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Central Appalachian paleofire reconstruction reveals fire-climate-vegetation dynamics across the last glacial-interglacial transition

Richard S. Vachula[a,b,c,*], Nicholas L. Balascio[b,**], Ambarish V. Karmalkar[d], JaneAnne Stockton[b], Ben Landolt[b]

[a] Department of Geosciences, Auburn University, Auburn, USA
[b] Department of Geology, William & Mary, Williamsburg, USA
[c] Virginia Institute of Marine Science, William & Mary, Gloucester Point, USA
[d] Department of Geosciences, University of Rhode Island, Kingston, USA

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ABSTRACT

Understanding fire-climate relationships in eastern North America is difficult due to human impacts on fire in the region. Predicting future wildfire activity in the region is further complicated by the changing climate-vegetation interactions that will accompany anthropogenic climate change. While the end-Pleistocene glacial-interglacial transition provides an informative climate analog to future warming and changing climatic conditions, there are very few paleofire records resolving this period in eastern North America. Here, we present the first paleofire record (charcoal and charcoal morphology) from central Appalachia to span the glacial-interglacial transition. We find that fire history of the last 27,000 years was characterized by three distinct periods: (1) the glacial (27–17.7 cal kyr BP) with low fire activity burning wood and needle fuels, (2) the deglaciation (17.7–11.1 cal kyr BP) with markedly increased fire activity but unchanged fuel types and vegetation compositions, and (3) the interglacial Holocene (11.1 cal kyr BP to present) with low fire activity, twig, deciduous leaf, rootlet, and herbaceous fuels, and vegetation-dependent fire activity. We further compare our paleofire data with variables (burned area fraction, precipitation, temperature) from the TraCE-21K-II transient simulation and discuss the feasibility of data-model comparisons in providing insights into fire-climate dynamics. Last, we explore the implications of our analyses from Twin Pond for the future of fire in the central Appalachia region of eastern North America. The clear link between fire and temperature evident in our analyses suggests that the region may experience increased fire activity in response to future warming. The roles of precipitation and vegetation on future fire, however, are less clear.

1. Introduction

Future climate warming is expected to drive shifts in species ranges in eastern North America (Morin et al., 2008; Morin and Thuiller, 2009). The role of projected fire disturbance in driving these ecosystem shifts in this region is less well understood (Liu et al., 2013). Further, wildfire management is expected to become more challenging (Kupfer et al., 2020). It is difficult to resolve fire-climate relationships and their impacts on vegetation due to the pronounced impacts of both Euro-American and Native American humans on modern and recent fire activity in eastern North America (Abrams and Nowacki, 2015, 2019). This lack of understanding is problematic, especially considering recent wildfires in eastern North America like the Great Dismal Swamp fire of 2008 that shrouded the Washington D.C. metropolitan area in smoke (Parthum et al., 2017; Williams, 2011), as well as the Gatlinburg, Tennessee fire of 2016 which forced widespread evacuations and disrupted daily life for thousands (Schneider, 2016).

Much of our current understanding of fire-climate relationships in eastern North America relies on Earth System Modelling (ESM) efforts focusing on the recent past, but the insights gained from these sources

* Corresponding author. Department of Geosciences, Auburn University, Auburn, USA.
** Corresponding author. Department of Earth and Climate Sciences, Bates College, Lewiston, USA.
E-mail addresses: rsv0005@auburn.edu (R.S. Vachula), nbalascio@bates.edu (N.L. Balascio).

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are limited in that future climate change will not be constrained by the same forcing parameters of the observational data with which these models have been calibrated and future climate changes will be accompanied by complex, perhaps unknown vegetation responses. In other words, modelling studies show significant fire risk throughout the eastern US by the end of the 21st century as a first order effect of increasing temperatures (e.g., lengthening of the fire season, variability of fire potential, seasonality), but they do not include the indirect impacts of fire potential resulting from ecosystem shifts (Bedel et al., 2013; Brown et al., 2021; Gao et al., 2021; Liu et al., 2013). Much work has focused on improving fire models within broader ESMs (Hantson et al., 2016; van Marle et al., 2017), though using observational fire data to calibrate these models is marred by the dominance of humans on modern fire regimes (Balch et al., 2017; Bowman et al., 2011). Paleoclimate model simulations have shown great utility for exploring Earth System responses to changing climatic conditions (Kageyama et al., 2018; Otto-Bliesner et al., 2017). For example, the Community Climate System Model (CCSM3)-based Simulation of Transient Climate Evolution over the past 21,000 years (TraCE-21ka and TraCE-21K-II), has explored climate and Earth System responses across a glacial-interglacial transition (He and Clark, 2022; Liu et al., 2009).

