathias et al., 2023), though the former two factors are unlikely to have been significant controls of iWUE during the Holocene prior to the industrial revolution. Pollen $\delta^{13}C$ values ($\delta^{13}C_{pollen}$) represent landscape- to population-level shifts in iWUE because multiple pollen grains must be combined to produce enough carbon for $\delta^{13}C$ analysis and each sediment sample comprises pollen grains from many individual plants within pollen source radii on the order of 10s of km (Prentice 1988). The $\delta^{13}C$ data from specific taxa can be coupled with pollen assemblage data to assess the influence of variations in iWUE on abundance changes for individual taxa and changes in community composition (Griener et al. 2013).

Here we seek to better understand the drivers of rapid changes in beech abundances in the southern Great Lakes region, through a new well-dated, multi-proxy record for Story Lake, Indiana. This record includes proxies for past vegetation composition (pollen), iWUE of beech ($\delta^{13}C_{beech}$), and fire regime (charcoal) from the same core. The Story records are compared to a recent lake level reconstruction from nearby Lake Lavine, MI (Ray-Cozzens 2023) as an independent indicator of past hydroclimate variations. We also compare the history of beech variations at Story with those at two nearby sites within 15 km of Story Lake (Appleman and Pretty Lakes), and one more distal lake located 120 km to the west (Spicer Lake). These comparisons allow us to test hypotheses about the synchrony of vegetation changes at landscape to regional scales and thereby assess the relative importance of local-scale vegetation-fire-climate feedbacks and regional-scale climatic drivers on rapid changes in mesic tree populations in the southern Great Lakes region.

Materials and Methods

Site Description

Our main study site, Story Lake (41.51237, -85.13500) is located in DeKalb County, northern Indiana (Fig. 1). Comparison pollen sites are also located in northern Indiana, including a new Holocene pollen record for previously studied Appleman Lake (Gill et al. 2009) and preexisting records from the Neotoma Paleoecology Database for Pretty Lake (Williams 1974) and Spicer Lake (Wang et al., 2016) and a comparison hydrological reconstruction located in southern Michigan from Lake Lavine (Ray-Cozzens 2023; Fig. 1). This region is situated in complex mosaic of three ecosystems: the prairie peninsula in the southwest, oak-dominated forest and woodlands in portions of the north, east, and west and beech-dominated forests in portions of the north, south and east (Fig. 1, McNab et al. 2007, Paciorek et al. 2016, Landfire 2020, Transeau 1935). Therefore, this area contains two major ecosystem transitions: the prairie-forest transition (Fig. 1a), whose Holocene dynamics that have been widely studied (e.g. Nelson and Hu 2008, Williams et al. 2009) and the oak-beech transition which is much less well studied (Fig. 1b, 1c , Abrams and Nowacki 2019, Wang et al. 2016). This makes northern Indiana an ideal region for studying the importance of the drivers of rapid vegetation shifts in complex ecosystem mosaics in the Great Lakes region and how they vary in time and space.

Pre-settlement vegetation of northern Indiana was a mosaic of oak-hickory and beech-maple forests with patches of wetland and prairie communities (Lindsey et al. 1965). Beech was a prominent taxon in these pre-settlement forests in northeastern Indiana as well as mid to late Holocene forests of southern Ontario, but it experienced widespread losses with Euro-American land conversion (Fig. 1; Paciorek et al. 2016, Lindsey et al. 1965, Bennett 1987). Contemporary mixed forests in northern Indiana are generally characterized by a mosaic of the maple-beech-birch, oak-hickory, and elm-ash-cottonwood communities (McNab et al. 2007). Elsewhere in the Great Lakes and northeastern North America, beech-dominated

mixed forests are compositionally diverse and associated with both fine-grained soils that retain moisture and low frequency fire disturbance (Abrams and Downs 2011, Engstrom et al. 1984, Henne et al., 2007, Landfire 2020, Lindsey et al. 1965). Oak communities in northeastern Indiana and elsewhere range from closed forests to open woodlands or prairies and are mostly found in xeric sites, often having well drained sandy soils, and are adapted to frequent low intensity fire regimes (Landfire 2020, Lindsey et al. 1965, Bennett 1987). However, both oak and beech forests prevail on the silt loams that are the dominant soils type in northern Indiana (Lindsey et al. 1965). The gradient between closed forests and open woodland in northern Indiana is also largely controlled by fire frequency and intensity, with frequent fire promoting oak woodlands while locations with low fire-return intervals allow for fire-sensitive species to dominate the overstory (Henderson and Long 1984). More broadly, semi-arid ecosystems in the Great Lakes region have been governed throughout the Holocene by feedbacks between aridity, vegetation composition, and fire regime, driving community shifts from fire-tolerant oak woodland and prairie systems to fire-intolerant mesic forests (Grimm 1983, Nelson et al. 2006, Nelson and Hu 2008, Shuman et al. 2009).

The climate of the southern Great Lakes region is continental with warm summers and cold winters, with northeastern Indiana experiencing monthly average temperature ranging from -4.6°C to 21.7°C with 988 mm annual precipitation (NOAA 2023). This region also has a large range of annual snowfall with some areas receiving high levels of lake effect snow, up to 70%, with annual snowfall between 60 and 80 inches on eastern shore of Lake Michigan with less snowfall inland. Annual snowfall near Story Lake averages 40 inches (NOAA 2023) and typically 30-50% of annual snowfall comes from lake effect snow (Jones et al. 2022).

Story Lake is a 30-ha kettle lake (Fig. 1), likely formed by remanent glacial ice embedded into glacial till from the Huron-Erie lobe during the retreat of the Laurentide Ice Sheet (Gray 1989). The terrain surrounding Story Lake is flat with small hills. Story Lake has two small islands and is connected by a narrow marsh and stream to an adjacent Lower Story Lake. Story Lake has no inlet stream. Soil conditions

range from fine-loam near the basin to fine to coarse-loam in the uplands (Soil Survey 2023). Forests border the lake to the north and west with a mosaic of agricultural fields in the surrounding area. Additionally, residential houses and a camping resort border the southeastern portion of the lake (Fig. 1).

Coring took place in June 2019 with the coring site located in the southern part of the lake, near the deepest part of the lake based on field depth surveys and pre-existing bathymetry maps (Fig. 1). The water depth at the coring location was 8.8 meters. We retrieved three closely adjacent and drive-offset cores, each 1-meter in length, extending from the sediment-water interface to basal glacial till. The top drive used a modified Livingston with a polycarbonate Bolivian adaptor and the remaining drives were extracted using the modified-Livingston steel barrel, with mud extruded after coring into PVC pipe for transport. Cores were taken to the Continental Scientific Drilling Facility at the University of Minnesota-Twin Cities for longitudinal splitting, high-resolution photographing, and logging for bulk density and magnetic susceptibility. After splitting and imaging, a 11.2 meter composite core was created by matching stratigraphy across cores to avoid samples at core breaks where possible. At the University of Wisconsin-Madison, the composite core was divided into 1 cm segments, from which all subsequent samples were obtained.

Radiocarbon dates and age-depth model

To create the Story Lake age-depth model, we submitted 16 terrestrial plant macrofossils for radiocarbon dating to the W. M. Keck Carbon Cycle Accelerator Mass Spectrometry Laboratory (Keck-CCAMS) at the University of California, Irvine (Table 1). One sample was determined to be too small for AMS analysis (642.5 cm, Table 1). The age-depth model was generated in R (R Core Team 2021) using the package *bchron* version 4.7.6 (Haslett and Parnell 2008). Of the 15 radiocarbon samples, two samples from near the top of the core were determined to be modern, and so likely contained excess ^{14}C from thermonuclear weapons testing (Table 1). To determine the age of those samples, the program *CALIBomb* was used

(Reimer and Reimer 2023) and ages are reported in calibrated years as the mean of the 98% confidence interval and error estimates from the 95% confidence curve. For both modern samples, this equated to an age of 1971 CE ± 12 years (Reimer and Reimer 2023). In addition to the radiocarbon dates, we used two age controls: the core top (set to 2019 CE ± 10 years, to represent uncertainty in sediment mixing) and the sharp increase of ragweed (*Ambrosia*) pollen relative abundances at 128.5 cm as an indicator of Euro-American land clearance. Indiana was actively settled between 1810 and 1870, with the largest rates of forest cutting between 1870 and 1910 CE, after the advent of the sawmill in 1860 CE (Denuyl 1953). We thus set the ragweed peak to 1860 CE ± 25 years to capture the full range of intense land clearing in Indiana. Age uncertainties for the two modern samples, core top, and ragweed rise were represented by a normal distribution and the uncertainties for the remaining 13 radiocarbon samples were estimated using the IntCal20 calibration curve (Reimer et al. 2020).

Laboratory Analyses: Pollen, Charcoal, and Carbon Isotopes

Pollen and charcoal analysis for Story Lake were performed at the University of Wisconsin-Madison. Sediment samples for pollen analysis were sampled using a 1 cm^3 metal sampler at 8-cm intervals and up to 4-cm intervals (average time interval: 85 ± 38 years). Pollen samples were processed to remove carbonates (10% hydrochloric acid), silicates (48% hydrofluoric acid), and organic matter (10% potassium hydroxide) and acetalize the pollen grains for identification following standard methods (Faegri and Iversen 1984). Processed pollen samples were analyzed at 400× magnification using a Zeiss Axiolab 5 microscope, pollen grains were identified using the reference key and images in Kapp et al. (2000), and at least 300 terrestrial pollen grains were identified for each sample. Pollen percentages were calculated using the sum of terrestrial pollen grains in R (R Core Team 2021) and graphical representation was completed the R package *riojaPlot* (Juggins 2022).

Macroscopic charcoal in sediment cores is used as a proxy for fire history (Whitlock and Larson 2001, Higuera et al. 2009, Higuera et al. 2010). Macroscopic charcoal was sampled contiguously with 1 cm^3 subsamples from core top to 746 cm, to encompass the times when beech was abundant near Story Lake. Sediment was treated with 6% hydrogen peroxide solution to oxidize organic matter and sodium hexametaphosphate to disaggregate clay particles, then heated at 50°C for 24-hours. Samples were then sieved using a 125-micron mesh, material remaining on the sieve was rinsed into petri dishes, liquid was evaporated in a drying oven for 12-48 hours, and all pieces of charcoal were counted using 40x magnification. To calculate charcoal accumulation rates (pieces cm^{-2} $year^{-1}$), charcoal concentrations (pieces cm^{-3}) were multiplied by the sediment accumulation rate obtained from the age-depth model (cm $year^{-1}$) for each depth. The signal-to-noise ratio was calculated using the R package *tapas* (Finsinger and Bonnici 2022)

The $\delta^{13}C$ analysis of beech pollen was performed at the University of Maryland Center for Environmental Science. Because of the effort involved, this analysis was only performed for samples younger than 5.0 ka BP. Sediment samples were processed to extract pollen grains using methods designed to avoid using carbon-containing chemicals (Nelson et al. 2006). To enable accurate and precise $\delta^{13}C$ analysis (Korasidis et al. 2022), aliquots of 15-20 beech pollen grains were extracted from each sample using an Eppendorf Transferman micromanipulator and rinsed in nanopure water at 200x magnification on a microscope slide. These grains were applied in a ~0.5 μl drop of nano-pure water to a spooling-wire micro-combustion device interfaced with an isotope-ratio mass spectrometer (SWiM-IRMS; Nelson 2012). Blanks (nano-pure water to which pollen grains were added and subsequently removed) were analyzed along with aliquots; in all cases the CO_2 yield of the pollen-containing aliquots was > 5x those of the blanks. Sample data were normalized to Vienna Peedee Belemnite using $\delta^{13}C$ measurements of 5 nmol C of dissolved in-house standards (leucine and sorbitol) that were previously calibrated to USGS40 and USGS41. Between one and six aliquots of beech pollen were analyzed from each sample depth and their $\delta^{13}C$ values were averaged.

