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A High-Resolution Paleoecological Perspective on Temperate Oak Forest Dynamics: Implications for Understanding Contemporary Oak Decline

Robert Anthony Mason
Lehigh University, bobmason54@gmail.com

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A High-Resolution Paleoecological Perspective on Temperate Oak Forest Dynamics:

Implications for Understanding Contemporary Oak Decline

by

Robert A. Mason

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"A High-Resolution Paleoecological Perspective on Temperate Oak Forest Dynamics: Implications for Understanding Contemporary Oak Decline"

Robert A. Mason

Date Approved

Robert K. Booth (Advisor)

David J. Anastasio (Department Chair)

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ABSTRACT

Recruitment failure of oak (*Quercus*) during the past century has raised concerns about ongoing changes in temperate forests of the eastern United States. Although the causes of oak decline and the associated forest changes are widely debated, most arguments have focused on the effects of fire suppression or moisture availability. Paleoecological records have provided long-term perspectives on oak forest dynamics, but these pollen and charcoal data are often limited by poor spatial, temporal, or taxonomic resolution. In this study I utilized pollen, charcoal, and plant macrofossils preserved in Turtlehead Rock Bog, a small floating peatland occupying a unique depositional basin in an oak-black birch (*Betula lenta*) forest in southwestern Pennsylvania to 1) reconstruct the depositional and wetland history of this unusual system, 2) compare the timing of wetland and upland changes with fire history and regional paleoclimate records, 3) develop a high-resolution record of fire and oak forest dynamics, and use these data to discuss oak decline and current management strategies.

Results indicate contemporaneous shifts in the arboreal pollen and wetland macrofossil records, along with changes in sediment accumulation rate, soil bulk density, organic matter content, and overall macrofossil preservation, suggesting a climate or disturbance driver for most vegetation changes. From 9000 to 2000 cal yr BP, sandy, charcoal-rich sediment accumulated slowly and preserved evidence of a changing upland forest and fern-dominated wetland. Then a >1000 year depositional hiatus occurred, likely caused by regional aridity. At 800 cal yr BP a sedge marsh

occupied the basin, followed by the establishment of a diverse sedge peat mat around 550 cal yr BP, associated with an increase in black birch and likely wetter conditions. Oak (likely *Q. prinus* and *Q. rubra*), American chestnut (*Castanea dentata*), and black birch have dominated the surrounding forest for the past 900 years, while fire occurrence and oak abundance both gradually declined. Comparisons of charcoal accumulation and oak pollen support a historical fire-oak linkage influenced by overall forest composition; however, oak has expanded in the past 75 years during a period of fire suppression. Recent oak recovery at the site may be attributable to a local fire event around 1930 and/or the eradication of American chestnut. Therefore, although prescribed burns likely increase oak recruitment in some forest types, human modifications to the landscape appear to have altered the historical relationship between fire and oak, warranting caution in using prescribed burns to increase oak recruitment on the modern landscape.

INTRODUCTION

Understanding the primary drivers of temperate forest community change is critical to successful ecosystem management and conservation (Dale et al., 2001; Salinger, 2005; Chazdon, 2008). Current knowledge of forest dynamics comes largely from observational data collected during the past several decades - or centuries if such records are available (Willis & Birks, 2006). These short-term data are useful for documenting recent and ongoing change (Sagarin & Pauchard, 2010), having identified significant shifts in abundance for some tree species and associated changes to forest ecosystems (Iverson & Prasad, 2001; Wyckoff & Clark, 2002; Cote et al., 2004; Schumacher & Carson, 2013). However, short-term studies provide limited information on the range of natural environmental variability experienced over centennial-to-millennial timescales (Willis & Birks, 2006), as well as ecosystem response to extreme climatic and disturbance events (e.g., Clifford & Booth 2015), particularly in regions where such events have been relatively rare during the past century (Pederson et al., 2014). Given current and expected climatic changes (Stocker et al., 2013), long-term perspectives are vital to inform conservation efforts and anticipate future ecological changes (Willis et al., 2007; Jackson & Hobbs, 2009). By revealing past forest responses to changes in climate and disturbance, paleoecological perspectives provide insight into the causes of recent and ongoing change and may inform adaptive management strategies (Willis & Birks, 2006; Millar et al., 2007; Willis et al., 2007; Jackson & Hobbs, 2009).

Observational studies have documented a widespread decline in populations of oak (*Quercus*) during the past century in the temperate forests of the eastern United States (Clark, 1992; McDonald et al., 2002; Abrams, 2003; DeSantis et al., 2010). At some locations declining oak abundance is associated with mortality; however, most attribute the changes to recruitment failure (McDonald et al., 2002). White oak (*Quercus alba*) appears to be declining faster than red oak (*Quercus rubra*) and other oak species (Abrams, 2003), and the effects of species-specific differences remain unclear. Since the early 1800s, the decline of oak populations and their replacement, usually by red maple (*Acer rubrum*) and sugar maple (*Acer saccharum*) (McDonald et al., 2002; McEwan et al., 2011), has been cited as a topic of concern because oaks have long been important to humans as a source of lumber (Clark, 1992) and are an irreplaceable food source for mast-dependent wildlife (McShea et al., 2007). The resulting ecological and economic consequences will likely grow until a viable management solution to oak decline is found, which depends on an accurate understanding of the problem (Foster et al., 2002; McShea et al., 2007). This issue has generated considerable debate within the scientific and management communities as studies from the stand- to regional-scale have suggested multiple interacting drivers including pests and pathogens, deer overbrowsing, forest fragmentation and parcelization, altered gap dynamics, and most commonly, fire suppression and/or increased moisture availability (Lorimer, 1992; Abrams & Seischab, 1997; Clark, 1997; Foster et al., 2002; McShea et al., 2007; McEwan et al., 2011).

Long-term, multi-decadally-resolved perspectives on the ecological dynamics of oak-dominated forests may discern the relative importance and interactions of forest composition, fire disturbance, and climate variability (Dale et al., 2001; Millar et al., 2007; McEwan et al., 2011). Although pollen and charcoal records have been developed in oak-dominated regions, these records have largely focused on regional scales and most have been poorly resolved temporally and/or taxonomically (Clark & Royall, 1996; Foster et al., 2002; Jackson & Booth, 2007; Booth et al., 2012; Clifford & Booth, 2015). Stand-scale perspectives with high temporal resolution and species-level taxonomic precision are necessary for comparison with modern investigations of ecological processes such as tree recruitment, growth, and mortality (Woods, 2000; Jackson et al., 2014). Forest hollows, which are small (~20 m^2) depositional basins within a forest, yield long-term pollen and charcoal records strongly weighted toward representation of local vegetation and fire events (Calcote, 1995; Kearsley & Jackson, 1997; Davis et al., 1998), and the adjacent and/or overhanging canopy often results in an abundance of terrestrial plant macrofossils which commonly allow species-level identifications, in contrast to pollen which typically allows only genus or family-level identification (Jackson & Booth, 2007). A stand-scale fire history coupled with a taxonomically-precise vegetation record may provide a novel perspective on oak-dominated forest dynamics and their sensitivity to changes in climate and disturbance (Booth et al., 2012; Jackson et al., 2014).

In this study I examined a sediment record of charcoal, pollen, and macrofossils from a small basin in an oak-black birch (*Betula lenta*) forest in southwestern

Pennsylvania. The small size of the basin and its overhanging forest vegetation make the site comparable to a forest hollow – an ideal environment for terrestrial plant macrofossil analyses (Jackson & Booth, 2007) and stand-scale paleoenvironmental reconstruction (Calcote, 1995; Davis et al., 1998), therefore Turtlehead Rock Bog is uniquely suited to provide a high-resolution long-term perspective on contemporary oak decline and associated forest changes. The primary objectives of this study were to 1) reconstruct the Holocene depositional and wetland developmental history of this unusual system, 2) compare the timing of wetland and upland changes, 3) develop a high-resolution record of fire and oak forest dynamics, and use these data to discuss oak decline and current management strategies.

STUDY SITE

Characteristics

Turtlehead Rock Bog is located in an oak-black birch forest in Fayette County, Pennsylvania (Figure 1A) in Ohiopyle State Park which has a mean annual temperature of 8.2°C and receives 1377 mm of precipitation (United States Climate Data [USCD], 2015). The wetland is within a small basin (~110 m^2, Figure 1B) confined by large rectangular boulders of Homewood sandstone positioned on the eastern flank of the Laurel Hill anticline at an elevation of approximately 840 m. The basin is likely artesian-fed by down-dip oriented joint openings that connect it to an aquifer with an estimated 15 m of hydrologic head and a 4 ha recharge area, possibly part of a perched aquifer system with an impermeable underclay or shale base associated with the Upper Mercer Coal seam.

The formation of the basin is not completely understood, though it may have formed through the fracturing of a resistant ledge of Homewood sandstone (J. Shaulis, personal comm.). The up-dip end of a large rectangular section may have loosened and rotated downslope about 30 m by solifluction, while the down-dip end remained relatively stationary (Figure 2). This rotation left a separation cavity with a narrow opening near the main ledge, which when healed, allowed water and sediment to accumulate upslope of an overflow spillway on the structurally down-sip side.

The floating peat mat which occupies the basin today is dominated by three-way sedge (*Duclichium arundinaceum*) along with other sedge species and cinnamon fern (*Osmunda cinnamomea*). *Sphagnum* moss (*Sphagnum sp.*) occurs in patches. The basin rock walls are covered in great laurel (*Rhododendron maximum*) and mountain laurel (*Kalmia latifolia*), and these boulders support a tree community of sassafras (*Sassafras albidum*), black birch, red maple, black gum (*Nyssa sylvatica*), and several oak species (e.g. *Q. prinus, Q. rubra, Q. macrocarpus*).

History

The first known inhabitants of this region were the Monongahela, who left as Europeans first arrived in the Americas, and were replaced by the Shawnee, Lenni Lenape, Seneca, and other native peoples during the 18th Century (Department of Conservation and Natural Resources [DCNR], 2015). The first European settlement near present-day Fayette County was established in 1752, but few immigrants followed until after 1762, when large groups from Virginia and Maryland emigrated in 1765 (Donaway, 1928). After the National Road was built in 1811, the population of settlers increased again, and by the turn of the 20th Century, the area had been logged extensively. In 1964 the land was sold to the Commonwealth by the Western Pennsylvania Conservancy, and the Ohiopyle State Park opened the following year (DCNR, 2015).