Climatic warming and fire regimes associated with the end-Pleistocene deglaciation serve as potentially informative analogs for ecosystem responses to future climate warming (Veloz et al., 2012; Williams et al., 2013). With the retreat of the Laurentide Ice Sheet and global climatic warming, terrestrial ecosystems with no modern analogs developed in the midst of widespread shifts of climatic niches (Jackson and Williams, 2004; Roberts and Hamann, 2012). Additionally, declining megafaunal populations and release of herbivorous pressures on fuel accumulation and subsequent fire activity are thought to have contributed to the development of these no-analog ecosystems through the so-called Megaherbivore Release Hypothesis (MRH) (Gill et al., 2009; Perrotti et al., 2022). A recent review compared fire and megafauna reconstructions from sites in interior and coastal plain southeastern North America (i.e. no sites in Appalachia), finding spatial heterogeneities in the influence of fire and megafauna extinctions on vegetation (Perrotti et al., 2022).

Despite the potential utility of resolving the deglacial fire history of southeastern North America, there are relatively few paleofire records resolving this period within the region. While there are a number of glacial-interglacial paleofire records in eastern North America (Fig. 1), the bulk of these sites are located in the continental interior (Perrotti et al., 2022). For example, Appleman Lake (Gill et al., 2009), Bonnet Lake (Fastovich et al., 2020), Silver Lake (Gill et al., 2012), and Stotzel-Leis (Watson et al., 2018) form a spatial cluster of sites south of the Great Lakes. In contrast, only two sites, White Pond (Krause et al., 2019) and Sheelar Lake (Perrotti et al., 2022) provide insights about glacial-interglacial fire history in southeastern North America, but are both located on the coastal plain (Fig. 1). In contrast, there are no paleofire records characterizing fire history across the glacial-interglacial transition in Appalachia.

Here we present the first paleofire record from central Appalachia which spans the glacial-interglacial transition. This record from Twin Pond consists of sedimentary charcoal accumulation rate and morphological classification data, enabling a reconstruction of fire activity and fuel type burned. This long-term paleofire record and timescale allow us to focus on non-human controls of fire in this region. Human impacts on fire in eastern North America during more recent time periods (e.g., last several millennia) are debated (Abrams and Nowacki, 2020; Oswald et al., 2020a, 2020b; Roos, 2020), but would be limited relative to the timespan of our dataset. In addition to providing novel insight into the paleofire history of central Appalachia, we compare our paleofire record with TraCE-21K-II modelled climate and fire history. Though the TraCE-21K-II experiment used the now dated CCSM3, it is the sole model