These individual aliquot measurements provide a measure of uncertainty that combines both analytical uncertainty (which is ± 1‰ or lower; Korasidis et al. 2022) and random variations in the $\delta^{13}C$ of the population of beech pollen grains drawn for isotopic analysis. Overall, we analyzed 101 aliquots across 44 samples.

Numerical Analyses

To determine changes in the prevalence of vegetation types through time, we used topic analysis, a machine-learning approach that categorizes taxa into assemblages and provides an estimate of the prevalence of each assemblage (Blei 2012). Topic analysis was originally developed for text mining, where documents are analyzed for patterns of associations among terms, based on iterative randoms draws from a statistical distribution (we used logistic normal distribution, see below). Associated terms within those documents are placed in groups, called topics, and then the prevalence of topics within documents becomes a primary way of describing documents. Topic analysis carries advantages for ecological applications due to its ability to provide robust and interpretable results, even for data with uneven sampling or for datasets with many variables or non-linear relationships among variables (Blei 2012, Valle et al. 2014, Christensen et al. 2018).

Topic analyses applied to ecological community data have two components: an estimate of importance of each taxon within an ecological community (beta) and an indication of the prevalence of each ecological community at a spatiotemporal locus (gamma). Topic analysis is thus very similar conceptually to standard ordination methods in ecology. For fossil pollen records, time series of gamma can provide information about shifts in prevalence of vegetation types.

Within topic analysis, two main algorithms can be used to categorize taxa into ecological communities: latent Dirichlet allocation (LDA) and correlated topic model (CTM). These two methods mainly differ with respect to the statistical distribution used to model variability among topics: LDA uses a Dirichlet

distribution while CTM uses a logistic normal distribution (Blei et al. 2003, Blei and Lafferty 2006). The Dirichlet distribution in LDA assumes that all topics are strongly independent, which is typically violated by ecological communities, given species interactions and shared responses to common environmental drivers. In contrast, the logistic normal distribution in CTM contains a correlation matrix that accounts for correlation among ecological communities. Therefore, the CTM method was used here. In CTM the user must specify how many topics to use; here we explored CTM with three to eight vegetation types and present the results for three vegetation types in the main text and alternate versions in Supplementary Information. All analysis was performed in R using the package *topicmodels* (Grün and Hornik 2011, Grün and Hornik 2023) using suggested control values from Grün and Hornik (2011).

Bayesian Change Point detection (BCP) for the gamma time series produced by the CTM analysis was used to determine the timing of rapid community shifts. BCP identified changes in prevalence of ecological communities, as identified as posterior probabilities of greater than 0.5, were interpreted as periods of rapid ecological community shifts. BCP analysis was performed using the R package *bcp* (Erdman and Emerson 2007).

Comparison Site Records

Appleman Lake, IN (41.6237, -85.2136) is a 21-ha kettle pond located 14 km northwest of Story Lake (Fig 1). Appleman Lake was cored in 2005 and the deglacial portion of the core was processed and analyzed by Gill et al. (2009). For this paper, we present a new pollen record for the Holocene portion of the core. The portion of the from 673 cm to the core top was subsampled at 8 cm resolution and processed for pollen analysis using the same technique as for Story Lake. Pollen was identified and counted at the University of Minnesota. The Holocene age-depth model for Appleman was based on the youngest two radiocarbon dates from Gill et al. (2009) at 627.5 cm (8397 calibrated years BP) and 618.5 cm (8106 calibrated years BD), the ragweed rise at 40.5 cm (1860 CE consistent with Story Lake), and core top (2005

CE). The age-depth model was generated using *bchron* version 4.7.6 (Haslett and Parnell 2008). Pretty Lake, IN (41.5760, -85.2498) is a 74.5 ha lake located 12 km northwest of Story Lake (Fig 1; Williams 1974). Spicer Lake, IN (41.7478, -86.5219) is a 5-ha kettle lake located 120 km west of Story Lake (Fig 1; Wang et al. 2016). Pollen and radiocarbon data for Pretty and Spicer Lakes were downloaded from the Neotoma Paleoecology Database (Williams et al. 2018) and their age-depth models were rebuilt using *bchron* version 4.7.6 (Haslett and Parnell 2008). Lake Lavine, MI (41.7693, -85.0376) is an 87-ha lake located 30 km north of Story Lake and was used as a hydrological comparison to Story Lake (Fig. 1). The lake level reconstruction for Lake Lavine was conducted by Ray -Cozzens (2022).

Results

Age depth model

The final age-depth model spans from 11.7 ± 0.6 ka BP (thousands of years before radiocarbon present, i.e. 1950 CE) to 2019 CE, however, we were unable to retrieve a basal date due to lack of dateable material in the last 300 cm of the composite core (Fig. 2). Sedimentation rates are nearly constant through much of the record, with an average sedimentation rate of 0.11 cm $year^{-1}$ (deposition time of 8.93 years cm^{-1}). However, near the top of the core, at 0.2 ka BP (138.5 cm), the sedimentation rate increases to an average of 0.63 cm $year^{-1}$ (deposition time decreases to 1.6 years cm^{-1}) (Fig. 2). See Supplementary Information for the *bchron* age-depth models for Spicer, Pretty, and Appleman Lakes.

Vegetation History

Pre-settlement vegetation changes at Story Lake were dominated by three taxa, beech (*Fagus*), oak (*Quercus*), and elm (*Ulmus*). Beech pollen abundances began to increase at 7.5 ka BP, with an acceleration at 7.1 ka BP, increasing from 5% to 25% over approximately 300 years (Fig. 3). During this initial increase, abundances of oak pollen declined from 57% at 7.9 ka BP to a low of 25% at 6.6 ka BP (Fig. 3). From 6.6 ka BP to 4.6 ka BP, oak abundances generally increased while beech decreased, with large centennial scale

316 variations superimposed on these millennial scale trends. From 4.6 ka BP to 3.0 ka BP, beech remained
317 low while oak reached its highest abundance of 61% at 4.3 ka BP. At 3.0 ka BP, beech abundances started
318 to rapidly increase from 3% to 22% in approximately 400 years, while oak decreased (Fig. 3). Starting at
319 2.6 ka BP, both beech and oak abundances fluctuated (e.g. beech varied from a high of 27% to a low of
320 7%) around a relatively constant mean, until the Euro-American intensification of land use at 0.09 ka BP
321 where both taxa abundances declined and have not recovered.

322 During the middle Holocene (8.0 to 5.0 ka), elm composed a substantial part of the pollen assemblage,
323 ranging from 12% to 28% with a mean of 18% (Fig. 3). After 5.0 ka BP, elm abundances declined but
324 fluctuated from 2% to 12% with a mean of 7% (Fig. 3). This pattern is consistent with other regional
325 records, where elm reached maximum abundance during the early to middle Holocene, perhaps due to
326 increased summer insolation (Wang et al. 2016, Williams and Jackson 2007). Other notable hardwood
327 taxa at Story Lake include hickory (*Carya*), hornbeam (*Ostrya*/*Carpinus*), ash (*Fraxinus*), walnut (*Juglans*),
328 sycamore (*Platanus*), and maple (*Acer*) (Fig. 3). These taxon abundances fluctuated but typically each were
329 <10% of the pollen assemblage (Fig. 3). Sycamore was generally more abundant in the middle Holocene
330 and decreases in the late Holocene. Hickory, ash, and maple conversely, were low during the middle
331 Holocene, then became more abundant in the late Holocene (Fig. 3). Both hornbeam and walnut remained
332 consistently low throughout the entire record (Fig. 3).

333 Herbaceous taxa were uncommon at Story Lake, except for ragweed (*Ambrosia*), which reached >40%
334 abundance in response to Euro-American land clearance (Fig. 3). Grass (Poaceae) first modestly increased
335 at 5.2 ka, then was moderately abundant after 3.0 ka BP, comprising approximately 5% of the pollen
336 assemblage until Euro-American land clearance, after which grass increased to its maximum abundance
337 of 15% at 0.0 ka BP (1950 CE, Fig. 3). Total non-arboreal pollen also peaked in response to Euro-American
338 land clearance with non-arboreal pollen dominating the assemblage at 0.01 ka BP (arboreal:non-arboreal
339 ratio = 0.67).

Three vegetation types, as determined by topic analysis, were robust to the choice of total number of vegetation types: beech-hardwood forest, oak forest/woodland, and open and cleared vegetation (Fig. 4, Supplementary Information). Vegetation types identified beyond these three generally further differentiate the oak forest/woodland into various communities that have oak as the dominant taxa but with different secondary taxa, while continuing to identify the beech-hardwood forest and open and cleared communities (Supplementary Information). One exception is the five topic model, which combines beech, oak, and elm into one community (Supplementary Information). However, the five-topic results have the worst model fit (highest AIC and BIC, Supplementary Information). The results for three vegetation types were chosen for further discussion here, with other variants available in Supplemental Information.

Beech-hardwood forest: This vegetation type is dominated by beech (beta = 0.34), with elm and oak as secondary taxa (beta = 0.20 and 0.12 respectively, Fig. 4b). Other important taxa include ash (beta = 0.08) and sycamore (beta = 0.07, Fig. 4b). This vegetation type is similar to the elm-ash-cottonwood vegetation type currently found in northern Indiana (McNab et al. 2007) as well as with pollen records from other beech forests in southern Ontario (Bennett 1987). Although cottonwood (*Populus*) pollen is not prevalent in the Story Lake pollen record, this modern vegetation type also contains sycamore and beech, which is consistent with the Holocene pollen record at Story Lake (Fig. 3). Over the Holocene, the prevalence of beech-hardwood forest changed rapidly five times, with two increases in prevalence (7.1 ka BP, and 2.8 ka BP) and three decreases (6.1 ka BP, 4.6 ka BP, and 0.02 ka BP).

Oak forest/woodland: This vegetation type is strongly associated with oak (beta = 0.57), with hickory and elm as secondary taxa (beta = 0.08 and beta = 0.07 respectively) (Fig. 4c). This vegetation type is similar to the oak-hickory vegetation type currently associated with northern Indiana, which is defined as having >50% of vegetation cover as oak and hickory (McNab et al. 2007). At Story Lake, the prevalence of oak forest/woodland changed rapidly five times, with timings that are synchronous with and opposite to

changes in prevalence of beech-hardwood forest. Hence, most of the vegetation changes at Story Lake during the Holocene can be characterized as a shift in prevalence between these two types. Both oak forest/woodland and beech-hardwood forest decreased in concert with Euro-American settlement at 0.02 ka, but oak forest/woodland rebounds slightly in the most recent pollen sample at 2019 CE, suggesting some recent reforestation.