METHODS

Field Methods

In October 2015 a series of sediment cores was collected from Turtlehead Rock Bog, and basin depth was measured with flexible probe rods along a transect through the site's long axis and at random grid points perpendicular to the transect (Figure 3). Not all areas of the peat mat were buoyant enough to support our weight, particularly combined with the weight of the coring equipment, thus cores were collected from two locations 7 m apart. At location 1 where the mat was thicker and more stable, we collected a 40 cm-long monolith (diameter~15 cm) from the surface mat, one 93 cm-long core using a modified, wide-diameter (10.5 cm) Livingston piston corer, and three 50 cm-long drives with a Russian peat corer (diameter=5 cm); these cores were used for high-resolution analysis of the recent record. At location 2 where the basin was deepest, we collected four 50 cm-long drives with a Russian peat corer, and these drives were used to develop the early portion of the record. All cores were wrapped in plastic wrap and aluminum foil, labeled, and stored in PVC tubing for transport to cold storage at Lehigh University in Bethlehem, PA.

Laboratory Methods

Each sediment core was sectioned into 1cm intervals, and the slices were divided into subsamples: 1 cm^3 for bulk density and loss-on-ignition analyses, 1 cm^3 for pollen analyses, and the remainder for macrofossil analyses (for the large monolith slices about 10 cm^3 were used for macrofossil analyses). Standard loss-on-ignition techniques were used to determine soil bulk density and organic matter content for each centimeter: drying at 90°C for 24 hr, heating at 550°C for 5 hr, and recording the sample weight before/after each step (Dean, 1974).

Pollen analyses generally followed standard procedures (Faegri & Iversen, 1989), although a sieving technique successfully used in previous studies to isolate both testate amoebae and pollen from peat was utilized for pollen preparations (Booth et al., 2010; Booth et al., 2012; Clifford & Booth 2015). *Lycopodium* tablets of known concentration (20848 spores/tab) were added to pollen subsamples to allow concentration calculations, and 200 arboreal grains were tallied in samples every other centimeter from 0-220 cm and every ten centimeters from 220-340 cm. Pollen percentages for arboreal pollen taxa were calculated as percentages using a total arboreal pollen sum, while percentages of wetland and non-arboreal upland pollen and spores were calculated using a total pollen sum. Charcoal fragments were tallied with pollen 0-220 cm (diameter=15-300 μm, hereafter referred to as “microscopic charcoal”), and charcoal concentrations were calculated based on the known concentration of the introduced *Lycopodium* spores. Influx (n/cm^2/yr) was calculated for microscopic charcoal fragments and dominant arboreal pollen using the age-depth model inferred deposition time of the sample and the concentration.

Each subsample for macrofossil analysis was measured by volumetric displacement in a graduated cylinder, and then sieved using a 150 μm mesh. All distinguishable macrofossils and charcoal fragments greater than this size were identified and tallied for each centimeter, and concentrations of charcoal (diameter>150 μm, hereafter referred to as “macroscopic charcoal”) and plant macrofossils were expressed per average sample volume (13 ml). Macroscopic charcoal influx was calculated using the age-depth model inferred deposition time of the sample and the concentration. Plant macrofossils or charcoal were collected from 16 depths and sent to the Woods Hole Oceanographic Institution NOSAMS facility and the University of Georgia Center for Applied Isotope Studies for radiocarbon dating (Table 1). All ages in this paper are expressed as calibrated years before present (cal yr BP), where the present is defined as 1950 AD.

Data Analysis

An age-depth model for the site was developed using a Bayesian approach and the software package *BACON* (Blaauw & Christen, 2011). In addition to the 16 radiocarbon-dated depths, dates were assigned for the top of the core (-65.8 cal yr BP), and for the pathogen-caused functional extinction of American chestnut in the 1920s (27.5±2.5 yr BP) observed in both the pollen and macrofossil records at 40 cm. This estimation was based on the *Final Report of the Pennsylvania Chestnut Tree Blight Commission* (1914), which noted that 11 infected chestnut trees were found and removed from Fayette County between 1912 and 1913, as well as J. E. Aughanbaugh's detailed report (1935), which indicated a nine-year infection timeline from blight introduction to chestnut eradication for Mont Alto State Forest in south-central Pennsylvania, and numerous map figures available online which placed the event between 1915 and 1930.

The software package *CharAnalysis* was used to identify likely local fire events in the macroscopic charcoal record from 0-220 cm (Higuera et al., 2009), as this portion of the record was analyzed contiguously (i.e., every cm). Background charcoal accumulation rate was estimated using a 100 year Lowess smoothing window, and peaks were isolated from residual data using locally-defined thresholds determined by a Gaussian mixture model and minimum count screen (Higuera et al., 2009; Higuera et al., 2010; Kelly et al., 2011). Influx of microscopic and macroscopic charcoal was compared to the vegetation history, and the potential ecological effects of the local fire events defined by *CharAnalysis* were also examined.

Stratigraphically-constrained cluster analysis (*Tilia-CONISS*) was used to objectively delineate major transitions in the arboreal pollen and wetland macrofossil records (Grimm, 1987). The pollen and macrofossil data were input as percentages and counts, respectively, and were square root transformed prior to utilizing Edwards and

Cavalli-Sforza’s chord distance as a dissimilarity index for the clustering (Grimm, 1987). The total sum of squares dendrograms were used to assist in the identification of upland and wetland vegetation zones and to facilitate discussion of the records by providing context for comparing vegetation and fire history.

RESULTS

Age-Depth Model and Depositional History

The age-depth model and physical sediment properties revealed several substantial changes since 9000 cal yr BP when deposition began (Figure 4). Sand and charcoal-rich sediments accumulated slowly (0.17 mm/yr) from 9000 cal yr BP until about 2000 cal yr BP (~219 cm). During these first 7000 years bulk density was high (1.03 g/cm^3), organic matter content was low (11%), and minimal macrofossil preservation occurred.

Sediment stratigraphy, soil bulk density, organic matter content, and total macrofossil concentration exhibited large shifts at about 219 cm in core drives from both coring locations, and radiocarbon dates above (216.5 cm) and below (225.5 cm) this horizon indicate a dramatic change in age between these depths (Figure 4). Based on the abrupt changes in bulk density, the sudden preservation of macrofossils as well as pollen changes (discussed later), a low in organic matter content, and the large amount of time represented between the dated horizons (~1200 years), it is very likely that there was a depositional hiatus in the sediment sequence at approximately 219 cm.

The hiatus in sediment accumulation lasted over 1000 years, until about 800 cal yr BP, at which point the basin began rapidly accumulating more organic-rich sediments, although sand from the adjacent sandstone boulders remained an important inorganic component. The mean sediment accumulation rate for about the first 150 years after the hiatus was about an order of magnitude greater (1.6 mm/yr) than the mean of the previous period, bulk density decreased by more than half (0.37 g/cm^3), and organic matter content nearly doubled (20%). The most apparent change observed during analysis of the transition was the surge of organic debris and macrofossils, quantified by the mean total plant macrofossil concentration which increased from 2 to 86 identifiable specimens per sample.

Accumulation and physical properties of the sediment experienced another important transition around 550 cal yr BP. Sediment accumulation rate increased (2.6 mm/yr), bulk density dropped to half its previous mean (0.15 g/cm^3), organic matter content tripled (60%), and mean total plant macrofossil concentration also increased (120 specimens per sample). About 250 cal yr BP bulk density was halved again (0.08 g/cm^3), organic matter content increased (88%), and these values plateaued around 25 cal yr BP (0.07 g/cm^3 and 96%, respectively) when sediment accumulation rate increased (4.4 mm/yr), mean total plant macrofossil concentration dropped to 66 specimen per sample.

Upland Vegetation and Fire History

Stratigraphically constrained cluster analysis of arboreal pollen data was used to guide the identification of five pollen zones to help summarize the upland vegetation of the site (Figures 5, 6). See Table 2 for information on the plant organs represented by the macrofossil analyses.

Zone P1 (9000-2000 cal yr BP)

Although Zone P1contains minimal plant macrofossils and is coarsely resolved with analyzed pollen samples separated by about 600 years, it represents a long period of time (~7000 years) with dramatic vegetation changes and forest compositions substantially different from today. When deposition began 9000 years ago, the area was dominated by eastern hemlock (*Tsuga canadensis*) and black birch, with oak increasing after 8000 cal yr BP (Figure 5). From 7500 to 5000 cal yr BP black gum, American beech (*Fagus grandifolia*), and American chestnut became more common alongside oak, and laurel (Ericaceae) increased in the subcanopy (Figure 6). Hickory (*Carya*) increased, and oak replaced chestnut, reaching its peak abundance in the record just prior to the hiatus, while chestnut dropped to its lowest pre-European levels. Zone P1 was characterized by very high macroscopic charcoal concentrations, and although the sediment accumulation rate was very low, charcoal influx rates are still relatively high (Figure 6).

Zone P2 (800-550 cal yr BP)

Given the depositional hiatus, the site history between 2000 and 800 cal yr BP is unknown; however, when the high-resolution record began about 900 years ago, the upland forest community was dominated by oak. The macrofossil record revealed that both white and red oak groups (*Quercus* subgenera *Eurythrobalanus* and subgenera *Leucobalanus),* likely corresponding to chestnut oak and red oak as these species are abundant today, were present along with American chestnut, black birch, sugar maple, black gum, and American holly (*Ilex opaca*) (Figure 5). The surrounding boulders and upland subcanopy were occupied by various shrubs, including winterberry (*Gaultheria procumbens*), great laurel, and mountain laurel, and charcoal influx values were high relative to the following zones (Figure 6).

Zone P3 (550-60 cal yr BP)

Zone P3 was characterized by increasing black birch macrofossils and birch pollen, decreasing oak pollen, and the consistent presence of red maple and other less prominent canopy taxa (Figure 5). Other than these changes, forest composition was similar to that of Zone P2. Charcoal influx decreased overall, but increased sharply in the mid-1800s (Figure 6).