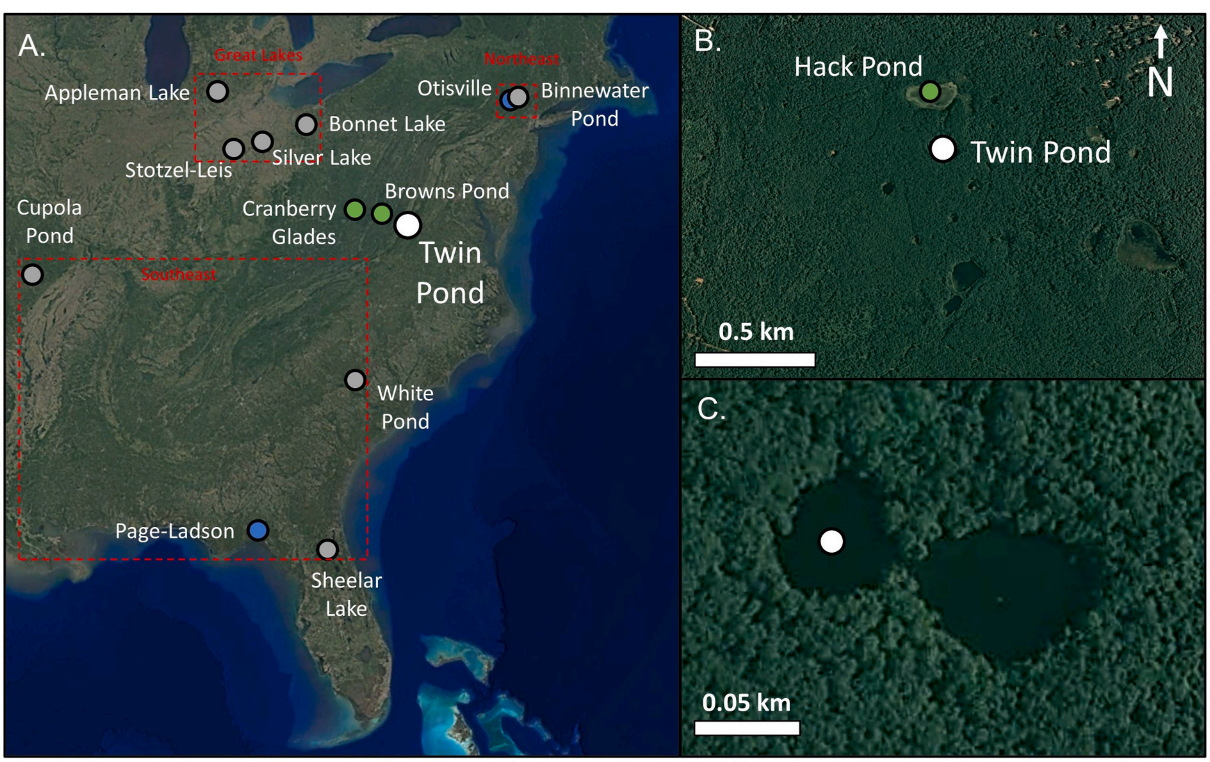

Fig. 1. (A) Twin Pond (white; 37.982529 °N, 78.995734 °W, 475 m a.s.l.) is located in the Shenandoah Valley of the Appalachian Mountains in eastern North America. Although other sedimentary charcoal records (gray) resolve fire history of eastern North America during the deglaciation (18–12 cal kyr BP), none are located in the central Appalachians. Pollen reconstruction sites referred to in the text are noted with green circles. Regional groups as defined by Perrotti et al. (2022) are noted in red, with several additional sites (blue) as discussed in Fig. 5. (B) Location of Twin Pond in the oak-dominated mixed forest of the Maple Flats Complex of sinkhole lakes. (C) Coring location in Twin Pond. Base map sourced from Google Earth imagery collected April 9, 2013.

experiment available for proxy-model comparisons on these glacial-interglacial timescales and thereby provides a unique opportunity to compare modelled parameterizations of fire with actual fire activity. Last, we compare the Twin Pond paleofire record with published paleoecological data to characterize fire's role in driving vegetation changes during a period of global warming, and interpret what these relationships might mean for the region in the face of future anthropogenic climate warming.

2. Materials and methods

2.1. Sediment core collection, dating, and analysis

Our study focuses on Twin Pond (37.982529 °N, 78.995734 °W, 475 m a.s.l.), a pond in the Maple Flats complex of sinkhole lakes in the Shenandoah Valley of western Virginia. The Maple Flats complex hosts more than twenty sinkhole ponds and is primarily managed by the US Forest Service, though some areas are privately owned (Buhlmann et al., 1999). Twin Pond is in an oak-dominated hardwood forest (Craig, 1969). In October 2017, a 130 cm core was extracted from Twin Pond by hammering a 2 m long PVC pipe with a 4-inch-diameter and internal core-catcher mechanism into the sediment. The core was split into archive and working halves prior to analyses.

Contiguous 1-cm resolution volumetrically-measured (1 cm^3) subsamples were collected from the core and loss-on-ignition analysis was used to determine the dry bulk density (by oven drying for 24 h at 105 °C) and organic matter (by combustion in an oven at 550 °C for 4 h) profiles of the sediment (Heiri et al., 2001). The magnetic susceptibility of the sediment core was measured along its length at contiguous 0.5 cm intervals using a Bartington MS2E sensor. The grain size distribution (% sand, silt, and clay) of the core was characterized at 4 cm intervals using a Beckman Coulter LS13320 laser diffraction particle size analyzer. Samples were pretreated with 10 ml of 30% hydrogen peroxide (48 h) and 10 ml of hexametaphosphate (24 h) prior to grain size analysis (Balascio et al., 2019).

Radiocarbon dating was performed on two macrofossil (charcoal) and four bulk sediment samples collected from the Twin Pond core. All samples were pretreated with the same acid-base-acid procedure (Oswald et al., 2005). Radiocarbon analyses were conducted at the University of California, Irvine and the National Ocean Sciences AMS Laboratory at Woods Hole Oceanographic Institution. Radiocarbon ages were calibrated to thousands of calendar years before 1950 CE (cal kyr BP) using the IntCal20 calibration curve (Reimer et al., 2020). The age-depth relationship for the Twin Pond core was modelled as a smooth spline curve using the clam age modelling package in R (Blaauw, 2010).

2.2. Sedimentary charcoal analysis

Charcoal was analyzed in 1-cm intervals along the length of the Twin Pond sediment core. Volumetric subsamples (0.25–1 cm^3) were collected and soaked in 12 mL of a 50:50 mixture of 2.5% bleach and sodium hexametaphosphate for 48 h before the samples were sieved through a 125 μm sieve with deionized water. Sieved samples were transferred to a gridded Petri dish, suspended in deionized water, and examined under a binocular dissecting microscope. Charcoal particles were distinguished from minerals on the basis of fully black color, vitreous luster, low particle density, and identifiable vegetal structures. Previous research has shown that the use of oxidants degrades charcoal formed at lower temperatures, so our data may reflect a bias towards charcoal formed at higher temperatures (Constantine and Mooney, 2022; Schlachter and Horn, 2010). Charcoal particles were identified and tallied while simultaneously being classified into morphotype groups following Mustaphi and Pisaric (2014). Previous research has tied charcoal morphologies to fuel types (Cheung et al., 2021; Enache and Cumming, 2006; Mustaphi and Pisaric, 2014). Guided by this previous research and the recommendations provided with the classification system (Cheung et al., 2021; Mustaphi and Pisaric, 2014), we classified the morphotypes into the following groups to characterize shifts in fuel: wood (A1, B1, B2, B3), needles (C1, C2, C3, C4), twigs (C5, C6, C7, D1, D2), deciduous non-grass leaves (A4, A5, B5), herbaceous material (A2, C4), and rootlets (C6, C7). Although we note that the fuel source designations provided by Mustaphi and Pisaric (2014) were developed in Canadian boreal forest, these morphotypes have been applied to charcoal from a range of latitudes and biomes (Feurdean et al., 2023; Feurdean and Vasiliev, 2019; Frank-DePue et al., 2022; Krause et al., 2019; Unkelbach and Behling, 2022). Additionally, we note that several morphologies belong to multiple fuel type groups.