Open or cleared vegetation: This late-Holocene-to-Anthropocene vegetation type is dominated by the herbaceous taxa ragweed (beta = 0.46) and grass (beta = 0.13). Prominence of open or cleared vegetation is low prior to Euro-American land-use intensification, with small peaks (0.17 gamma) at 2.5 ka BP. During the Euro-American period, this vegetation type prevailed, with a 0.96 gamma at 0.01 ka BP.

Fire History

The macroscopic charcoal record at Story Lake has a low signal-to-noise ratio (mean SNI = 2.7), with few individual peaks clearly distinguishable from the background trend (Fig. 5b). A SNI >3 is needed to confidently detect discrete fire events (Kelly et al. 2011). Low SNI values may indicate fire regimes characterized by high frequency but low severity fires, in which charcoal produced by individual fire events does not differ substantially from background values (Kelly et al. 2011). Alternatively, low SNIs can be due to low sampling resolution or high sediment mixing (Kelly et al. 2011), neither of which are likely at Story Lake due to high and contiguous sampling resolution and because the linear sedimentation rates observed (Fig. 2) are higher than the median and mean rates (0.076 cm yr^{-1}, 0.14 cm $year^{-1}$) for other kettle lakes in eastern North America (Goring et al. 2012), implying less time-averaging and mixing. Therefore, here we focus on variations in total charcoal accumulation rates (CHAR) at Story Lake and interpret CHAR as a proxy for shifts in the overall prevalence of low-intensity fires in the Story Lake watershed.

Charcoal was found in every sample, so times with zero charcoal represent a break in sampling due to core breaks and not a lack of charcoal in a sample (Fig. 5b). Total CHAR appears to have a quasi-cyclical

pattern in the middle Holocene (8.0 to 4.5 ka BP) with gradual rise and fall of CHAR over approximately 1000-year periods, ranging from 3 pieces cm^{-2} yr^{-1} to 56 pieces cm^{-2} yr^{-1} (Fig. 5b). From 4.4 ka to 3.3 ka CHAR is high, with an average of 38 pieces cm^{-2} yr^{-1}. CHAR steadily rises between 4.7 and 3.7 ka, reaching a maximum of 94 pieces cm^{-2} yr^{-1} at 3.7 ka (Fig. 5). After 3.5 ka, CHAR remains low (average of 12 pieces cm^{-2} yr^{-1}), with particularly low values after 1.0 ka (average of 8 pieces cm^{-2} yr^{-1}), until Euro-American land clearance, when CHAR increases to an average of 20 pieces cm^{-2} yr^{-1} (Fig. 5).

Hydroclimate History

Lake levels and $\delta^{13}C_{beech}$ record different phenomena and so provide different perspectives on the hydroclimate history of northern Indiana. The Lake Lavine reconstruction of past water level, which is governed by the watershed-scale balance between precipitation and evapotranspiration, shows a general increase in lake level over the Holocene, starting at 8.0 ka BP with a water depth 333 cm below modern levels (Fig. 5d). This increase suggests a generally positive water balance across much of the Holocene (Ray-Cozzens 2022). This trend was interrupted by several reversals, indicating periods of negative water balance. The first period of lake level increase lasted from 7.2 ka BP to 6.7 ka BP, followed by a subsequent decrease from 6.7 ka BP to 6.4 ka BP (Fig. 5d). There were three distinct periods of drought identified by sharp but short-duration decreases in lake level at 5.7 ka BP, 5.1 ka BP, and 4.7 ka BP, plus three more prolonged periods of lowered lake level from 6.4 to 6.0 ka BP, 3.9 to 3.5 ka, and 2.9 to 2.5 ka BP (Fig. 5d).

The values of $\delta^{13}C_{beech}$ at Story varies between -29.7 ‰ and -21.0 ‰ and thus indicate a fairly large range of variation in the iWUE of beech trees around Story Lake during the past ~5,000 years (Fig. 5c). The mean analytical range among individual aliquots from the same sample is 1.6‰. For most time periods $\delta^{13}C_{beech}$ values are highly negative, indicating low iWUE and prioritization of carbon gain over water loss. There are brief periods of higher iWUE ($\delta^{13}C_{beech}$ > mean $\delta^{13}C_{beech}$ [-25.1‰]) at 4.8 ka BP, 4.4 ka BP, 3.3 ka BP, 2.9 ka BP, 2.7 ka BP, 2.6 to 2.4 ka BP, 1.7 to 1.6 ka BP, and 0.6 to modern (Fig. 5c), possibly indicating

prioritization of water conservation. The time series of $\delta^{13}C_{beech}$ at Story Lake shows both some similarities to and differences from sub-regional hydroclimate changes deduced from water levels at nearby Lake Lavine (Fig. 5d). For example, two periods of decreased water level at 5.1 and 4.7 ka BP are followed by excursions towards more positive $\delta^{13}C_{beech}$ and higher iWUE at 4.8 and 4.4 ka BP (Fig. 5c, d), with a 300 year lag in iWUE for each event. If these proxies are recording the same events, the lags may result from chronological uncertainties in both records, or may indicate a differential sensitivity or response time. The records differ in that there are other periods when iWUE fluctuated but lake levels remained relatively constant (e.g. after 2.0 ka BP). Moreover, $\delta^{13}C_{beech}$ and iWUE show no long-term increase (Fig. 5c), unlike the long-term increase in lake levels during the past 5.0 ka BP (Fig. 5d).

Correlations among Proxies

Simple correlation relationships suggest a significant relationship between charcoal accumulation rates (CHAR) and the abundances of both beech and oak pollen abundances (Fig. 6). CHAR shows a positive correlation with oak abundance (slope = 37.0, p-value <0.001, r^2 = 0.11, Pearson's correlation = 0.33) and a negative correlation with beech abundance (slope = -58.9, p-value < 0.001, r^2 = 0.14, Pearson's correlation = -0.38) (Fig. 6). The 95th quantile regression shows an even stronger relationship between CHAR and oak (slope = 76.8, p-value < 0.001) and CHAR and beech (slope = -152.1, p-value < 0.001), suggesting that beech and oak abundances may be particularly sensitive to more intense fire regimes.

In contrast, there is no significant relationship between the relative abundance of beech pollen and $\delta^{13}C_{beech}$ (p-value = 0.06, Fig. 7), although the Pearson's correlation (0.28) suggests a modestly positive correspondence. Comparison of the $\delta^{13}C_{beech}$ and beech abundance time series shows possible evidence that the correlational structure has shifted over time. For example, between 5.0 and 4.0 ka two positive but single-point excursions of $\delta^{13}C_{beech}$ (higher iWUE) correspond to declines in beech abundance (Fig. 7). Conversely, at 2.2 and 1.5 ka BP negative excursions in $\delta^{13}C_{beech}$ (lower iWUE) match declines in beech

abundance whereas a positive excursion in $\delta^{13}C_{beech}$ (higher iWUE) at 1.7 ka BP is associated with a peak in beech abundance (Fig. 7).

Relative timing of beech fluctuations at Story, Appleman, Pretty, and Spicer Lakes

Fluctuations of beech populations are synchronous at the landscape scale but asynchronous regionally (Fig. 8). Two lakes located within 15 km of Story Lake, Appleman and Pretty Lakes, show positive correlation with Story Lake (Pearson's correlation 0.79 and 0.66 respectively; Fig. 8), suggesting that the rises and declines in beech populations recorded at Story Lake were part of broader vegetation phenomena recorded across northeastern Indiana. Of these three sites, the Holocene record at Story Lake is the best dated. Uncertainties in the Holocene age-depth models at Appleman and Pretty Lake are large enough (Appleman) or confounded by hardwater effects (Pretty) that lead/lag relationships among these records cannot be assessed (Supplemental Information). The number and timing of rapid change events in beech are not correlated between Story Lake and Spicer Lake (p-value=0.39; Fig. 8). The age-depth models for Story and Spicer Lakes records are well constrained, with 17 age controls at Story Lake and 17 age controls at Spicer Lake (Wang et al., 2016), and generally linear sedimentation rates at both sites. At Spicer Lake, beech experienced three rapid but short-lived decreases (5.3 ka BP, 4.3 ka BP, and 1.2 ka BP) and one rapid decrease followed by a prolonged period of low abundance (3.2 ka BP to 1.8 ka BP, Fig. 8) (Wang et al. 2016). None of these rapid changes are apparent at Story Lake (Fig. 8). To test whether the Story and Spicer records show synchronous events given age uncertainty, we identified three events that could be plausibly correlated between the Story and Spicer records: the initial rise at ca. 7.5 ka and the beginning and end of a prolonged period of low beech abundances during the middle to late Holocene (Fig. 8, red points with whiskers). Initial expansion is similar (within 200 years) but not synchronous (p-value <0.05). For the middle-Holocene decline in beech abundances at Story Lake at 4.6 ka we identified

two possible matches at Spicer, at 4.2 ka BP and 3.2 ka BP (Fig. 8b). Although the patten of the middle Holocene beech low period is similar the timing of the onset of low beech at Story Lake (4.6 ka BP) and both potential onsets at Spicer Lake (4.2 ka BP and 3.2 ka BP) are significantly different (p-value <0.05), as is the timing of recovery (2.8 ka BP at Story Lake and 1.8 ka BP at Spicer Lake, p-value <0.05; Fig. 8). These inter-site comparisons thus demonstrate apparent synchrony of beech dynamics at a landscape scale (i.e. among sites in northeastern Indiana) and regional-scale asynchrony (i.e. between northwestern and northeastern Indiana).

Discussion

Shifts in sensitivity to fire and climate drivers of oak-beech transitions in the Southern Great Lakes

Multiple lines of evidence suggest that ecosystem-type conversions and the prevalence of mesic beech-hardwood forests and oak forest/woodland at the northern margin of the former Prairie Peninsula were closely regulated by shifts in fire regime and secondarily by hydroclimate and other factors. These dynamics acted to synchronize beech fluctuations at local to landscape scales and produce asynchronous changes at regional scales (northwest Indiana versus northeast Indiana). The positive and negative feedbacks among hydroclimate, fire, and vegetation appear to have varied in strength and direction over time (Fig. 9). Consequently, the ecoclimatic sensitivity of vegetation shifted over time, including periods of relatively high sensitivity to extrinsic drivers and other periods where beech-hardwood forests persisted despite strong extrinsic forcing.