Zone P4 (60-10 cal yr BP, 1890-1940 AD)

Widespread logging in the late 1800s and early 1900s was reflected by dynamic changes in pollen and macrofossil abundances during Zone P4 (Figure 5). Oak pollen fell dramatically, but briefly, around 50 cal yr BP with a concomitant increase in birch pollen and black birch macrofossils. American chestnut pollen declined, and both pollen and macrofossils disappeared at the time of its pathogen-caused functional extinction. Black birch macrofossils remained high during and shortly after the demise of American chestnut. Charcoal influx decreased again, as macroscopic charcoal was rare in this zone and microscopic charcoal showed continued decline (Figure 6).

Zone P5 (the last ~75 years)

During the time that the area has been under the management of Ohiopyle State Park, the forest has continued to change, likely because of post-logging and post-chestnut blight succession. Zone P5 was characterized by a unique forest community compared to the forest that existed prior to logging and human disturbance (Figure 5). A precipitous drop in birch pollen and black birch macrofossils characterized the start of the zone, and this shift was followed by increasing oak, black gum, and red maple. Many of the less prominent canopy taxa peaked during this period, including sugar maple, white and black ash (*Fraxinus americana, F. nigra*), walnut (*Juglans*), hophornbeam (*Ostrya virginiana*), cherry (*Prunus*), and elm (*Ulmus*). Ericaceae pollen and macrofossils of great laurel and mountain laurel decreased (Figure 6), although these shrubs currently dominate the basin boulders. Today the surrounding forest is dominated by chestnut oak, red oak, and black birch, and these species form a canopy over the basin along with sassafras, burr oak, red maple, and black gum. No macroscopic charcoal occurred during this interval, but microscopic charcoal influx declined (Figure 6).

Wetland Vegetation History

Like the upland vegetation community, plant macrofossils indicate that the local wetland vegetation community underwent several major shifts during the last 9000 years (Figure 7). These changes were summarized by defining five wetland zones through stratigraphically-constrained cluster analyses performed using the wetland macrofossil data.

Zone W1 (9000-2000 cal yr BP)

Zone W1 was characterized by abundant ferns, including *Osmunda* and *Polypodium*, and some sedges, like woolgrass (*Scirpus cyperinus*) (Figure 7). Overall, poor macrofossil preservation during this interval prevents a more detailed reconstruction.

Zone W2 (800-550 cal yr BP)

After the depositional hiatus, wetland macrofossil preservation increased significantly and revealed that a diverse group of sedges and rushes occupied the basin (Figure 7). *Osmunda*, the most abundant fern prior to the hiatus, was less abundant in Zone W2, although leaf fragments revealed that it was represented here by cinnamon fern. This zone was characterized by macrofossils of green bulrush (*Scirpus atrovirens*), river bulrush (*Bolboschoenus fluviatilis*), woolgrass, and common rush (*Juncus effusus)*.

Although standing water was indicated in this period by the presence of *Daphnia* and obligate wetland plants, the abundance fungal sclerotia indicated at least seasonally aerobic conditions likely due to drying.

Zone W3 (550-150 cal yr BP)

Zone W3 was characterized by the establishment of a floating peat mat similar to what occupies the site today (Figure 7). Wetland macrofossils showed abruptly increasing amounts of three-way sedge and white beaksedge (*Rhynchospora alba*), rising amounts of fringed sedge (*Carex crinita*), and the appearance of hardstem bulrush (*Schoenoplectus acutus*) and star sedge (*C. echinata*). White beaksedge, and three-way sedge to a lesser extent, are commonly found on floating peat mats where the hydrology is relatively stable. *Scirpus* species decreased as three-way sedge expanded, *Sphagnum* moss macrofossils were first observed in this zone, and fungal sclerotia decreased consistent with less seasonal drying.

Zone W4 (150-10 cal yr BP, 1700-1940 AD)

Coincident with the timing of the ragweed (*Ambrosia*) pollen rise (Figure 6), likely associated with European settlement, three-way sedge increased and reached its peak, but all other previously-mentioned mat sedges decreased or disappeared from the record at the onset of this zone except star sedge which remained stable (Figure 7). Macrofossils of knotweed (*Polygonum*), devil’s beggartick (*Bidens frondosa*), and *Hypnum* moss are common in this zone.

Zone W5 (the last ~75 years)

Sedges have continued to dominate the peat mat, although only macrofossils of three-way sedge, dominant on the mat surface today, occurred in this zone (Figure 7). Although knotweed pollen increased in this zone, macrofossils were also much rarer than in Zone W4.

Identification of Local Fire Events

CharAnalysis results from the macroscopic charcoal record of the last 900 years showed an overall decrease in the background charcoal accumulation rate, and identified nine peaks likely corresponding to local fire events adjacent to Turtlehead Rock Bog (Figure 8, See Methods, Data Analysis for details). The first five peaks were concentrated in the early portion of the record when the background rate was more variable, with the fifth peak (~550 cal yr BP), followed by a relatively steady decline in background charcoal. The background rate decreased quickly between the sixth (~270 cal yr BP) and seventh peaks (~140 cal yr BP), and the eight peak (~60 cal yr BP) was associated with the highest macroscopic charcoal concentrations and background accumulation rates since European settlement. The final peak (~30 cal yr BP) occurred during fire suppression when few macroscopic charcoal fragments were observed in the record, and the resultant background rate was virtually negligible. The global signal-to-noise ratio for these data was slightly lower than the preferred threshold determined by Kelly and others (2011), but this was likely caused by the presence of local fires of intermediate intensity throughout much of the last 900 years.

DISCUSSION AND CONCLUSIONS

A Unique Paleoecological Record: Source Area, Preservation, and Taxonomic Precision

Although the origin of this depositional environment is not entirely clear, Turtlehead Rock Bog is uniquely suited to record local forest conditions given its small size, saturated floating peat mat, and the surrounding vegetated boulders. The system is similar to a forest hollow, and these small basins have a rich history in paleoecology because of their ability to provide stand-scale reconstructions of vegetation and fire history (Calcote, 1995; Kearsley & Jackson, 1997; Davis et al., 1998) and to serve as a potential means of bridging the gap between the spatial scales of short-term observational ecological studies and long-term paleoecological investigations. Furthermore, the floating peat mat with seasonal standing water preserved a richly detailed plant macrofossil record of the past 900 years, including some taxa and/or specific plant organs that have seldom or never been recovered as macrofossils from Holocene sediment records (e.g., many American chestnut seed burs, a sassafras seed, several acorns, etc.).

The Turtlehead Rock Bog basin (~110 m^2) is slightly larger than a typical forest hollow (~20m^2) (Calcote, 1995); therefore, it likely has a relevant pollen source distance around 100-150 m (Sugita, 1994), but this distance may be limited by the ~10 m-tall boulders around the basin. These rock walls likely decrease the source area of terrestrial plant macrofossils which is usually much smaller than that of pollen (10-100

m) (Jackson et al., 2014). However, a comparison of pollen and macrofossil data for arboreal taxa with well-dispersed and easily quantified macrofossils (e.g. birch pollen and black birch macrofossils, American chestnut pollen and macrofossils) indicates very similar patterns (Figure 5), suggesting overlapping source areas for terrestrial plant macrofossils and pollen at Turtlehead Rock Bog.

Analyzing plant macrofossils and pollen in the same core also increases overall taxonomic precision and aids in the interpretation of pollen percentage data. Macrofossils preserved in Turtlehead Rock Bog over the last 900 revealed that birch pollen changes were largely attributable to black birch, oak pollen reflected red and white oak subgenera, Ericaceae pollen was contributed by three unique species, and Cyperaceae pollen trends resulted from at least eight unique species. Macrofossils also indicated the presence of taxa that were underrepresented (e.g. maple) or not observed in the pollen record (e.g. *Liriodendron tulipifera*, sassafras). Furthermore, fluctuations in pollen taxa reflected by similar fluctuations in macrofossil concentrations (e.g., birch pollen and black birch macrofossils) demonstrate that such shifts reflect real changes in population abundance rather than artifacts of proportional shifts potentially associated with pollen percentages.

Depositional and Paleoecological History: Climate, Wetland Development, and the Forest Community

The record from Turtlehead Rock Bog is characterized by two fundamentally different depositional environments separated by a >1000 year depositional hiatus.

Sandy, charcoal-rich sediment accumulated slowly from 9000 to 2000 cal yr BP and preserved evidence of a dynamic upland and fern-dominated wetland. Then mixed sandy and organic sediment, likely deposited while the site was occupied by a sedge-dominated marsh, accumulated rapidly around 800 cal yr BP under conditions favorable to the spectacular preservation of plant macrofossils. A sedge-dominated peat mat established about 550 cal yr BP, and rapid accumulation continued as the sediments became more organic rich, and an ecosystem similar to what occupies the site today was established.

The depositional hiatus that lasted from 2000 to 800 cal yr BP was likely caused by periods of extended drought. Oak and hickory pollen reached their highest values in the entire record just prior to the hiatus (Figure 5) when organic matter drops to near its lowest levels (~5%) (Figure 4). Other regional records provide tentative support for drought episodes during this interval, including Sr:Ca ratios measured from speleothems in West Virginia about 95 km southwest of Turtlehead Rock Bog. These records suggest two multi-centennial arid periods beginning at 2000 and 1200 cal yr BP, and the magnitude of change in Sr:Ca ratios at 2000 cal yr BP was one of largest departures in the 7000 year-long record (Springer et al., 2008). At Cranesville Bog (~30 km south) a peatland established about 1200 cal yr BP as the forest community shifted abruptly from beech- to oak and pine-dominated, consistent with drought conditions (Booth et al. 2016), and drought conditions around 1300 and 1400 cal yr BP have been inferred from low lake levels based on paleomagnetic records from White Lake in northern New Jersey (Li et al., 2007) and from peatland succession and lithology changes at Tannersville Bog in eastern Pennsylvania (Cai & Yu, 2011), respectively. Furthermore, bog water-table depth records inferred from testate amoebae in eastern lower Michigan revealed large multi-decadal-scale drought events at two major intervals in the late Holocene: from 1900 to 1600 cal yr BP and again between 1000 and 700 cal yr BP (Booth et al., 2006; Booth et al., 2012). The later episode of drought and high moisture variability is well-documented at sites spanning from the western United States to portions of the east (e.g. Hubeny et al., 2011). Although there is considerable uncertainty when comparing ^{14}C-dated chronologies across multiple sites and regions, it appears likely that drought, or multiple episodes of drought, caused the depositional hiatus at Turtlehead Rock Bog by facilitating aerobic conditions not conducive to organic matter preservation.