In several high charcoal concentration samples, the volumetric sample size was halved to expedite the time required to quantify charcoal in the sample. Comparisons between full and halved sample volume results confirm this introduced negligible error into our charcoal concentration measurements. Charcoal measurements are expressed as charcoal accumulation rates (CHAR) by dividing the volumetric sedimentary charcoal concentrations by the sediment interval accumulation rate following standard practice (Frank-DePue et al., 2022; Long et al., 1998; Vachula et al., 2018; Whitlock and Larsen, 2002). To identify temporal zones of CHAR variation, we used MATLAB's findchangepts algorithm, which identifies points at which the summed residual error of each period is minimized from its local mean.

2.3. Comparison to published paleoecological data

We compare our Twin Pond charcoal data with several published datasets. First, we compare charcoal morphology assemblage changes with sedimentary pollen data from Hack Pond in the Maple Flats complex (Craig, 1969). Although the Hack Pond pollen record is constrained by only two radiocarbon dates, the reliability of its age-depth model is supported by its correspondence to changes in the Browns Pond pollen record ~50 km to the northwest (Kneller and Peteet, 1993). The Browns Pond chronology is supported by six radiocarbon dates and its pollen record shares several correspondences in the timing of peaks and increases of taxa with that of Hack Pond (e.g., *Corylus* peak at ~10.5 cal kyr BP, *Tsuga* peak at ~8.8 cal kyr BP, and *Picea* decline ~10 cal kyr BP), supporting the reliability of the Hack Pond chronology. Likewise, we compare our charcoal data with pollen data from Cranberry Glades (Watts, 1979), which exhibits contemporaneous vegetation shifts, is located ~100 km to the northwest of Twin Pond, and has chronology supported by three radiocarbon dates. We opted to include and show the pollen data from Browns Pond, Hack Pond, and Cranberry Glades to (1) prevent criticism of comparison with Hack Pond's poor chronological constraints, and (2) to show that vegetation compositions in this region (central Appalachia) were generally consistent across space and that our comparison of Twin Pond charcoal with Hack Pond pollen is not necessarily locally limited in its implications.

Pollen groups were defined using plant codes (e.g., trees and shrubs, upland herbs) provided by the Neotoma database (Williams et al., 2018), as well as published pollen groups (Perrotti et al., 2022). For example, hardwood pollen abundance was tabulated by summing pollen percentages of *Acer*, *Alnus*, *Betula*, *Carya*, *Castanea*, *Cornus*, *Corylus*, *Fagus*, *Fraxinus*, *Juglans*, *Liquidambar*, *Morus*, *Nyssa*, *Ostrya/Carpinus*, *Platanus*, *Populus*, *Quercus*, *Salix*, *Tilia*, and *Ulmus* (Perrotti et al., 2022).

2.4. Comparison to TraCE-21K-II

We compared our paleofire data with paleoclimate model output. The paleoclimate model experiment used in this study is the CCSM3-based global coupled model experiment Transient Climate Evolution over the past 21,000 years (TraCE (He and Clark, 2022; Liu et al., 2009)). A recent update by He and Clark (2022), dubbed TraCE-21K-II, improved the earlier TraCE-21ka simulation runs by correcting an overestimation of the Atlantic Meridional Overturning Circulation to freshwater fluxes. Rather than use the more established TraCE-21ka simulation results, we opted to use the more recently published TraCE-21K-II simulation results as they have been shown to be more reliable (He and Clark, 2022). We compare our Twin Pond paleofire data to the TraCE-21K-II simulation results and outputs. Since these data are the result of extremely complex and established modelling frameworks, we do not explore their calculation in this paper. We use the decadally averaged simulated surface air temperature, precipitation, net primary productivity, and burned area fraction (BAF) variables obtained from the full-forcing TraCE-21K-II simulation. Within the CCSM3 model framework, vegetation and fire disturbance are simulated by the Lund-Potsdam-Jena Dynamic Vegetation Model (LPJ-DGVM) (Bonan et al., 2003; Sitch et al., 2003). Fire in LPJ-DGVM is parameterized and calculated from the dynamic variables of fire season length, fuel load, litter moisture, and plant functional type (Sitch et al., 2003; Thonicke et al., 2001), while the empirical relationship between these variables is derived from observations of historical fire activity (Minnich, 1998; Russell-Smith et al., 1997; Thonicke et al., 2001; Viegas et al., 1992; Viegas, 1998). Previous studies show that the TraCE simulations capture many important features of the climate of the past 21 kyr (Buizert et al., 2018; Otto-Bliesner et al., 2014) and are therefore suitable to study the transient evolution of climate and fire variables in eastern North America.