8.0 to 4.6 ka: High sensitivity to fire and climate (Fig. 9a) - The initial expansion of beech-hardwood forests in the Story Lake region between 7.3 and 7.1 ka was rapid, which is consistent with other sites in the regions which show similar rapid expansions of beech upon arrival (Bennett 1988) and occurred during a period of low fire prevalence and net positive water balance, as indicated by low CHAR and rising lake

levels (Fig. 5). The subsequent decline in beech-hardwood forests between 5.0 ka and 4.6 ka appears to have been largely governed by disturbance regime and extrinsic climatic factors, because the decline corresponds closely to an intensifying fire regime (as indicated by a rise in CHAR beginning at 6.0 ka, Fig. 5b) and brief periods of increased iWUE and likely water stress in beech (Fig. 5c). During this period of beech-hardwood forest declines, the individual fluctuations in total CHAR show no clear connection to fluctuations in vegetation prevalence. Rather, the multi-centennial decline in beech-hardwood forests is matched by a multi-centennial increase in fire activity.

Coincident with the increase in fire activity, Mg/Ca data from Lake Geneva on the Wisconsin-Illinois border indicate potential regional warming from 5.2-4.6 ka, with high temperatures then persisting until 3.8 ka (Puleo et al., 2020). The warming would be expected in Indiana as part of a large-scale change in atmospheric patterning reconstructed in the northeast U.S. (Shuman et al., 2023). If this temperature record applies regionally, the warming may explain the increased fire activity, even though the Lake Lavine water levels increased substantially from 5.0 to 4.4 ka BP. Both fire and warming could have worked in concert to reduce beech-hardwood forests, while favoring oak-derived fuels conducive to increased wildfire. Oak and beech have differing temperature preferences; just as beech populations extended further north historically into Michigan than oak (Fig. 1), oak pollen abundances peak today where mean July temperatures exceed 20°C whereas beech abundance peaks below 20°C (Williams et al., 2006). The lake-level and charcoal records further suggest that effective moisture availability declined during and preceding periods of intensified fire regime and increased iWUE (and possibly water stress) of beech, for example at 5.2-5.0 ka BP and 4.9-4.6 ka BP (Fig. 5b-d). Hence, for this initial period (8.0 to 4.6 ka), one hypothesis is that climate variations were the primary determinant of fire regime and thus also of beech/oak prevalence (Fig. 9).

4.6 to 3.7 ka: Strong fire-vegetation coupling (Fig. 9b) - The period from 4.6 ka BP to 3.7 ka BP is marked by prominence of oak forest/woodland, an active fire regime, potentially high regional temperatures, and

503 an initial increase but then stable or slightly declining lake levels (Fig. 5). The iWUE of beech appears to
504 be moderate to low (Fig. 5c), suggesting low moisture stress. Hence, during this period, a positive feedback
505 loop between fire-tolerant oak and a high-frequency but low-intensity fire regime may have been the
506 primary factor governing the dominance of oak forest/woodland and scarcity of mesic beech-hardwood
507 forests. Fire as an agent of maintaining prairie and oak woodland type ecosystems has been widely seen
508 during the Holocene in the eastern Prairie Peninsula and eastern US (Nelson et al. 2006, Vose and Elliot
509 2016, Nowacki and Abrams 2008). Many oak species are particularly well adapted to frequent low
510 intensity fire regimes due to their thick bark, suitability of fire disturbed landscapes for seeding, ability to
511 resprout after fire, deep root systems, and suppression of fire sensitive competitors (Vose and Elliot 2016,
512 Abrams 1992). Therefore, frequent low intensity fires can promote establishment and spread of oak
513 woodlands through suppression of fire-intolerant species (e.g., beech), which could modify the understory
514 to suppress fires (Nowacki and Abrams 2008). Therefore, a prolonged period of oak woodland dominance
515 could have facilitated a positive feedback loop (Fig. 9) that supported the increased and sustained low
516 intensity fire regime at Story Lake from 4.6 ka BP to 3.4 ka BP, even during periods when $\delta^{13}C_{beech}$ and
517 iWUE suggests low water stress (Fig. 5). Notably, a peak in beech abundance at 4.0 ka BP when beech
518 pollen accumulation rates equal those at other times of beech dominance (Supplemental Information)
519 may have been limited by wildfire at Story, in contrast to Spicer where fire was limited and beech
520 abundance was high until 3.2 ka BP (Fig. 8).

521 *3.7 to 2.8 ka: Rapid ecosystem transition linked to shifting fire and climate (Fig. 9c) -* After 3.7 ka BP, fire
522 activity sharply declines until a low point at 3.2 ka BP (Fig. 5b), which coincides with increased water
523 availability and decreased iWUE (Fig. 5). These relationships suggest a direct regulation of fire regime by
524 climate, which is consistent with current controls on wildfire in the Great Lakes Region where winter and
525 early spring precipitation and snow cover are major controls over fire frequency and thus the presence of
526 mesic, fire intolerant forests (Henne et al. 2007, Cardille et al. 2001). Late summer precipitation is also an

important deterrent for wildfire in the Great Lakes region (Cardille et al. 2001). However, $\delta^{18}O$ Holocene records in northeastern Indiana, southeastern Wisconsin, and eastern North America indicate no change in precipitation seasonality (Stuiver 1968, Puleo et al. 2020, Stefanescu et al. 2023); therefore a combination on increased summer and winter precipitation may have resulted in the decreased fire regime seen at Story Lake. Regional cooling at 3.8-3.2 ka BP may have also been a factor (Puleo et al., 2020; Shuman et al., 2023). Based on inferred changes in the latitudinal temperature gradient in eastern North America, the warmest conditions would been expected from 4.8-3.8 ka BP when oak-hickory communities replaced cool-tolerant hardwood forests in Pennsylvania, New York, and Massachusetts (Shuman et al., 2023) and the Mg/Ca ratio peaked in southern Wisconsin (Puleo et al., 2020). Today, climate patterns show that cool north-central areas of North America tend to decrease wildfire activity; temperature has a strong influence on wildfire activity via vapor-pressure deficits and effects on fuel moisture (Gedaloft, 2010).

An increase of hickory at 3.6 ka (Fig. 3) suggests that the climate changes and diminished fire resulted first in in-filling of oak woodlands and establishment of oak-hickory forests. Then, 400 years after the decline of fire, mesic beech-hardwood forests rapidly increase in prevalence at 2.8 ka BP. This sequence thus could suggest a prolonged two-stage successional change that is obscured by the lack of species-level resolution for many pollen taxa, particularly oak. For example, a plausible infilling of oak woodlands to oak forests and shift from more fire-tolerant (e.g. *Q. macrocarpa, Q. alba, Q. ellipsoidalis*) to fire-sensitive oak species (e.g. *Q. velutina, Q. rubra*) that cannot be differentiated by pollen analysis. Alternatively, regional temperatures, a factor not captured at Story Lake, may have continued to decline until 2.9 ka (Shuman et al., 2023). The continued cooling thus could have directly or indirectly affected the ability of mesic beech-hardwood forests to outcompete oak forest/woodland and would explain why oak remained dominant until 2.8 ka BP, even though fire activity declined after 3.7 ka BP.

550 The differences between beech histories at Spicer and Story (Fig. 8) argue somewhat against strong direct
551 regulation by temperature, because temperature variations tend to be spatially autocorrelated at
552 landscape to regional scales. However, prior work in Minnesota's Big Woods indicates that regional-scale
553 temperature variations, combined with local- to landscape variations in fire exposure and moisture
554 availability, can produce a spatial and temporal mosaic of rapid vegetation changes (Shuman et al. 2009,
555 Umbanhower 2004). Additionally, an increase in winter precipitation between 7.0 ka BP and 4.0 ka BP is
556 observed in western Michigan, at sites immediately downwind of Lake Michigan, suggesting localized lake-
557 effect snow (Henne and Hu 2010), which could be a factor in the difference between Story and Spice Lake
558 to the west. The proximity of Spicer Lake to Lake Michigan (Fig. 1) may have made it more subject to lake
559 effects and hence differing Holocene variations in temperatures, moisture, and fire history than the
560 northeastern sites (Story, Appleman, and Pretty, Fig. 8).

561 With or without a direct temperature influence, the rapid ecosystem transition at 2.8 ka (Fig. 4, 5a)
562 involved a first-stage establishment of nearly fire-free oak-hickory forests that allowed beech and other
563 fire-sensitive hardwoods, such as maple, to establish in the understory and later become widely prevalent.
564 The lag time between cessation of fire regime and the rapid establishment of beech forests is
565 approximately 400 years, suggesting that some abrupt ecosystem transitions may occur centuries after
566 the original triggering event. A positive feedback loop between increasing beech abundance and
567 establishment of microclimates inimical to fire establishment and spread may have further accelerated
568 this transition (Nowacki and Abrams 2008, Alexander et al. 2021). The low beech iWUE during this
569 transition (Fig. 5c), suggests that the combination of high-water availability and suppressed fire regime
570 may be essential for enabling this rapid ecosystem transition (Fig. 9).

571 *2.8 ka to European Settlement: Vegetation Persistence and Stable State (Fig. 9d) -* After 2.8 ka, the
572 prevalence of oak forest/woodland and beech-hardwood forests around Story Lake fluctuated but
573 remained roughly even on the landscape from 2.8 ka until the onset of Euro-American land clearance

(1860 CE), despite large fluctuations in $\delta^{13}C_{beech}$ (Fig. 5). Moreover, the Lake Lavine record suggests a period of lowered lake levels between 3.0 and 2.5 ka, soon after the rapid re-establishment of mesic beech-hardwood forests without re-establishment of oak forest/woodland dominance. This vegetation persistence despite ongoing hydroclimate variability suggests that a new stable state had been reached in which beech is maintained internally through a stabilizing negative feedback loop that is resilient to hydroclimate variability (Fig 9). In this negative feedback loop, high beech abundances create microclimates favorable to beech recruitment and inimical to fire spread, thus reducing ecosystem sensitivity to environmental variability (Nowacki and Abrams 2008, Alexander et al. 2021). Nonetheless, some of the brief excursions in prevalence of oak forest/woodland and beech-hardwood forest may be linked to hydroclimate perturbations or to small shifts in fire regime (Fig. 5b), or to intrinsic ecosystem processes such as frequency dependent species interactions (Ramiadantsoa et al. 2019). Overall, we hypothesize that the persistence of beech-hardwood forest during the late Holocene, prior to Euro-American arrival is primarily governed by intrinsic processes and stabilizing vegetation feedbacks (Fig. 9).

Other possible drivers not directly analyzed

In addition to internal ecosystem processes and climate, humans may have also affected fire and vegetation dynamics at Story Lake, although human activities are not directly captured in our proxy network. Archaeological records from the middle Holocene suggest that human societies in Indiana were highly mobile foragers, although the population and community dynamics of peoples in this time-period and region are not well understood (Stafford et al. 2000, Jones and Johnson 2016). Summed probabilities for calibrated radiocarbon dates from archaeological contexts in the Great Lake Region (calculated from Kelly et al. 2022 using the method in Surovell et al. 2009), which are often used as a simple indicator of human population abundances, suggests a population increase from 6.5 ka BP to 5.5 ka BP, then a period of low population from 5.5 ka KP to 3.9 ka BP, and a gradual increase from 3.9 ka BP to a peak at 0.7 ka BP. These fluctuations in radiocarbon date summed probabilities do not appear to correspond to changes

598 in fire intensity, which peaks from 4.4 ka BP to 3.7 ka BP during a low point of human population. The
599 rapid beech increase at 2.9 ka BP occurs during the middle of the population increase, but at a point when
600 population is still low. Native American communities at other sites in the Upper Midwest and
601 Northeastern US have managed landscapes using fire (Abrams and Nowacki 2019, Abrams and Nowacki
602 2008, Clark and Royall 1996), likely with localized and patchy impacts (Munoz et al., 2014). Many late-
603 Holocene pollen records in eastern North America do not have clear signals of human activity (Gajewski
604 et al. 2019). To further elucidate the effects of human societies and environmental change on ecosystem
605 dynamics in the Great Lakes region, more work is needed with paired pollen, charcoal, and hydroclimate
606 proxies at sites with known human occupation, as has been done in Ontario (Munoz and Gajewski 2010,
607 McAndrews and Boyko-Diakonow 1989, Burden et al. 1986).