The Turtlehead Rock Bog record of the last 900 years shows several analogous changes in upland and wetland vegetation, suggesting a climatic and/or disturbance driver (Figure 9). For example, Pollen Zone P2, characterized by high oak abundance (Figure 9A) and regionally widespread fires (Figure 9B), corresponds with when the basin was occupied by a sedge-dominated marsh from about 800 until 550 cal yr BP (Figure 9C). The establishment of a floating peat mat at 550 yr BP is associated with a local fire event, but with fewer regional fires, and increasing amounts of birch pollen and black birch macrofossils occur immediately after, suggesting a shift toward wetter conditions. Large short-term fluctuations in soil bulk density and organic matter content at this time, and the local fire event indicate that a transient drought may have occurred immediately before the increase in moisture, and the aforementioned West Virginia speleothem record suggests a drought beginning at about 600 (Springer et al., 2008). Although wetter conditions must have prevailed to allow the persistence of a floating peat mat, enhanced hydroclimatic variability has been linked to floating mat initiation and episodic expansion in other depressional ecosystems (Ireland et al., 2012; Ireland et al., 2013; Ireland & Booth 2011; Booth et al., 2016). Interestingly, bog records from Maine indicate widespread fire and drought at 550 cal yr BP – the only time in the past 2000 years that all studied southern Maine bog sites record both drought and fire (Clifford & Booth 2013; Clifford & Booth 2015).

Lasting Effects of Local Human Disturbance

Humans have radically altered forest community dynamics around Turtlehead Rock Bog through clear-cutting, pathogen introduction, and changes to the fire regime. The earliest evidence of human disturbance around Turtlehead Rock Bog is the increase of ragweed pollen in the late 18th Century when the area was settled by immigrants from surrounding states (Figure 9A), but human influence on the record was generally subtle at this time. During the 19th Century, however, several forb taxa (e.g., devil's beggartick, knotweed) were introduced or expanded within the wetland, and extensive logging fundamentally changed the upland community. Birch and oak pollen reached their extreme high and low values, respectively, around 1900 when regional fire suppression efforts began (Stout et al., 2000). Within a few decades the local population of American chestnut was eradicated by the blight, and the resulting canopy gaps were likely temporarily filled by black birch, a known gap-colonizing species (Matlack, 1992). After a nearby forest fire, and in the absence of American chestnut, oak recovered to pre-settlement pollen levels, and red maple and black gum expanded into the oak-black birch canopy around the site (Figure 5). State-wide post-blight surveys conducted by Aughanbaugh (1935) indicated that American chestnuts in southwestern Pennsylvania (five counties including Fayette) were replaced by advanced regeneration and new growth of red oak, red maple, chestnut oak, sassafras, black cherry, and black gum, and that chestnut oak was the primary replacement in the entire state.

Stand-Scale Oak and Fire Dynamics: Implications for Understanding Contemporary Oak Decline

Analyses of the pre-land-clearance relationships between charcoal accumulation rate, local fire events, and oak pollen support a historical linkage between oak dominance and fire, but the recent recovery of oak under minimal charcoal accumulation rates suggests that anthropogenic-induced disturbances have influenced this linkage. To further assess fire-oak dynamics, oak pollen percentages were compared to microscopic and macroscopic charcoal accumulation data within each upland vegetation zone, and similar patterns emerged (Figure 10). This similarity reflects the overlap in size of microscopic and macroscopic charcoal fragments, and suggests an overlap in source area, like that of pollen and plant macrofossils. For example, Pollen Zone P2 (800-550 cal yr BP) was characterized by consistently high oak abundance across high, but variable accumulation rates for both microscopic (Figure 10A) and macroscopic charcoal (Figure 10B), suggesting that local-to-regional fires may help sustain oak dominance but not continually increase oak abundance. In Zone P3 (550-60 cal yr BP) when the forest contained more substantial components of black birch and other species, charcoal accumulation (particularly macroscopic) showed a positive correlation with oak. Within Zones P4 (60-10 cal yr BP) and P5 (10 cal yr BP-present), which reflect the time periods of extensive logging and post-logging succession during fire suppression, oak reached high levels while microscopic and macroscopic charcoal accumulation rates were at their lowest in these two zones. Therefore, oak increased in the absence of local-to-regional scale fire.

At the stand scale, do local fires facilitate oak recruitment and lead to increasing amounts of oak on the landscape in subsequent decades (Elliott et al., 1999; Brose et al., 2013)? The high-resolution charcoal and pollen data allow an assessment of this question by examining the response of oak pollen to individual, local fire events. Nine such fire events were identified by *CharAnalysis*, and the trajectory of oak pollen percentages for 30 years after each event demonstrates that in most cases oak increased and in no cases did it decrease (Figure 10C). Six of the peaks were followed by a net increase in oak pollen percentage (three significant, three insignificant), and three showed no substantial change. Interestingly, these three events were all in Zone P2, when oak was dominant and showed no increase in response to higher charcoal accumulations in the previous analysis (Figure 10A, 10B). The most recent fire event which was followed by a large overall increase in oak, coincided with the functional extinction of American chestnut; therefore, oak faced minimal competition for canopy dominance. The highest concentrations of white oak group macrofossils were recorded after this event – higher than red oak group macrofossils – suggesting that it led to the expansion of chestnut oak which is common in forest around Turtlehead Bog today.

Oak Forest Management Implications

Prescribed burns have been used to facilitate oak regeneration in temperate mixed-oak stands where oak has declined (Elliott et al., 1999; Brose et al., 2013), yet there is much debate about this practice. For example, some have argued that the simplistic interpretation of fire as the solution to oak decline may threaten an already-damaged and currently-changing ecosystem (Arthur et al., 2012; Vose & Elliot, 2016). These forests have been severely impacted by humans (clear-cutting, overbroswing, fire regime change, pest and pathogen introduction, fragmentation, climate change, etc.), and some tree-ring records suggest that the climate of the past century has been unusually wet (Pederson et al., 2013). My study demonstrates that oak populations in southwestern Pennsylvania were supported in-part by local-to-regional fires prior to clear-cutting in the late 19th Century (Figure 10), and therefore supports a historical linkage between fire and oak, albeit one that is dependent of the overall forest composition. Over the last century, however, human impacts appear to have substantially altered historical fire and oak dynamics, as oak has expanded around Turtlehead Rock Bog in the absence of regional fire (Figure10). Whether this expansion was due to a local fire event in the 1930s, the loss of American chestnut, or other factors is not entirely clear, but enough uncertainty exists to suggest caution in using prescribed burns to increase oak recruitment on the modern landscape, particularly given climatic trends. Ultimately, management strategies must be informed not only by historical ecological relationships, but also by our continually evolving understanding of today’s temperate forests which are constantly adapting to a rapidly-changing climate.

TABLES

Table 1: Radiocarbon-Dated Depths and Material

laboratory code	depth (cm)	dated material	^{14}C date (cal yr BP)	calibrated age (cal yr BP)		
				weighted mean	2σ range	
OS-127435	46.5	*B. lenta* macrofossils	145+15	51	25	96
OS-127438	75.5	*B. lenta* macrofossils	125+15	161	85	256
OS-127439	127.5	*B. lenta* macrofossils	265+15	369	297	442
UG-26760	127.5	*D. arundinaceum* macrofossils	350+20	369	297	442
OS-127440	131.5	*B. lenta* & *D. arundinaceum* macrofossils	670+15	384	318	456
UG-26761	166.5	*D. arundinaceum* macrofossils	460+20	515	484	545
OS-127441	184.5	*B. lenta* & *D. arundinaceum* macrofossils	575+15	606	552	642
OS-127443	185.5	*D. arundinaceum* macrofossils	625+20	612	556	646
UG-26762	212.5	*B. lenta* macrofossils	850+25	781	723	894
OS-127444	214.5	*B. lenta* macrofossils	1000+15	794	738	906
OS-127442	216.5	*B. lenta* macrofossils	985+20	807	750	925
UG-27725	225.5	charcoal	2410+25	2284	2023	2574
UG-26763	257.5	charcoal	4000+25	4295	4107	4433
UG-26764	277.5	charcoal	4630+25	5276	5127	5416
UG-26765	293.5	charcoal	5720+25	6284	6096	6454
OS-127445	335.5	charcoal	8180+40	8947	8659	9200