3. Results

3.1. Sediment analyses and chronology

The age-depth model for the Twin Pond sediment core is based on four radiocarbon dates and shows the core has a basal age of at least 27 cal kyr BP (Fig. 2A). We considered the two radiocarbon ages from depths of 84 and 104 cm to reflect landscape reservoir effects (i.e., their radiocarbon ages not being contemporaneous with their deposition in the sediments, as supported by their inversion and significantly older ages), and so were not included in the age depth model (Table 1). Likewise, sediments below a depth of 75 cm in the core were not included in any of the paleofire analyses given their lack of age control.

The dry bulk density of the core was generally consistent below a depth of 20 cm (average (μ) = 1.26 g/cm^3; standard deviation (σ) = 0.17 g/cm^3) and decreased between 20 cm and the surface of the core (Fig. 2B; μ = 0.53 g/cm^3; σ = 0.16 g/cm^3). Below 20 cm depth sediments were dominated by equivalent percentages of silt and clay, with relatively low proportions of sand (Fig. 2C). Grain size shifted to a dominance of clay above 20 cm depth. Magnetic susceptibility of the core was relatively uniform (μ = 1.28 SI *10^{-5}; σ = 3.74 SI *10^{-5}), apart from a peak reaching 40.2 SI *10^{-5} centered at 17 cm depth (Fig. 2D). The organic matter content of the core was generally low below a depth of 10 cm (μ = 6.71 %; σ = 2.44 %), and increased between 10 cm depth and the top of the core (μ = 17.60 %; σ = 4.84 %).

3.2. Sedimentary charcoal analysis

Charcoal concentrations in the Twin Pond sediment core are generally low between 52 and 75 cm depth (Fig. 3; average (μ) = 409.1 #·cm^{-3}; standard deviation (σ) = 350.4 #·cm^{-3}) as well as between the surface of the core and 26 cm depth (μ = 111.3 #·cm^{-3}; σ = 124.9 #·cm^{-3}). In contrast, charcoal concentrations were elevated between 26 and 51 cm depth (μ = 3114.4 #·cm^{-3}; σ = 1391.9 #·cm^{-3}). Charcoal morphological assemblages in the Twin Pond sediment core were dominated by Types A1, A2, and A3, as well as lower quantities of Types A4, B1, B2, and B3 (Fig. 3). Types C, D, E, F and G are also present in the core in lower quantities. Type C morphologies are most abundant in the glacial and deglaciation time periods.

Charcoal accumulation rates (CHAR) in the Twin Pond core range greatly (0.02–15.38 cm^{-2} yr^{-1}) over the last 27,000 years (Fig. 4). Our changepoint analysis of the CHAR time series identified two age points at which the mean of CHAR changed most significantly: 11.1 and 17.7 cal kyr BP. Therefore, the CHAR values in the Twin Pond core can be divided into three time periods: the glacial (27–17.7 cal kyr BP), deglaciation (17.7–11.1 cal kyr BP), and Holocene (11.1 cal kyr BP to present). CHAR values were greatest during the deglaciation (average (μ) = 10.33 cm^{-2} yr^{-1}; standard deviation (σ) = 2.87 cm^{-2} yr^{-1}) and were relatively low during the glacial (μ = 1.95 cm^{-2} yr^{-1}; σ = 2.04 cm^{-2} yr^{-1}) and Holocene (μ = 0.52 cm^{-2} yr^{-1}; σ = 0.94 cm^{-2} yr^{-1}). During the Holocene, CHAR values were greatest from 11.1 to 6.0 cal kyr BP (μ = 1.22 cm^{-2} yr^{-1}; σ = 1.29 cm^{-2} yr^{-1}), followed by the lowest CHAR values from 6.0 to 2.9 cal kyr BP (μ = 0.07 cm^{-2} yr^{-1}; σ = 0.04 cm^{-2} yr^{-1}), and low but relatively variable CHAR values between 2.9 cal kyr to present (μ = 0.18 cm^{-2} yr^{-1}; σ = 0.12 cm^{-2} yr^{-1}).

4. Discussion

4.1. New insight into the paleofire history of central Appalachia

Macroscopic charcoal particles (>125 μm) preserved in lake sediment records generally record area burned within ~50 km of a lake, with more proximal areas having a more pronounced influence on charcoal accumulation than more distal areas (Higuera et al., 2007; Peters and Higuera, 2007; Vachula, 2021; Vachula et al., 2018). We