608 Pests and pathogens have also been invoked as possible mechanisms for rapid declines in tree populations
609 during the Holocene. Hemlock looper outbreaks have been suggested as a cause for the eastern hemlock
610 declines (Davis, 1981, Bhiry and Filion 1996, Booth et al. 2012a), but other studies have failed to find
611 evidence of looper outbreaks (Oswald et al. 2017). Beech is a thin-barked species that has been highly
612 susceptible to the introduction of the beech scale insect (*Cryptococcus fagisuga*) from Europe in the 1890s
613 and the outbreak of beech bark disease, which arises from the infection of various fungal species after
614 beech scale insect infestation (Beckman et al. 2021). Modern studies on European beech (*Fagus sylvatica*)
615 have found that stands are susceptible to pathogen damage, such as from the fungus *Kretzschmaria*
616 *deusta*, which has been found in beech forests during the Holocene, with high abundances of fungal
617 ascospores traced to flood events (van Geel et al. 2013, Cordin et al. 2021). However, pests and pathogens
618 are difficult to detect using traditional palaeoecological approaches, such that even in ecosystems with
619 regular insect outbreaks (e.g. bark beetles), the outbreaks can only be detected through indirect means
620 (Morris and Brunelle, 2012) or at small forest hollow sites (Schafstall et al. 2020). Hence, whether pests

621 and pathogens had any effect on American beech dynamics during the Holocene remains possible but
622 unknown and unstudied.

623 Interpreting and reconciling the $\delta^{13}C_{pollen}$ record

624 Much of the insight gained in this study into past fire-climate-vegetation interactions comes from having
625 multiple proxies from the same core, with precise relative depth positioning. In particular, the analysis of
626 $\delta^{13}C_{beech}$ enables a more direct understanding of whether beech water use responds to changes in water
627 balance (from lake level proxies) and whether those responses scale to changes in beech population
628 abundance. Several prior studies have shown a positive correlation between $\delta^{13}C_{pollen}$ and drought stress
629 for many plant species including *Cedrus* (Bell et al. 2017), *Nothofagus* (Griener et al. 2013), *Artemisia*, and
630 *Ambrosia* (Nelson et al. 2012). Other studies have shown that Holocene shifts in vegetation in eastern and
631 midwestern North America are linked to past hydroclimate variations, e.g. the mid-Holocene abrupt
632 declines of hemlock (Booth et al. 2012a, Shuman 2012, Marsicek et al. 2013), mid- to late-Holocene
633 declines in beech (Booth et al. 2012b, Wang et al. 2016), and shifts in the prairie-forest ecotone (Nelson
634 et al. 2006, Williams et al. 2010). Most of these studies have paired fossil pollen records with paleoclimatic
635 proxies that are sourced from lacustrine or palustrine archives (Clifford and Booth 2015, Shuman et al.
636 2009). However, trees, lakes, and bogs have different sensitivities to hydroclimate fluctuations, with
637 differently scaled integrations across watershed ecohydrology and different response times to
638 atmospheric shifts in water supply and demand. Therefore, even paleo-hydrological proxies from the
639 same sediment cores as fossil pollen or paired well-dated sites may not provide a direct measure of plant
640 responses to changes in hydroclimate. This differential response of proxies to changing water availability
641 has hampered understanding of the direct vegetation response to changes in hydroclimate.

642 The analyses here generally suggest some correspondences between the hydrological water balance at
643 Lake Lavine (Fig. 5d) and iWUE of beech at Story Lake (Fig. 5c), but also notable differences. Some

individual events appear to correlate drought periods with high iWUE and high beech abundance, e.g. at 5.1 ka Bp and 4.7 ka BP, while others periods show the opposite pattern with no apparent correlation between moisture availability, iWUE, and beech abundance, e.g. after 2.4 ka BP. However, small fluctuations in lake level may not be apparent in the lake level reconstruction due to low sampling in shallow cores. Additionally, the long-term wetting trend from 8.0 ka BP to present in the lake level reconstruction is not apparent in $\delta^{13}C_{beech}$. One possible explanation is that biological systems are often characterized by homeostatic mechanisms, while physical hydrological systems might or might not. Hence, the ratio of photosynthesis to stomatal conductance is only expected to vary within physiological limits that prevent the $\delta^{13}C$ values of C_3 plants from becoming too positive or negative. It is also possible that there is intraspecific variation in iWUE among beech trees and successional dynamics across the lifetime of individual trees may favor individuals with generally higher or lower iWUE, thus acting to stabilize population-level shifts in iWUE inferred from $\delta^{13}C_{beech}$ across centennial-millennial scales. Conversely, if atmospheric annual water balance is positive, lake water level should continue to increase, until water levels are high enough that a stream outlet or other balancing outflow is reached. Therefore, a one-to-one relationship between pollen $\delta^{13}C$ values and lake levels is not to be expected.

The absence of a significant relationship $\delta^{13}C_{beech}$ and beech abundance at Story Lake (Fig. 7) is surprising given that a positive correlation between $\delta^{13}C$ and drought stress is reported in modern studies of various taxa (Bell et al. 2017, Griener et al. 2013, Nelson et al. 2012). As explained above, one hypothesis for this lack of a relationship is that water availability is the main regulator of $\delta^{13}C$, but that, as fire-climate-vegetation feedbacks shift in strength and direction over time, water availability is a secondary and intermittent regulator of beech population abundances, with periods of direct hydroclimate control on beech populations and periods of indirect regulation though mediating fire regimes (Fig. 9). Alternatively, variations $\delta^{13}C_{beech}$ and iWUE during the Holocene might be affected by other factors beyond moisture availability. For example, increased photosynthesis has been a major driver of increased iWUE in response

668 to increased atmospheric CO_2 during the past century (Mathias and Thomas, 2021); however, during the
669 Holocene, the effects of CO_2 on iWUE should be muted, given that atmospheric CO_2 variations were
670 modest, with a linear rise of only 260 to 280 ppm between 8.2 ka and 1800 CE (Indermuhle et al., 1999).
671 Changes in temperature during the Holocene (Shuman et al. 2023) may have also influenced iWUE
672 through the influence of temperature on photosynthesis (Dusenge et al. 2018), potentially interacting
673 with changes in water availability.

674 Landscape to regional controls on beech declines and beech-oak dynamics

675 The multiple rapid beech fluctuations throughout the Holocene in northern Indiana appear to be
676 synchronous at the landscape scale (less than 15 km distance between Story, Appleman, and Pretty Lakes)
677 but are clearly asynchronous at regional scale (120 km distance between Story and Spicer Lakes). This
678 pattern of landscape-scale synchrony and regional asynchrony suggests that local- to landscape-scale
679 interactions between species, fire regime, and climate are the dominant drivers of vegetation change,
680 including rapid vegetation change (Fig. 9). Note also that Story Lake shows a close correspondence
681 between fire regime and vegetation dynamics (Figs. 5, 7) whereas Spicer Lake has little to no charcoal and
682 no clear correspondence between fire regime and vegetation change (Wang et al., 2016). Hence, the
683 importance of fire-vegetation feedbacks appear to vary intra-regionally, with fire an important driver of
684 ecological change at Story Lake and generally unimportant at Spicer Lake.

685 Within-landscape correlations among sites in beech abundance (within 15 km) suggests that small scale
686 factors, such as disturbance, have a local synchronizing effect in northern Indiana. Although proxies for
687 fire and water stress were not collected at Appleman or Pretty lakes, the synchrony between sites
688 suggests that the same factors are driving vegetation change at all local sites. Therefore, the interactions
689 between fire and hydroclimate that are seen at Story Lake are likely important at all three sites. The
690 controlling effects of fire on forest transitions are well documented during the Holocene such as the

691 prairie peninsula (Nelson et al. 2006, Nelson and Hu 2008), Minnesota's big woods (Calder 2016,
692 Umbanhower 2004, Shuman et al. 2009), and eastern North America (Abrams and Nowacki 2019).

693 Intra-regional differences in hydroclimate and vegetation dynamics might also be governed by the lake-
694 effect snow, which intensifies local hydroclimate variability (Booth et al., 2012b) and has been shown to
695 affect vegetation composition in Michigan (Henne et al. 2007). Spicer Lake, which is 17 km from the
696 southeastern shore of Lake Michigan, may be more affected by variations in lake-effect snow, while Story
697 Lake, further east, may be more directly regulated by past shifts in fire regime. This lake-effect hypothesis
698 is consistent with the pre-settlement distribution of beech which positively correlated with total snowfall
699 (Seely et al. 2019) with the importance of lake-effect snow in maintaining snow cover throughout the
700 winter being especially important in areas with coarse textured soils which do not retain water and rely
701 on snowmelt for establishment of mesic species in the spring (Henne et al. 2007). This is also seen during
702 the MCA, where both droughts and beech declines were heterogenous on the landscape with sites that
703 had more pronounced drought also having larger beech declines (Booth et al., 2012b). Hence, just as the
704 importance and directionality of fire, vegetation, and climate interactions at Story Lake appears to vary
705 during the Holocene (Figs. 5, 9), the relative importance of these drivers and interactions likely varied
706 spatially as well, across all scales considered here: local, landscape, and regional.

707 Additional multi-proxy and high-resolution records are needed to further disentangle the interacting
708 effects of climate, fire, and vegetation dynamics at local to sub-regional scales. Further insight can be
709 gained also by more advanced statistical analyses than the relatively simple correlational analyses shown
710 here. In particular, advances in ecological modeling, such as state-space models, allow more precise
711 testing of hypotheses about drivers of community dynamics and allow separation of process-based drivers
712 from observational errors inherent in palaeoecological data e.g., time uncertainty and sampling errors
713 (Auger-Méthé et al. 2021). Combining a large network of multi-proxy high-resolution sites with state-
714 space models can provide further quantification of regional drivers of ecological change.