Table 2: Turtlehead Rock Bog Complete List of Taxa (continued on next page)

group	scientific name	common name	form	fossil type(s)
arboreal	*Acer rubrum*	red maple	tree	pollen, leaf, seed
arboreal	*Acer saccharum*	sugar maple	tree	pollen, leaf, seed
arboreal	*Acer undiff.*	maple	tree	twig
arboreal	*Alnus*	alder	tree	pollen
arboreal	*Betula*	birch	tree	pollen
arboreal	*Betula lenta*	black birch	tree	flower, bract, seed, leaf, twig
arboreal	*Carya*	hickory	tree	pollen
arboreal	*Castanea dentata*	American chestnut	tree	pollen, seed burr, seed
arboreal	*Fagus grandifolia*	American beech	tree	pollen, seed
arboreal	*Fraxinus americana*	white ash	tree	pollen
arboreal	*Fraxinus nigra*	black ash	tree	pollen
arboreal	*Ilex*	holly	tree	pollen
arboreal	*Ilex opaca*	American holly	tree	seed
arboreal	*Juglans*	walnut	tree	pollen
arboreal	*Liriodendron tulipifera*	tulip poplar	tree	seed
arboreal	*Nyssa sylvatica*	black gum	tree	pollen, leaf, seed
arboreal	*Ostrya virginiana*	hophornbeam	tree	pollen, seed pod
arboreal	*Picea*	spruce	tree	pollen
arboreal	*Pinus subg. Pinus*	pine subg.	tree	pollen
arboreal	*Pinus subg. Strobus*	white pine subg.	tree	pollen
arboreal	*Pinus undiff.*	pine	tree	pollen
arboreal	*Prunus*	cherry	tree	pollen
arboreal	*Prunus serotina*	black cherry	tree	seed
arboreal	*Quercus*	oak	tree	pollen
arboreal	*Quercus subg. Eurythrobalanus*	red oak subg.	tree	leaf
arboreal	*Quercus subg. Leucobalanus*	white oak subg.	tree	leaf
arboreal	*Quercus undiff.*	oak	tree	leaf, seed, twig
arboreal	*Salix*	willow	tree	pollen
arboreal	*Sassafras albidum*	sassafras	tree	seed
arboreal	*Tilia*	linden	tree	pollen
arboreal	*Tsuga canadensis*	eastern hemlock	tree	pollen
arboreal	*Ulmus*	elm	tree	pollen

upland	*Ambrosia*	ragweed	forb/herb	pollen
upland	*Asteraceae*	aster	forb/herb	pollen
upland	*Phytolacca americana*	American pokeweed	forb/herb	seed
upland	*Poaceae*	grass	forb/herb	pollen
upland	*Pteridium aquilinum*	western brackenfern	forb/herb	spore
upland	*Solidago*	goldenrod	forb/herb	seed
upland	*Viola*	violet	forb/herb	seed
upland	*Ericaceae*	heather	shrub	pollen
upland	*Gaultheria procumbens*	wintergreen	shrub	seed
upland	*Kalmia latifolia*	mountain laurel	shrub	leaf, seed, seed pod, twig
upland	*Rhododendron maximum*	great laurel	shrub	bract, seed, seed pod, twig
upland	*Rubus occidentalis*	black raspberry	shrub	seed
upland	*Sambucus*	elderberry	shrub	pollen
upland	*Sambucus nigra*	black elderberry	shrub	seed
upland	*Vitis*	grapevine	vine	pollen
wetland	*Bidens frondosa*	devil's beggartick	forb/herb	seed
wetland	*Huperzia lucidula*	shining clubmoss	forb/herb	spore
wetland	Monolete spores	fern	forb/herb	spore
wetland	*Osmunda*	osmunda	forb/herb	spore
wetland	*Osmunda cinnemomea*	cinnamon fern	forb/herb	spore
wetland	*Polygonum*	knotweed	forb/herb	seed
wetland	*Polygonum*	knotweed	forb/herb	pollen
wetland	*Polypodium*	polypody	forb/herb	spore
wetland	*Bolboschoenus fluviatilis*	river bulrush	graminoid	seed
wetland	*Carex crinita*	fringed sedge	graminoid	seed
wetland	*Carex echinata*	star sedge	graminoid	seed
wetland	*Cyperaceae*	sedge	graminoid	pollen
wetland	*Dulichium arundinaceum*	three-way sedge	graminoid	seed
wetland	*Juncus effusus*	common rush	graminoid	seed, seed pod
wetland	*Rhynchospora alba*	white beaksedge	graminoid	seed
wetland	*Schoenoplectus acutus*	hardstem bulrush	graminoid	seed
wetland	*Scirpus atrovirens*	green bulrush	graminoid	seed
wetland	*Scirpus cyperinus*	woolgrass	graminoid	seed
wetland	*Hypnum imponens*	hypnum moss	moss	leaf
wetland	*Leucobryum glaucum*	leucobryum moss	moss	leaf
wetland	*Plagiomnium*	plagiomnium moss	moss	leaf
wetland	*Polytrichum*	polytrichum moss	moss	leaf
wetland	*Sphagnum*	sphagnum moss	moss	spore, leaf
other	*Daphnia*	waterflea	other	ephippia
other	Fungi	Fungi	other	sclerotia
other	*Polystepha pilulae*	oak gall	other	gall

FIGURES

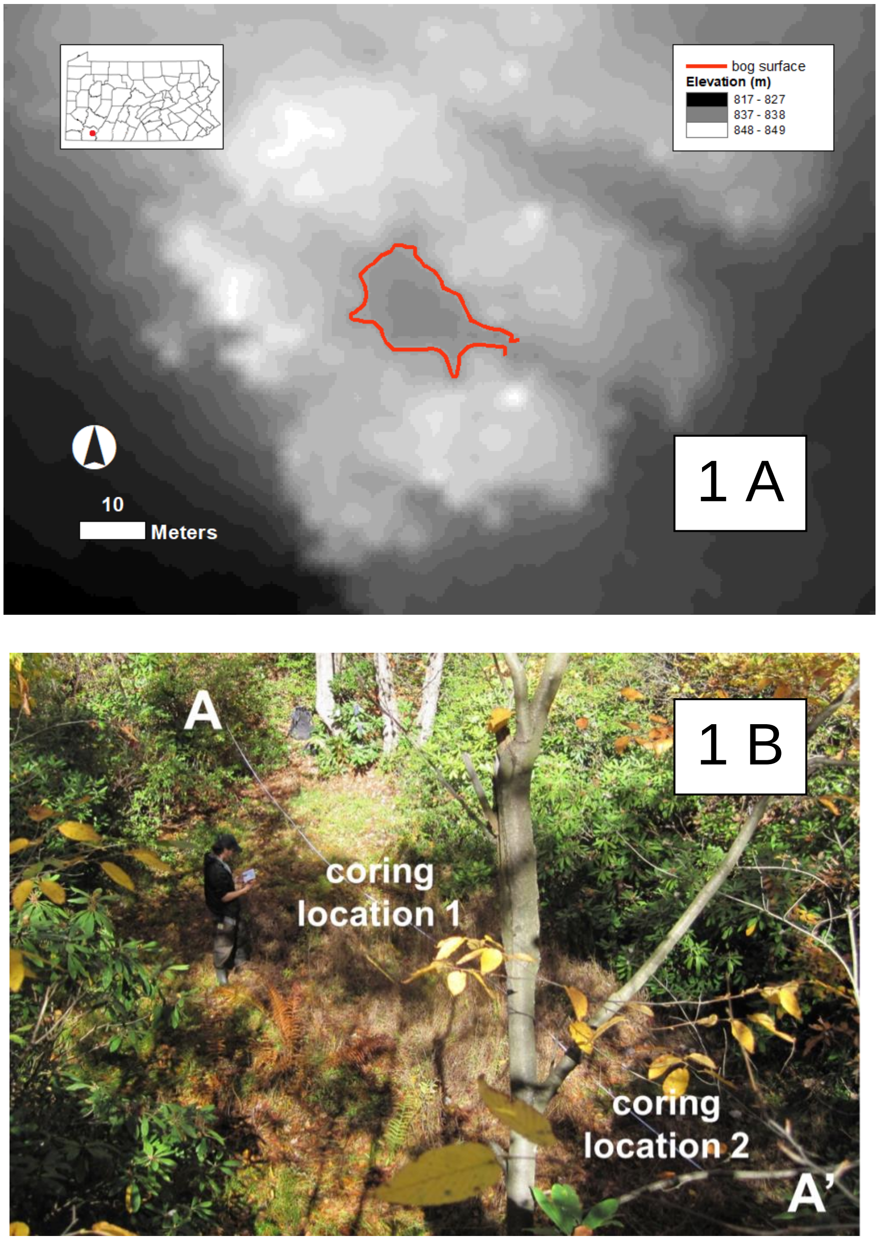

Figure 1: Turtlehead Rock Bog Site Map
A 1 m shaded contour map constructed in ArcGIS using LiDAR elevation data with inset county map of Pennsylvania indicating Fayette County (dot) (1 A); photo of vegetated basin indicating transect (A-A') and coring locations (1 B)

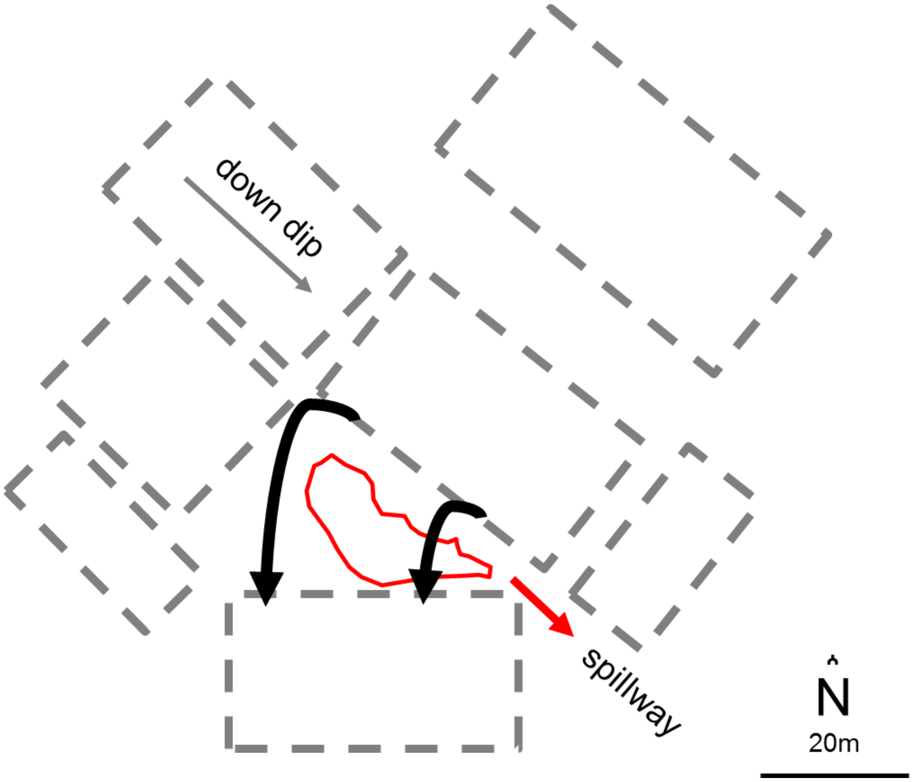

Figure 2: Diagram of Hypothesized Basin Formation
Cartoon depicting the proposed break-up of Homewood sandstone boulders to form the present-day Turtlehead Rock Bog basin