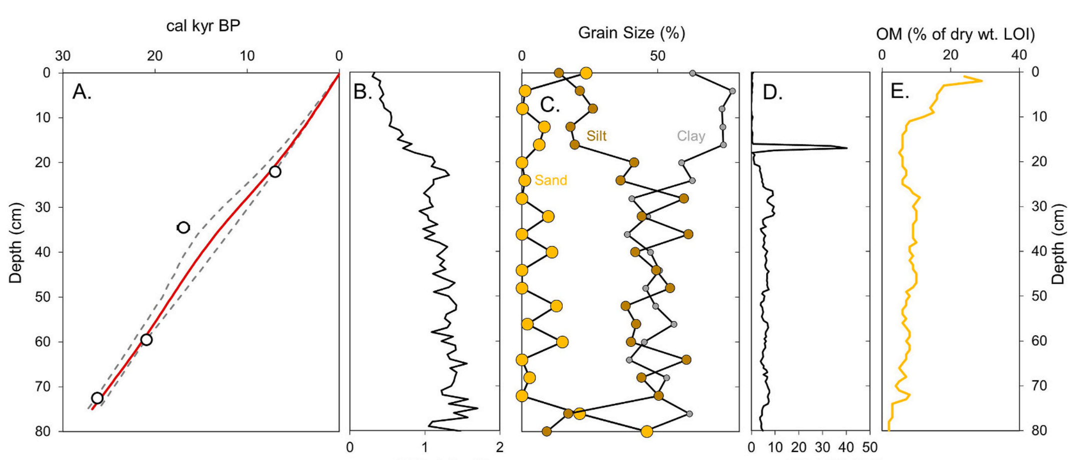

Fig. 2. Age-depth model and sedimentological characteristics of the Twin Pond core. A.) Radiocarbon ages (Table 1) and age-depth model generated using the clam age modelling software (Blaauw, 2010). Gray dashed lines show the 95% confidence intervals around the median age (red line). Subsequent subplots show down-core variations in dry bulk density (B), sediments grain size (C), magnetic susceptibility (D), and organic matter as percent of dry weight lost on ignition (E).

Table 1
Radiocarbon sample information for the Twin Pond record. All radiocarbon ages are calibrated using the IntCal20 calibration curve (Reimer et al., 2020).

Site	Laboratory ID	Depth (cm)	Radiocarbon age (^{14}Cyr BP)	Calibrated age (cal yr BP, 2σ)	Material dated
Twin Pond	UCI- 210699	21	6090 ± 20	6888–7002	bulk sediment
	UCI-204839	34	13980 ± 200	16347–17475	charcoal
	UCI-206819	59	17330 ± 40	20810–21004	bulk sediment
	UCI-210700	72	22130 ± 100	25990–26514	bulk sediment
	UCI-206820	84	53500 ± 2000	–	bulk sediment
	OS-137955	104	41600 ± 2800	–	charcoal

UCI: University of California Irvine Keck-CCAMS Facility; OS: National Ocean Sciences AMS Facility.

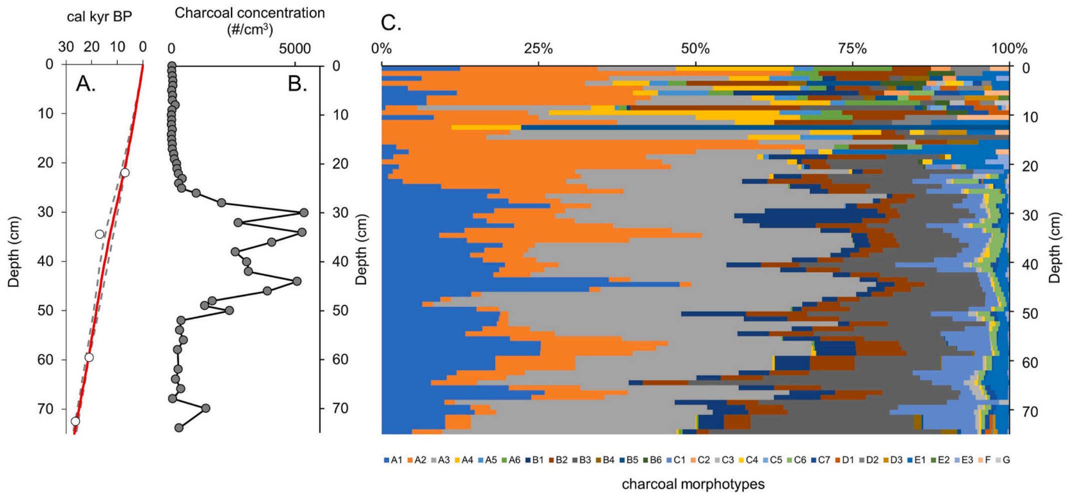

Fig. 3. Comparison of the Twin Pond age depth model (A), sedimentary charcoal concentrations (B), and the assemblages of charcoal morphotypes associated with each sample (C).