Conclusions

The interacting effects of fire and climate on ecosystem-type conversions is a major societal concern and the beech-oak mosaic in northern Indiana offers a useful model system for understanding how these changes in mesic forests are governed by past shifts in climate variability and fire regime. At Story Lake, variations in the prevalence of beech-hardwood forests and oak forests/woodlands throughout the Holocene, including rapid changes, are mediated by multiple and shifting feedbacks among climate, fire, and vegetation. At Story Lake, fire appears to a strong regulator of vegetation composition changes, with climate also exerting direct effects on fire regime and vegetation dynamics. Temperature variations may also have played a role, a critical need is more independent paleotemperature proxies in this region. Possible contributing factors that are mostly unexplored here include human activity and pests or pathogens. The timing of beech declines differs from those observed at Spicer Lake, where fire is not prevalent, suggesting that variation in local fire regime (and perhaps also moisture availability via lake-effect snow) drives intraregional differences in beech population dynamics. This work has shown the potential for $\delta^{13}C_{beech}$ in assessing both the sensitivity of beech to hydroclimate perturbations and identifying periods of beech forest persistence despite apparently large changes in iWUE and moisture availability. These periods of persistence may indicate strong stabilizing feedbacks.

Climate change is one of the main threats to American beech and, in Indiana, climates are expected to get warmer and wetter with more extreme events and less snowfall (Beckman et al. 2021, Widhalm et al. 2018). With beech bark disease now introduced and fire events mostly suppressed, the interactions between climate variability, disturbance regime, and disease are likely to be very different between the Holocene dynamics studied here and those of the 21st century. Nonetheless, fire-climate feedbacks are an underappreciated source of risk in the Great Lakes region, and rising temperatures and future drought events may have profound effects on beech populations in the Great Lakes region through initiating more

738 fires and favoring oak forests over beech forests as seen at Story Lake during the Holocene.
739 Recommendations for future work include 1) the continued building of a high-resolution multi-proxy
740 network to further disentangle the interacting effects between vegetation, fire regime, climate, and
741 human activity, 2) furthering our understanding of the behavior of $\delta^{13}C$ (e.g. through paired high-
742 resolution $\delta^{13}C$ analyses of pollen grains from lake sediments and tree rings of the same taxa) to
743 disentangle stand- and landscape level signals of tree physiological reactions to changes in water
744 availability; 3) the development and application of state-space modeling approaches to further establish
745 causality of vegetation change within and across networks of sites at local to subcontinental scales, and
746 4) conducting forward looking studies to better understand how climate change, disturbance regime, and
747 pathogens may impact feedbacks between climate, fire, and vegetation in the Great Lakes region which
748 will both advance our understanding of the underlying fundamental processes and help direct future
749 conservation efforts.

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Tables

Table 1: List of all macrofossils and radiocarbon dates and additional points used to build the age–depth model for Story Lake, Indiana. The date that was identified by the age-depth model as an outlier is indicated with an asterisk (*), radiocarbon dates that represent post-1950 CE samples (identified with a cross †) have age estimates were provided by *CALIBomb*. NA indicates that there is no radiocarbon date associated with that sample either because the sample does not come from radiocarbon dated material (coretop and *Ambrosia* rise), the two samples determined to be modern (27.5 cm and 29.5 cm), and a sample that was too small for dating (642.5 cm). Calibrated years BP is equal to the mean ± 1σ or for ^{14}C the calibrated median age (years before 1950 CE)

Laboratory ID	Core Depth (cm of sample midpoint)	^{14}C age and error (radiocarbon years before 1950 CE)	Calibrated years BP	95% Calibrated credible interval age range (year BP)	Dated material
Coretop	0.5	NA	-69± 10	NA	Core top
STOR191A1B-27.5	27.5	NA	-21 ± 12†	NA	Leaf fragment
STOR191A1B-29.5	29.5	NA	-21 ± 12†	NA	Leaf fragment
STOR191A2L-128.5	128.5	NA	90 ± 25	NA	*Ambrosia* rise
STOR191A2L-138.5	138.5	170 ± 15	187	5-279	Leaf fragment
STOR191A2L-151.5	151.5	400 ± 60	440	315-523	Wood fragment
STOR191A2L-181.5	181.5	970 ± 15	851	801-920	Root fragment
STOR191A3L-262.5	262.5	2085 ± 15	2040	1996-2108	Fibrous plant
STOR191A2L-296.5	296.5	2505 ± 15	2576	2501-2716	Fibrous plant
STOR191A2L-304.5	304.5	2530 ± 20	2620	2509-2729	Fibrous plant
STOR191A4L-332.5	332.5	42440 ± 840*	45093	43591-46554	Fibrous plant
STOR191A6L-519.5	519.5	4590 ± 60	5296	5052-5461	Leaf fragment
STOR191C6L-575.5	575.5	5520 ± 25	6308	6283-6389	Leaf fragment
STOR191A2L-615.5	615.5	6270 ± 70	7183	6992-7333	Leaf fragment
STOR191A2L-642.5	642.5	NA	NA	NA	Plant fiber

STOR191A8L-668.5	668.5	7660 ± 360	8524	7808-9373	Leaf fragment
STOR191A8L-717.5	717.5	8025 ± 20	8890	8781-9001	Wood fragment
STOR191A9L-836.5	836.5	10110 ± 210	11740	11124-12519	Cone fragment

Figures

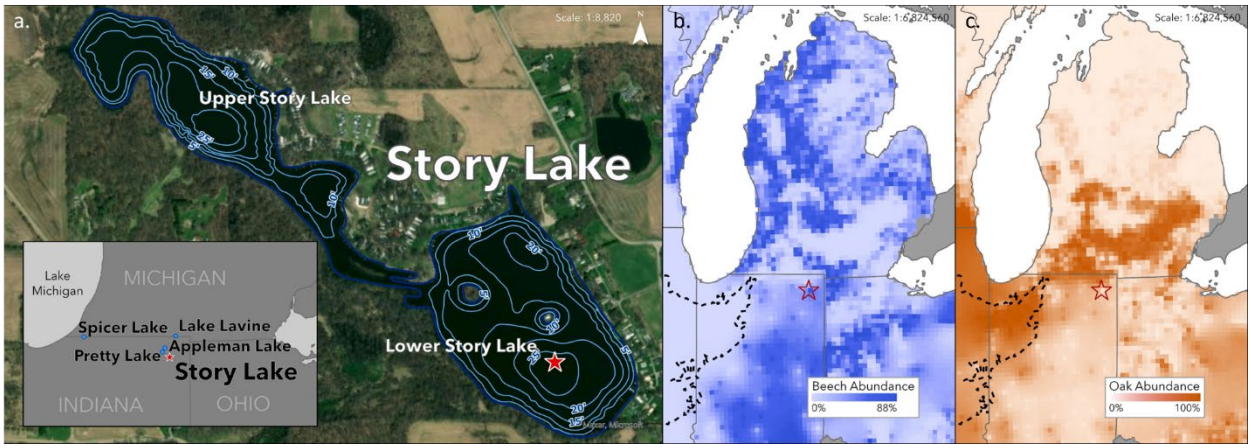
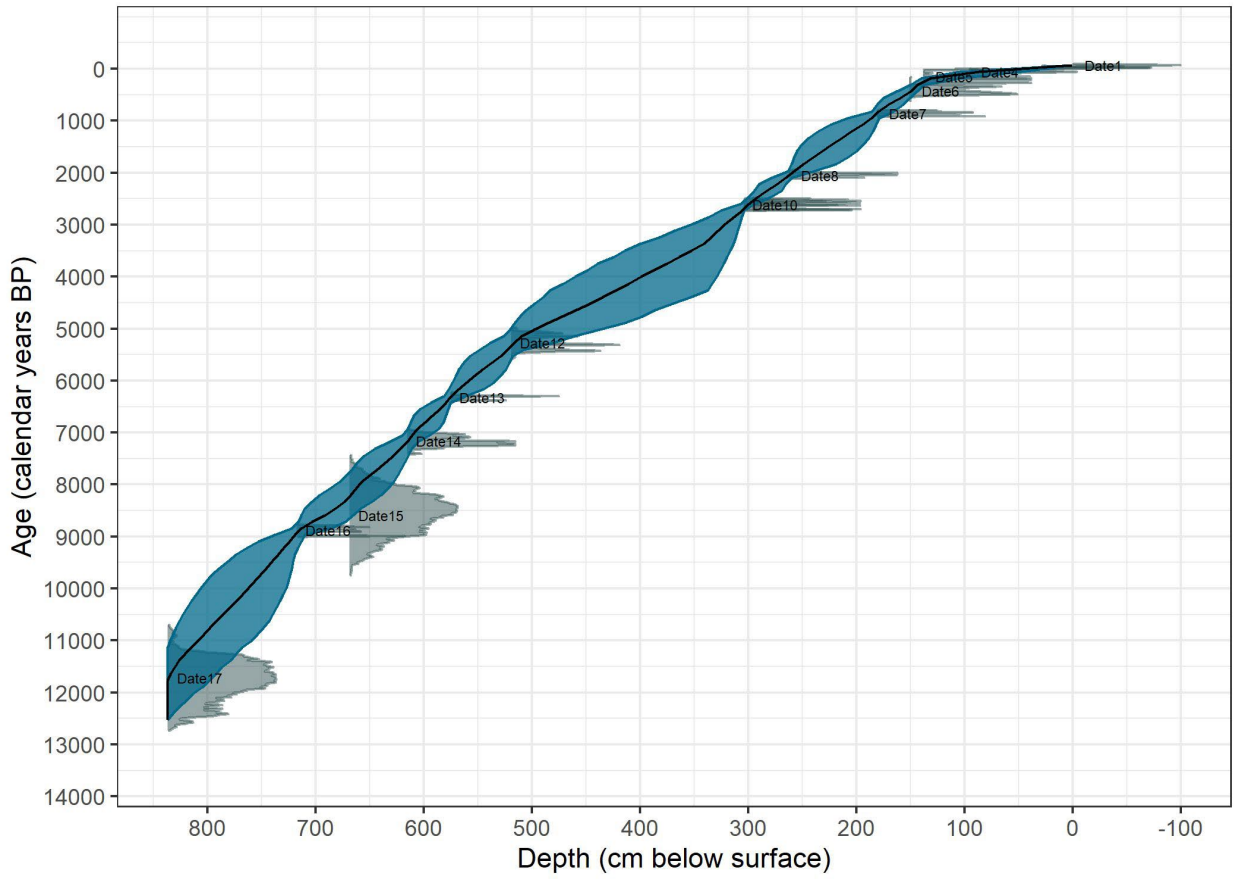
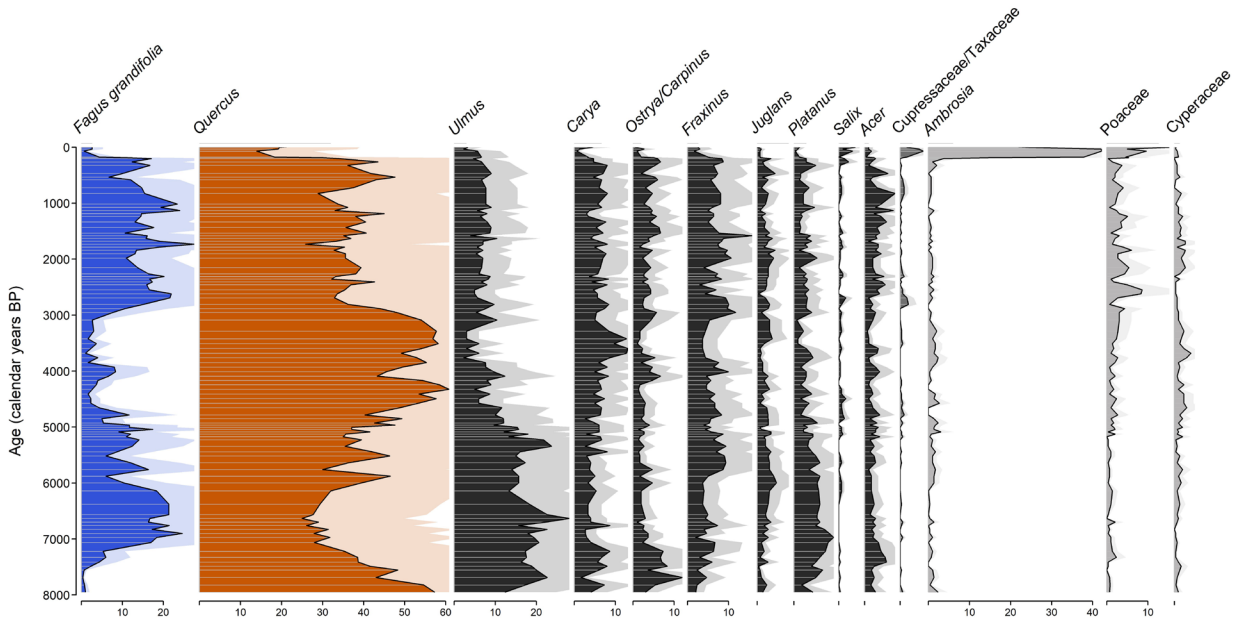