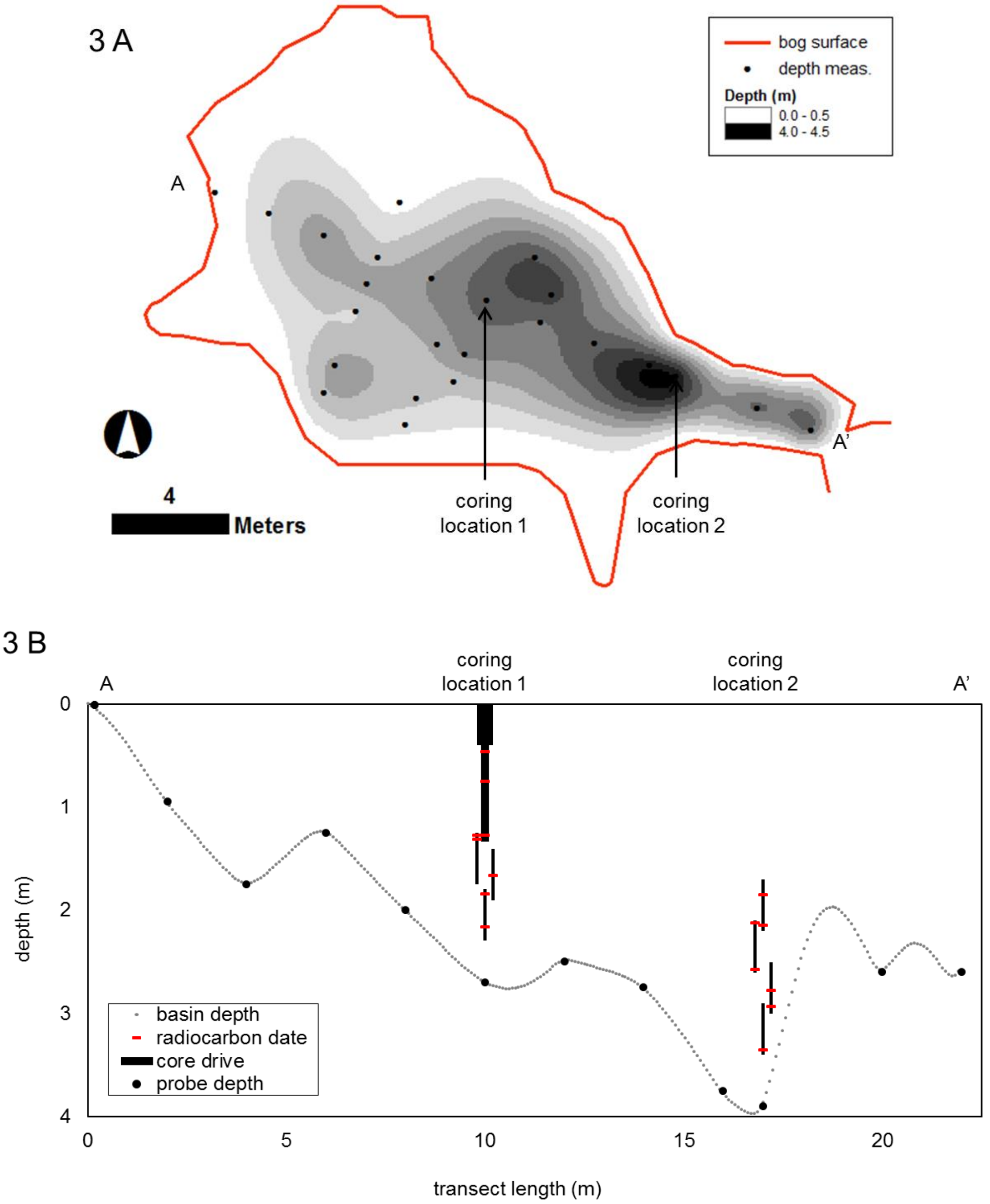

Figure 3: A 0.5 m shaded contour map constructed in ArcGIS using LiDAR elevation data and field probe-depth measurements along a transect (A-A’) and random perpendicular grid points (3 A); basin transect depth profile based on ArcGIS depths, showing core drives and radiocarbon-dated depths (3 B).

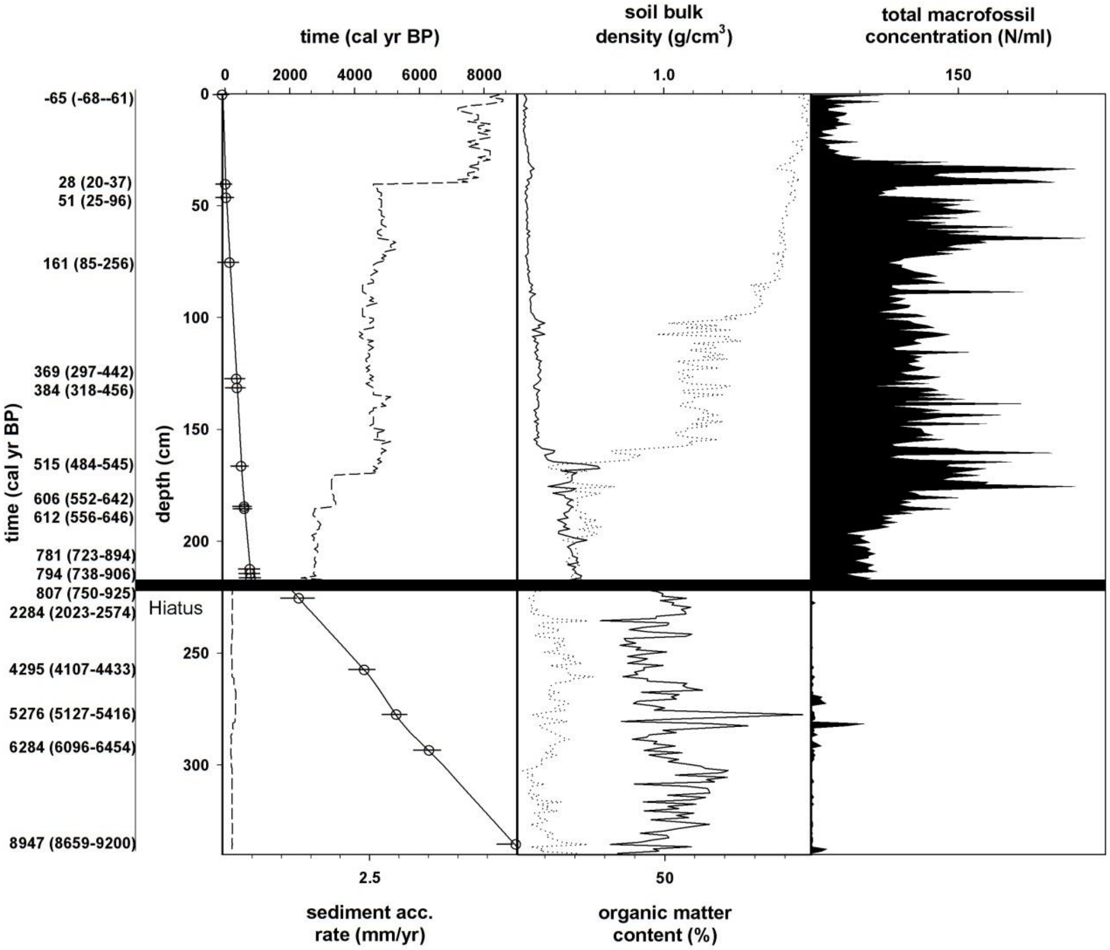

Figure 4: Age-Depth Model and Depositional History
BACON age-depth model (solid line with markers, based on 16 radiocarbon dates and two assigned dates), sediment accumulation rate (dashed line), soil bulk density (solid line), organic matter content (dotted line), and overall macrofossil concentration (area)

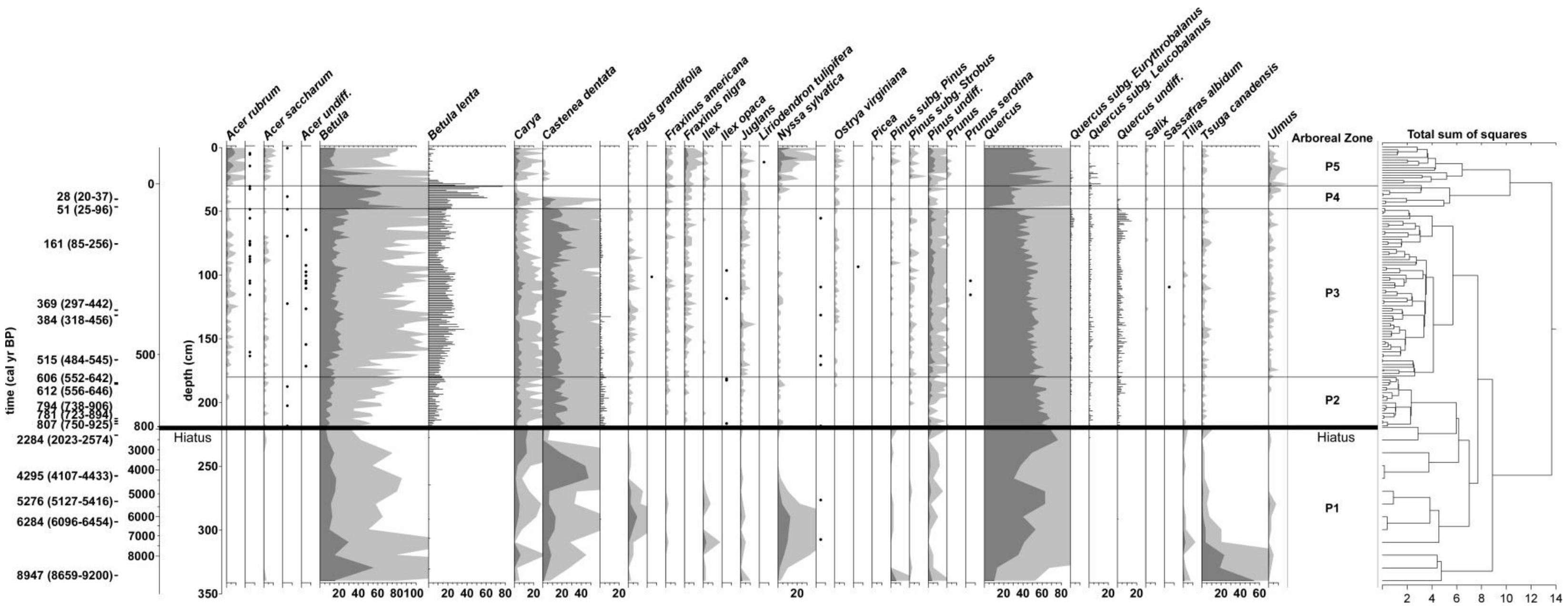

Figure 5: Arboreal Vegetation History
Pollen (% gray, 5x exaggeration light gray) and plant macrofossil (n/ml bar, presence/absence dot) records of Turtlehead Rock Bog arboreal vegetation over the last 9000 years with zonation based on CONISS stratigraphically-constrained cluster analysis of arboreal pollen