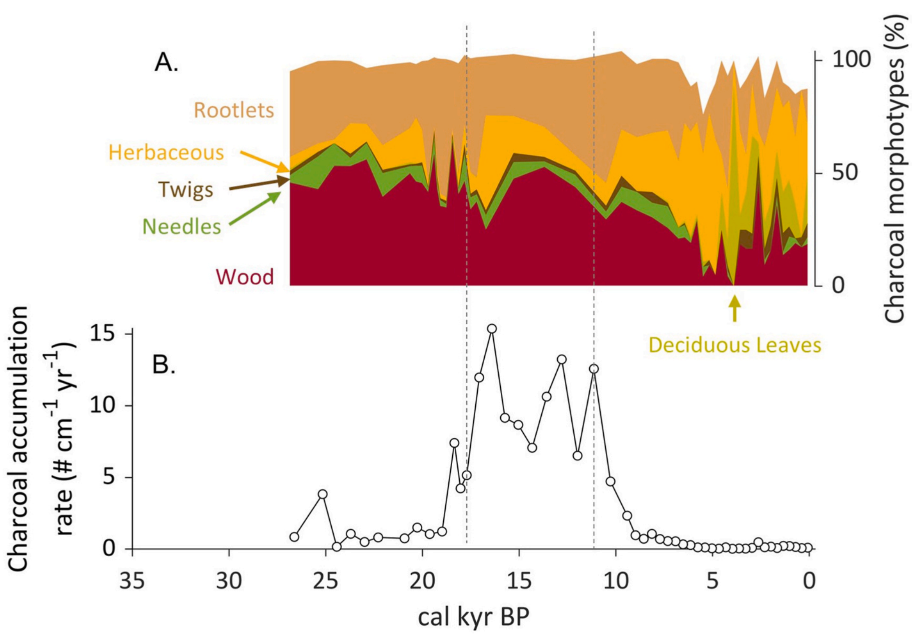

Fig. 4. Twin Pond fuel type changes inferred from sedimentary charcoal morphotypes (A), and fire activity recorded by charcoal accumulation rates (B). Dashed lines divide the Twin Pond paleofire record into the glacial (27–17.7 cal kyr BP), deglaciation (17.7–11.1 cal kyr BP), and Holocene (11.1 cal kyr BP to present) periods. The glacial paleofire record is characterized by decreased fire activity and a dominance of charcoal morphotypes characteristic of wood (red) and needles (green). In contrast, fire activity of the Holocene decreased and charcoal morphotypes exhibit a fuel-type shift towards charcoal morphotypes characteristic of more twigs (brown), deciduous leaves (light green), herbaceous material (yellow), and rootlets (tan). During the deglaciation, fire activity was elevated and charcoal morphotypes broadly mirrored those of the glacial.

therefore interpret the Twin Pond charcoal record to reflect the regional fire history (e.g., burned area within ~50 km) around the Maple Flats. We used the morphotype classification scheme developed by Mustaphi and Pisaric (2014) to quantify changes in charcoal morphological characteristics. Although these morphotypes are not necessarily fuel-specific, they can indicate likely fuel sources (Enache and Cumming, 2006; Rehn et al., 2021). For example, whereas some morphotypes are more unique and therefore better diagnostics of fuel types, others are common to multiple fuel sources (Frank-DePue et al., 2022; Mustaphi and Pisaric, 2014).

The Twin Pond paleofire record provides the first perspective on central Appalachia's fire history across the glacial-interglacial transition. Sedimentary charcoal (CHAR) preserved in the Twin Pond sediment record show that over the last 27,000 years, fire history in central Appalachia was characterized by three distinct periods, as supported by our changepoint analysis. First, during the glacial (27–17.7 cal kyr BP), fire activity was relatively low and charcoal morphotypes were characteristic of wood and needle fuels being burned (Fig. 4). These fuel types were consistent during the deglaciation (17.7–11.1 cal kyr BP), but increased charcoal accumulation rates show that fire activity increased markedly during this period (Fig. 4). Fire activity decreased sharply during the interglacial Holocene (11.1 cal kyr BP to present), and charcoal morphologies preserved during this period show that fuel types also shifted towards more twigs, deciduous leaves, herbaceous material, and rootlets (Fig. 4).

4.2. *Glacial vs. interglacial state determines whether vegetation composition and fire are linked in central Appalachia*

The Twin Pond charcoal data provide new perspective on the paleoecological history of eastern North America across the glacial-interglacial transition. Charcoal accumulation rates show that fire activity in central Appalachia increased during the deglaciation, in agreement with published paleoecological records (Fig. 5). Indeed, across multiple regions of eastern North America (e.g., Great Lakes, Northeast, Southeast; Fig. 5D), charcoal records show general agreement for increased fire activity during the deglaciation and Pleistocene-Holocene transition.

Paleofire and pollen data from central Appalachia show that elevated fire activity during the deglaciation occurred without broad changes in vegetation composition. When the Twin Pond CHAR data are compared with pollen data from Hack Pond (Craig, 1969), Browns Pond (Kneller and Peteet, 1993), and Cranberry Glades (Watts, 1979), it is clear that despite relative stability of vegetation compositions during the glacial and deglaciation, fire activity increased markedly during the deglaciation (Fig. 5). The stability of fuel types burned is also reflected in charcoal morphology data from Twin Pond, which show that fuel types burned changed little across the glacial-deglaciation transition, despite a significant increase in fire activity (Fig. 4). This juxtaposition is puzzling, especially in light of previous paleoecological research in other areas of eastern North America, which show the glacial-interglacial transition is typically associated with the subsequent development of ecosystems with no modern analogs as forests shifted from coniferous to deciduous (i.e., hardwoods) tree dominance (Jackson and Williams, 2004; Roberts and Hamann, 2012). By extension, this lack of a clear linkage between vegetation and fire during a period of marked temperature and precipitation change (Fig. 5) implicates these variables as likely drivers of fire in central Appalachia.