Figure 1: Panel a shows the coring location for Story Lake, Indiana (IN), with bathymetric contours showing lake depths in 1.52m (5 foot) increments (blue lines, IDNR 2019). Inset map shows location of Story Lake (red star) and four comparison sites: Lake Lavine, MI, Spicer Lake, IN, Appleman Lake, IN, and Pretty Lake, IN (blue points). Panels b and c show the location of Story Lake relative to pre-settlement distributions of American beech (middle) and oak (right; Paciorek et al. 2016). The dashed line indicates the boundary of the temperate prairie parkland from the USDA Ecological Subregions (McNab et al. 2007). Areal imagery Sources: Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community.



1133

1134 Figure 2: Age-depth model for Story Lake, based on the *bchron* R package (Haslett and Parnell, 2008),
1135 constructed from 17 age controls (15 ^{14}C dates, *Ambrosia* rise, coretop, Table 1), shows a continuous
1136 sediment record spanning from 11.7 ka BP to present with an average deposition time of 9.25 years/cm.
1137 Individual radiocarbon dates are shown as the density distributions of their calibrated ages (grey). The
1138 95% confidence interval of the age-depth model is shown in blue. One ^{14}C date at 332.5 cm was
1139 determined as an outlier by *bchron* (Table 1) and is not shown here.



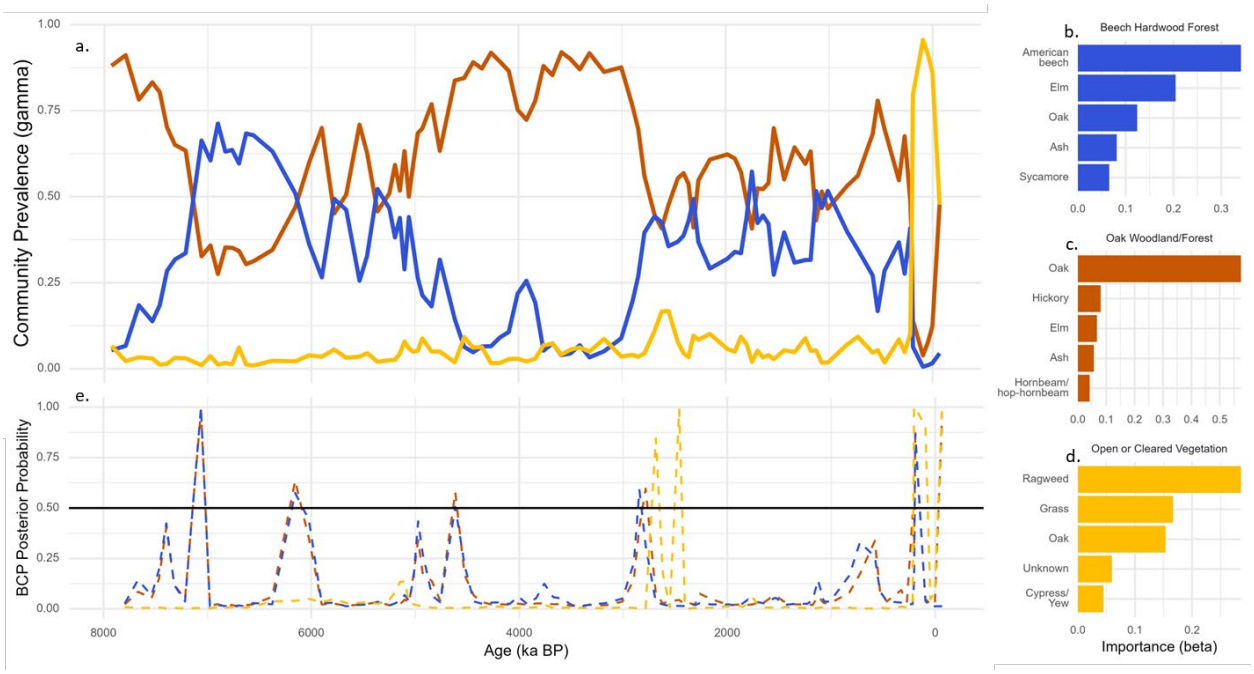
1140

1141 Figure 3: Pollen percentages of major taxa (>3.5% abundance) for Story Lake, Indiana from 8 to 0 ka BP.

1142 American beech (*Fagus grandifolia*, blue) and oak (*Quercus*, orange) are highlighted. Arboreal pollen types

1143 have a black fill, while non-arboreal pollen types have a gray fill. Exaggerated pollen curves (pollen percent

1144 x2) are shown in lighter colors. Individual samples are indicated by horizontal light lines.



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1146 Figure 4: Prevalence of vegetation types through time at Story Lake as identified by the CTM topic model
1147 (panel a). Colors correspond to vegetation types: beech-hardwood forest (blue), oak forest/woodland
1148 (orange), and open/cleared vegetation (yellow). The importance of taxa within each vegetation type is
1149 displayed as bar graphs (panels b-d). Dashed lines in panel e show the probability of change points for
1150 each community type based on Bayesian change point analysis, with the black horizontal bar indicating
1151 the 0.5 posterior probability threshold used to identify change points.

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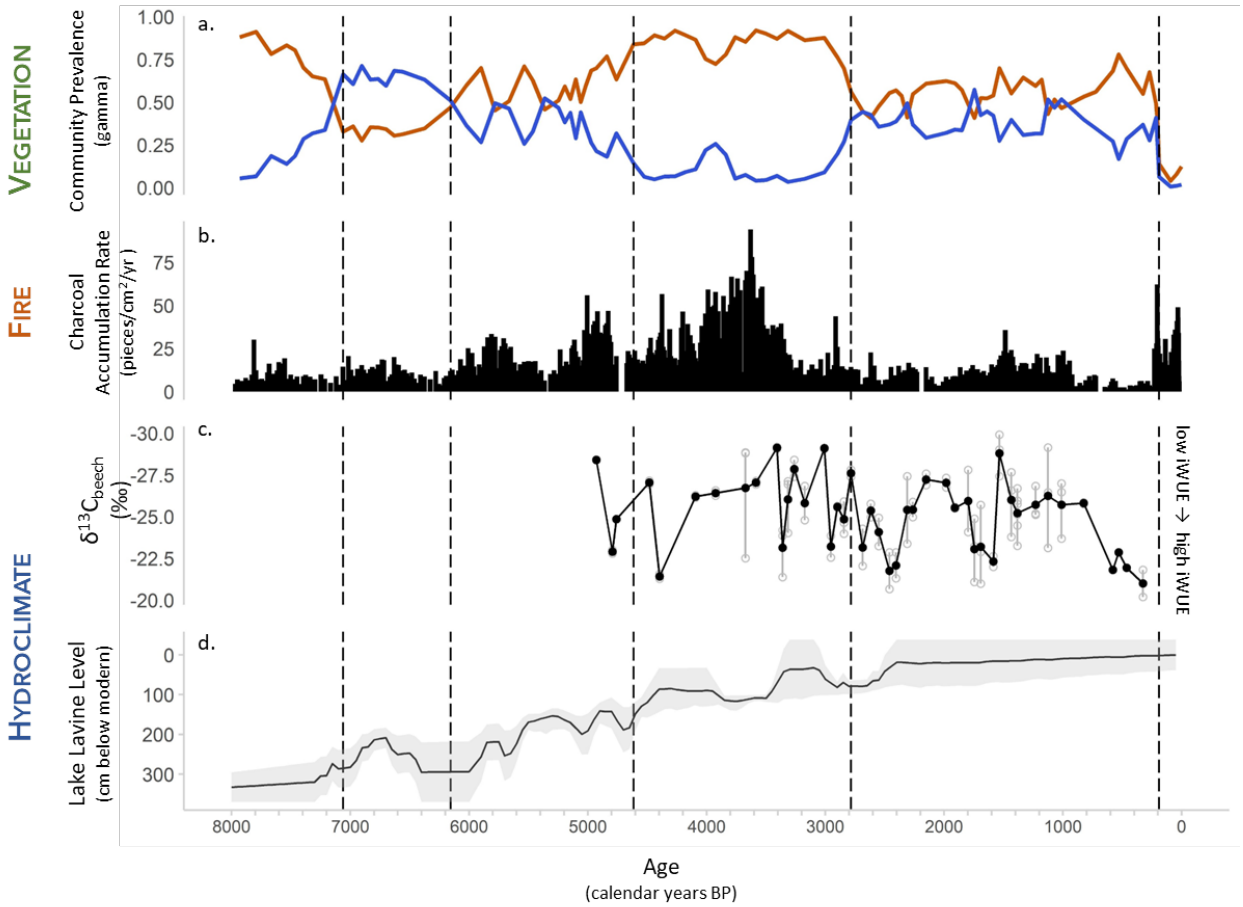


1153

1154 Figure 5: Combined time series for vegetation, fire, and hydroclimate proxies. Panel a shows the
1155 community prevalence of beech forest (blue) and oak woodland (orange), based on CTM gamma scores.
1156 Panel b shows, charcoal accumulation rate (pieces/cm^2/yr), an indicator of fire history (panel b). Panels c
1157 and d show indicators of plant iWUE and hydroclimate, expressed as $\delta^{13}C_{beech}$ (panel c) and lake level
1158 variations of Lake Lavine, IN (panel d, from, Ray-Cozzens 2022). In panel c, individual aliquots of $\delta^{13}C_{beech}$
1159 are indicated by grey hollow circles connected by a vertical line. Vertical dashed lines are based on change
1160 point analysis of the topic model (Fig. 4e) and indicate times when both beech forest and oak woodland
1161 have probability of a change point greater than 0.5.