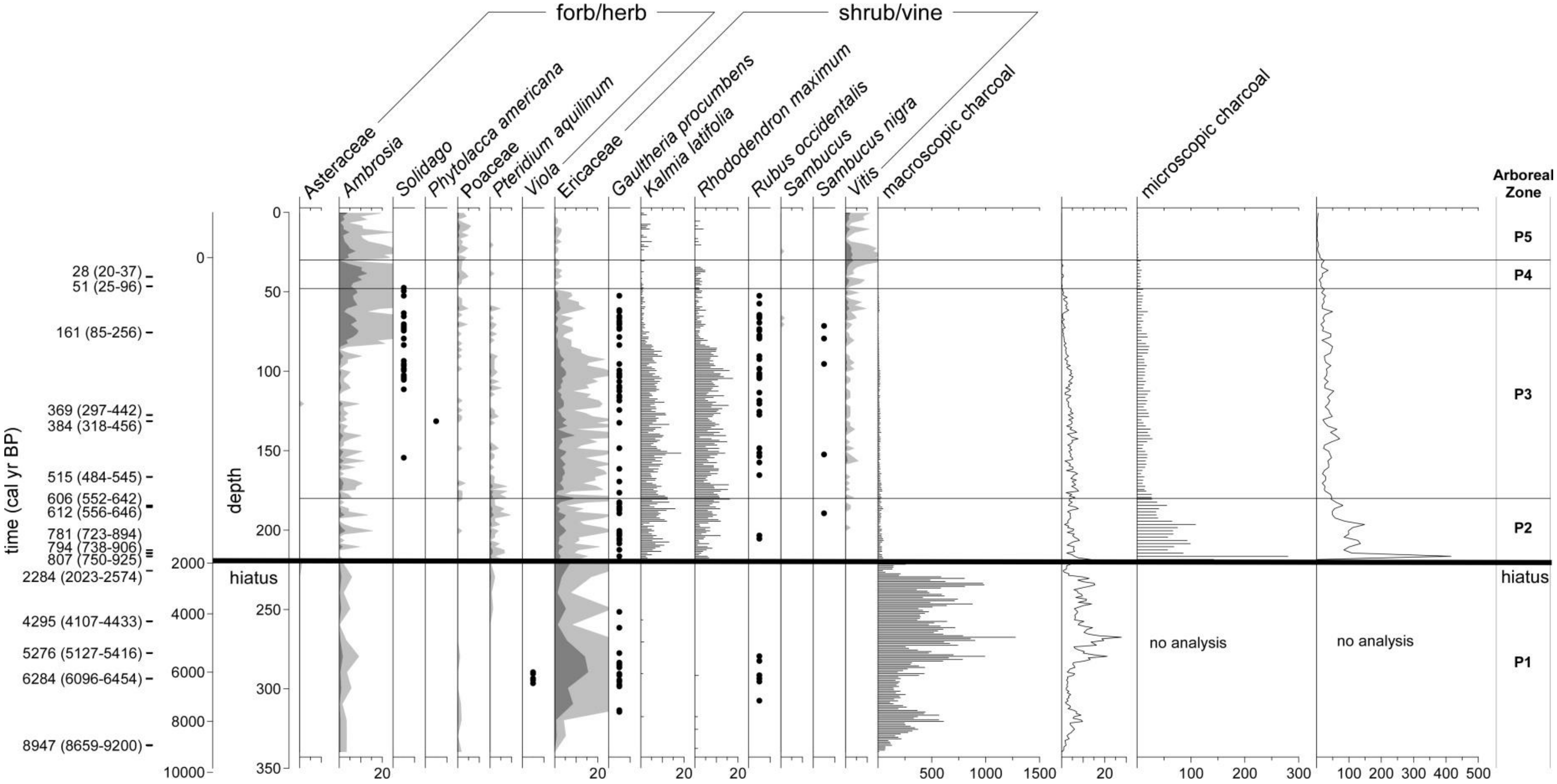

Figure 6: Upland (Non-Arboreal) Vegetation and Fire History
Pollen (% gray, 5x exaggeration light gray) and plant macrofossil (n/ml bar, presence/absence dot)records of Turtlehead Rock Bog non-arboreal upland vegetation and macroscopic and microscopic charcoal concentrations (n/ml bar) and accumulation rates (n/cm^2/yr solid line) over the last 9000 years with zonation based on CONISS stratigraphically-constrained cluster analysis of arboreal pollen

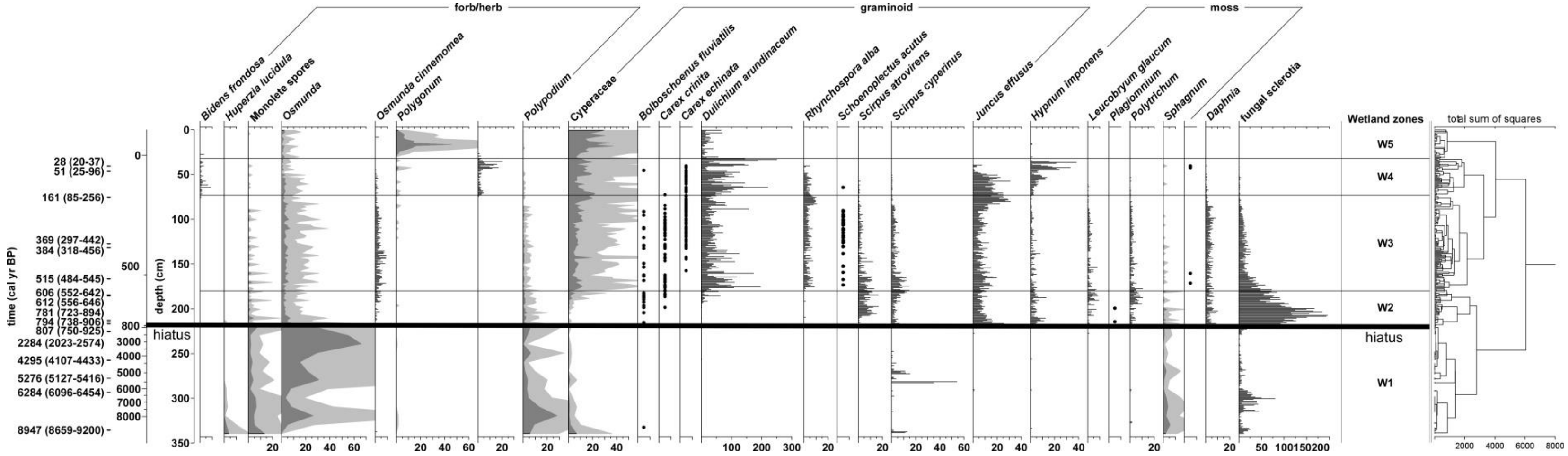

Figure 7: Wetland Vegetation History and Non-Plant Macrofossil Record

Pollen (% gray, 5x exaggeration light gray) and plant macrofossil (n/ml bar, presence/absence dot)records of Turtlehead Rock Bog wetland vegetation and non-plant macrofossil concentrations over the last 9000 years with zonation based on CONISS stratigraphically-constrained cluster analysis of arboreal pollen

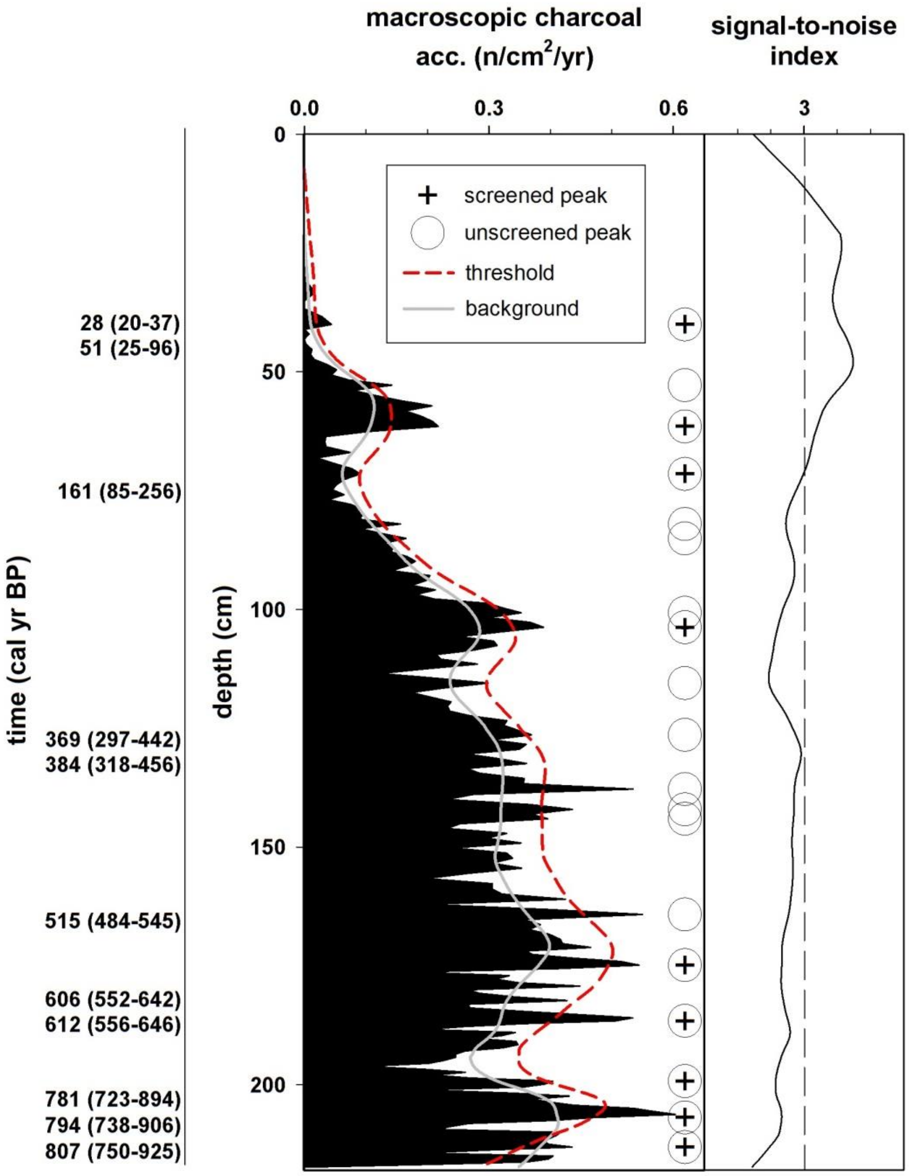

Figure 8: Identification of Local Fire Events
CharAnalysis-calculated macroscopic charcoal accumulation rate (area), background rate (solid line), peak threshold (dashed line), unscreened peaks (circle), and screened peaks (plus) interpreted as local fire events; signal-to-noise index; see methods for details

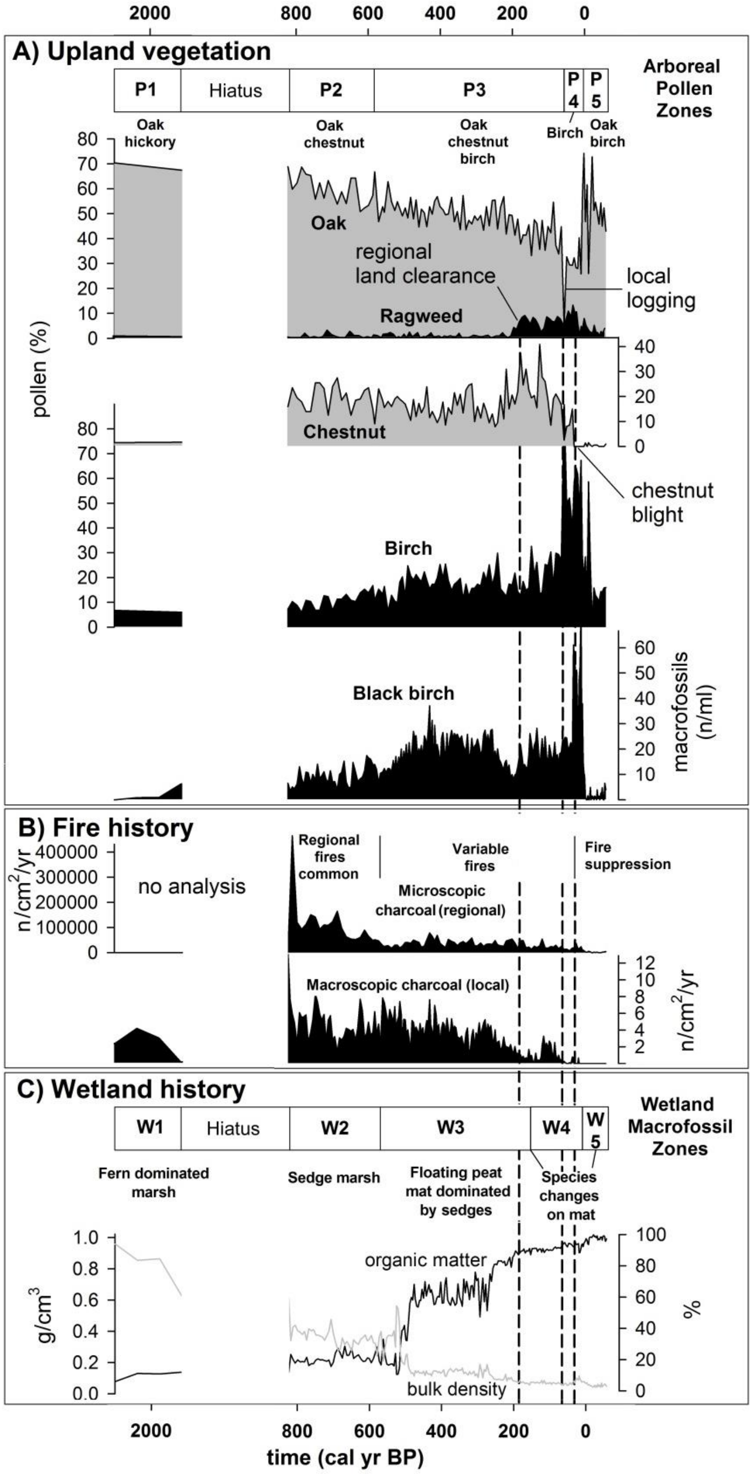

Figure 9: Upland, Wetland, Fire Synthesis

Synthesis of select upland vegetation (A), microscopic and macroscopic charcoal records (B), and wetland characteristics (C) to show contemporaneous shifts

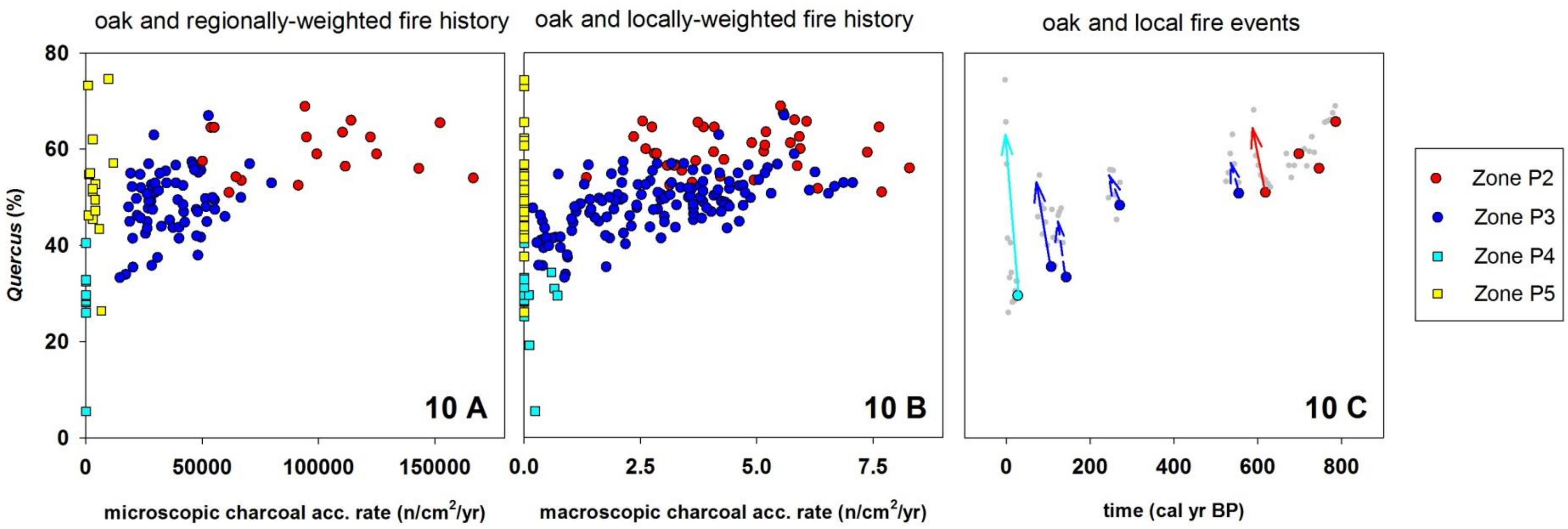

Figure 10: Oak Abundance and Fire
Comparisons of oak pollen percentage with microscopic (A) and macroscopic charcoal accumulation rates (B) to examine oak response to regional and local fire occurrence; comparison of local fire events identified by *CharAnalysis* with oak pollen percentages of the following 30 years (gray dots) (C) to examine oak response to individual local fires (arrows indicate regression trend lines: solid – significant, dashed – insignificant)

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VITA

Robert Anthony Mason

Education

Lehigh University (May 2017)
- Master of Science in Earth and Environmental Sciences (GPA 4.0)
- Master of Science Thesis: "A High-Resolution Paleoecological Perspective on Temperate Oak Forest Dynamics: Implications for Understanding Contemporary Oak Decline"
- Positions Held: Graduate Student Senator
- Awards: NE Section Geological Society of America – Kenneth N. Weaver Student Travel Award (2017); Lehigh University – EES Research Funding (2017, 2016)

Lehigh University (May 2015)
- Bachelor of Science in Earth and Environmental Sciences (GPA 3.8)
- Honors Thesis: "The Influence of White-tailed Deer Herbivory on Tree Recruitment in Forest Canopy Gaps Created by Hurricane Sandy"
- Position(s) Held: Society of Environmental Scientists President
- Awards: Lehigh University – EES Undergraduate Research Symposium Best Talk (2015), EES Donnell Foster-Hewett Award for Professional Excellence (2015), President's Scholar Award (2015), EES Research Funding (2013), Lee Iacocca International Internship (2012)

Penn State Extension (March 2016)
- Community Forestry Online Short Course

University of Pittsburgh, Pymatuning Lab. of Ecology (June 2015, May 2014)
- Disease Ecology, Forest Ecology 3-week Summer Field Courses

Employment

Lehigh University (2013-Present)
- Program Coordinator
- Grader
- Teaching Assistant
- Laboratory Research Assistant
- Field Research Assistant

City of Bethlehem, Public Works, Bureau of Urban Forestry (May-Aug.2015)
- Urban Forestry Intern

Bethlehem's Bounty, Community Supported Agriculture (May-Aug.2014)
- Farm/Garden Intern

Osa Conservation, University of Georgia in Costa Rica (June-Aug. 2012)
- Research Intern

Certifications

Lehigh University (April 2017)
- Teacher Development Training, Level I

Penn State Extension (March 2017)
- Tree Tenders Training