1162

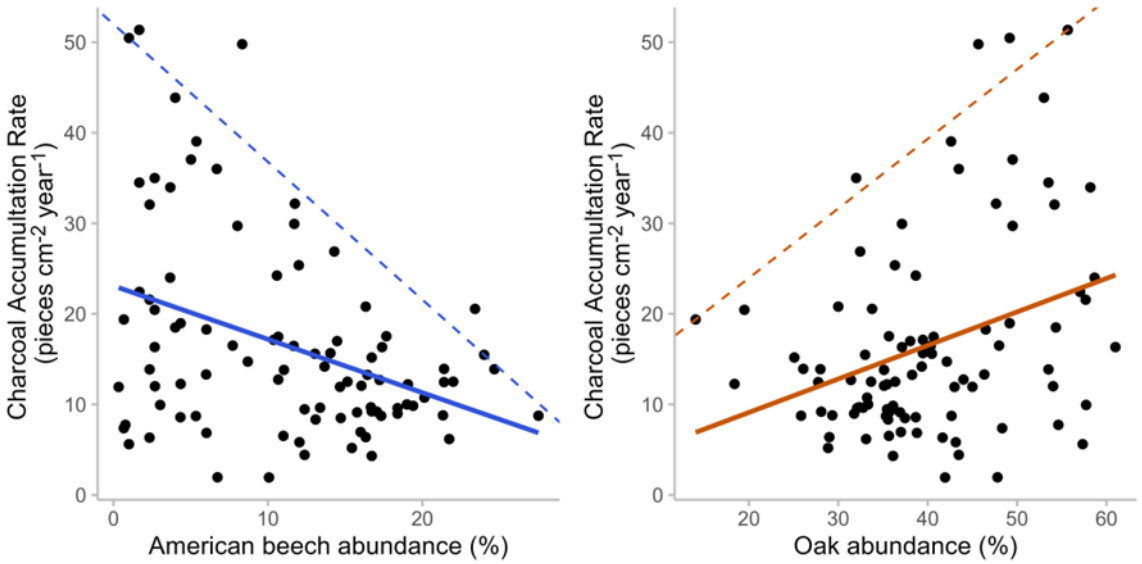


Figure 6: Correlation between charcoal accumulation rate and American beech (*Fagus grandifolia*) abundance (left, p-value < 0.001, r^2 = 0.14, Pearson's correlation = -0.38) and oak (*Quercus*) abundance (right, p-value <0.001, r^2 = 0.11, Pearson's correlation = 0.33). Dashed lines represent the 95th quantile regression.

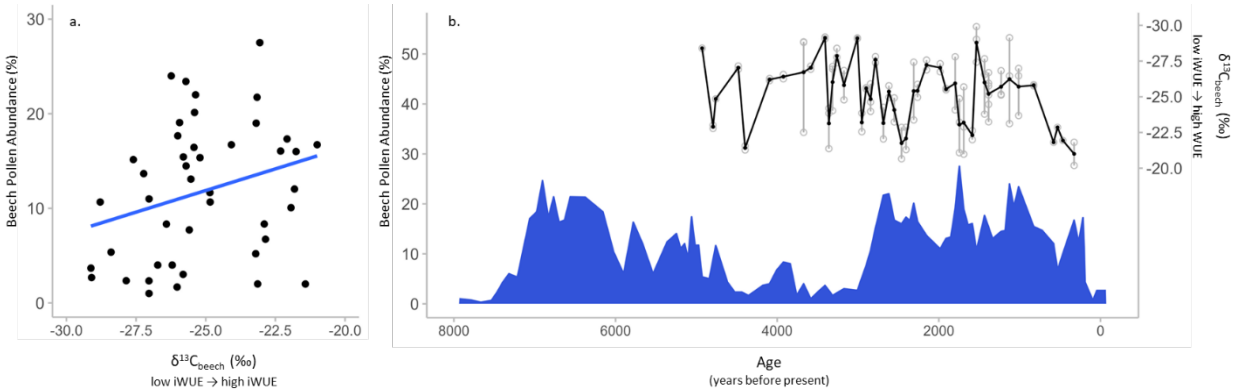


Figure 7: Comparison of American beech (*Fagus grandifolia*) pollen abundance (panel a, y-axis and panel b left y-axis) and $\delta^{13}C$ of American beech pollen grains ($\delta^{13}C_{beech}$, panel a x-axis and panel b right y-axis). Individual aliquots of $\delta^{13}C_{beech}$ are shown on panel b, indicated by grey hollow circles connected by a vertical line. Direct comparison of American beech abundance and $\delta^{13}C_{beech}$ (panel a) shows no significant correlation (p-value = 0.06, r^2 = 0.06, Pearson's correlation = 0.28).

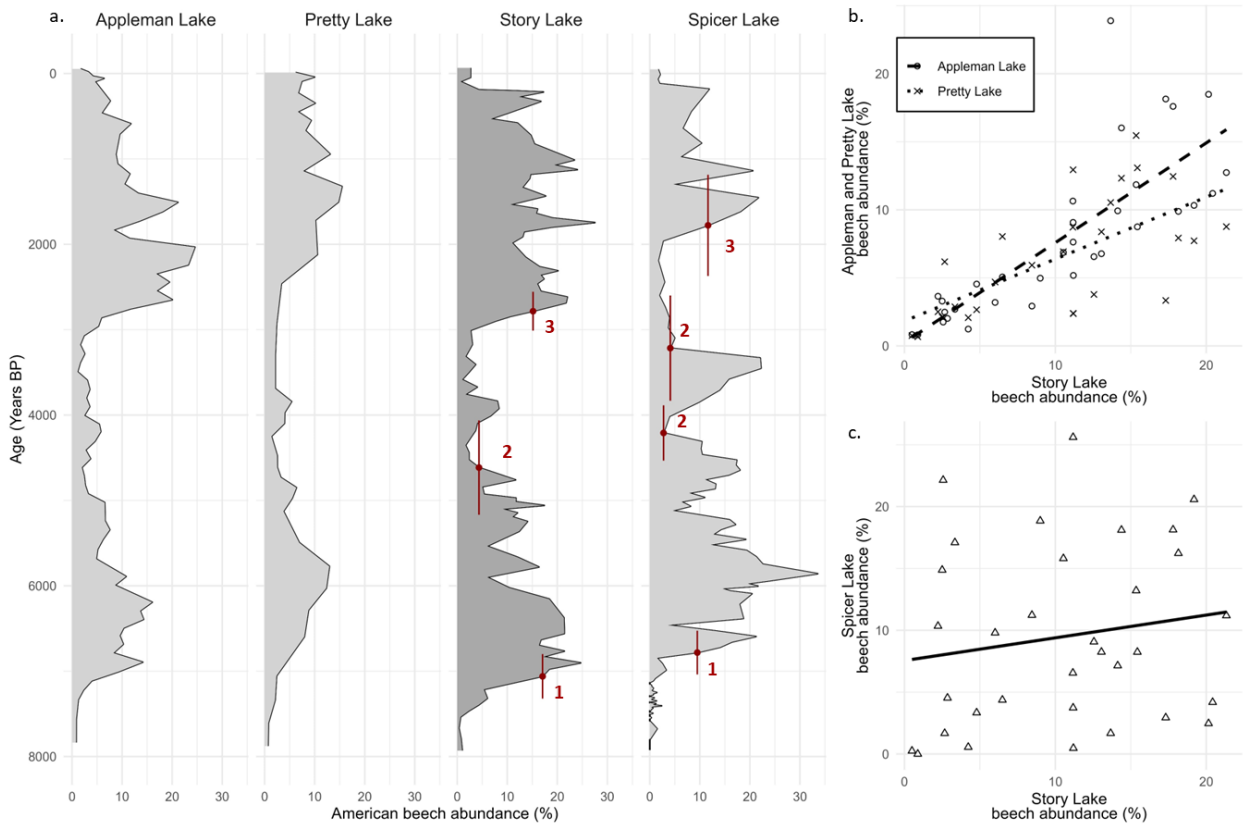
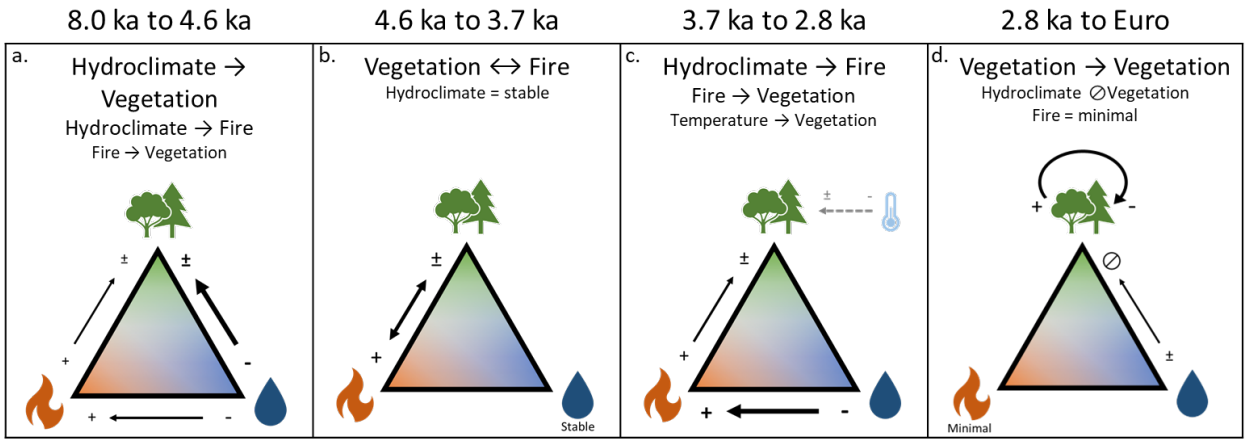


Figure 8: a) Comparison of Holocene variations in American beech (*Fagus grandifolia*) pollen abundances for Story Lake and nearby Appleman and Pretty Lakes, and the more distal lake, Spicer Lake. To compare regional timing of beech fluctuations, red bars represent the 95% confidence interval as inferred by *bchron* for selected points in the Story and Spicer Lake records with possible visual correspondences: the initial early-Holocene rise (1), the beginning of the mid-Holocene low period compared to two potential matches in the Spicer Lake record (2) and the end of the mid-Holocene low (3). b) Correlation of American beech abundances between Story Lake and local lakes, Appleman (p-value < 0.05, $r^2 = 0.64$, Pearson's correlation = 0.80) and Pretty (p-value < 0.05, $r^2 = 0.44$, Pearson's correlation = 0.66). c) Correlation of American beech abundance between Story Lake and Spicer Lake (p-value = 0.39, $r^2 = 0.03$, Pearson's correlation = 0.15).



1187

1188 Figure 9: Schematic diagram, showing interpretation of the changing drivers and vegetation-fire-
1189 hydroclimate feedbacks of ecological change at different time periods (a-d) at Story Lake, Indiana.
1190 Regional-scale temperature changes, which were not directly analyzed here, but which may modulate
1191 these feedbacks are identified by a grey dashed arrow. The hypothesized relative importance of each
1192 factor is depicted by arrow width and font size.