The timing of fire and vegetation changes evident in central Appalachia stand in contrast to published paleoecological transitions identified in eastern North America. Although the timing of conifer-hardwood vegetation transitions varied across eastern North America (Fig. 5D), they tended to occur between ca. 16 and 14 cal kyr BP (Liu et al., 2012; Perrotti et al., 2022). The transitionary periods of mixed conifer and hardwood taxa represent terrestrial ecosystems without modern analogs (Jackson and Williams, 2004; Roberts and Hamann, 2012). Often,

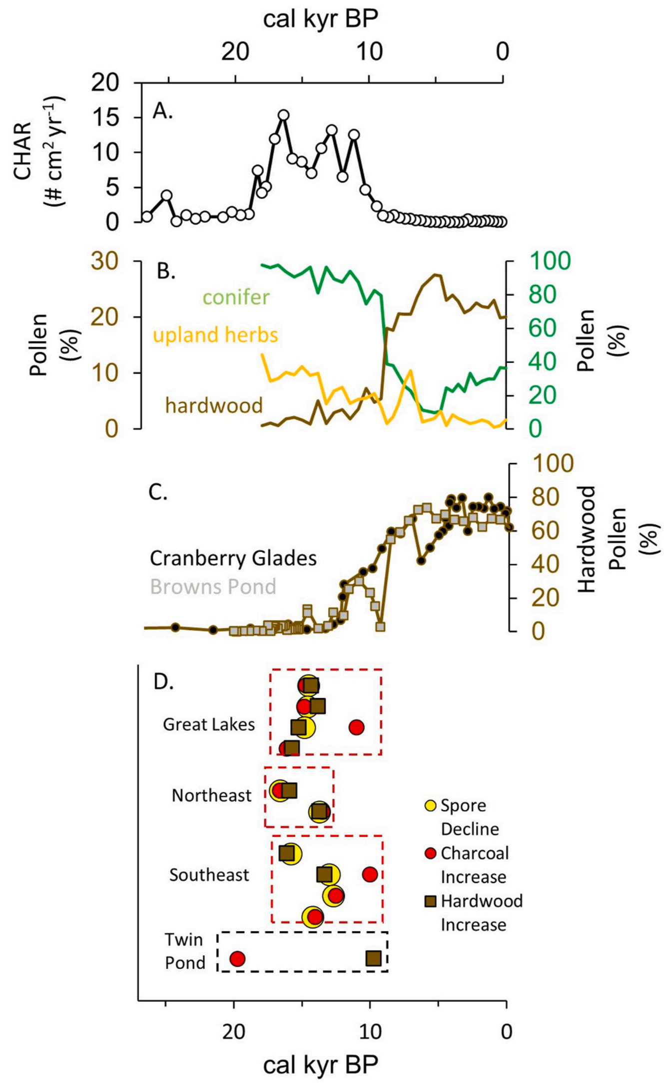

Fig. 5. Comparison of (A) Twin Pond charcoal accumulation rate and local as well as regional paleoecological data. (B) Pollen data from Hack Pond (Craig, 1969) show that a distinct vegetation shift from conifer to hardwood dominance occurred ca. 10 cal kyr BP (upland herbs are plotted on the left y-axis). The timing of this shift is corroborated by (C) hardwood pollen data from nearby Cranberry Glades (Watts, 1979) and Browns Pond (Kneller and Peteet, 1993). The fire and vegetation shifts evident in central Appalachia stand in stark contrast to (D) regional paleoecological reconstructions, which broadly support a link between the rise of hardwoods and fire, which have been traditionally interpreted to support the Megaherbivore Release Hypothesis (Perrotti et al., 2022). The regional groups (D) were defined by Perrotti et al. (2022) and are noted in Fig. 1.

though not in all cases, these no-analog vegetation states were accompanied by elevated charcoal accumulation rates and the decline of megafaunal dung spores, forming the evidentiary basis of the Megaherbivore Release Hypothesis (MRH) (Perrotti et al., 2022). The pollen records from Hack Pond (Craig, 1969), Browns Pond (Kneller and Peteet, 1993), and Cranberry Glades (Watts, 1979) (Fig. 5B and C) show that there was a relatively delayed hardwood increase in central Appalachia (between ca. 12 and 10 cal kyr BP). Further, the increase of charcoal accumulation rates in the Twin Pond sediment record dates to ca. 20 cal kyr BP, preceding the conifer-hardwood vegetation shift that occurred nearly 10,000 years later (Fig. 5A). Altogether, these data show that the paleoecological history of central Appalachia was marked by timings and sequences of ecosystem change and fire disturbance across the glacial-interglacial transition that were distinctly different than the prevailing paleoecological narrative (Fig. 5).

The Twin Pond charcoal data show that the hardwood increase was associated with a decline of fire activity (Fig. 5), whereas previous paleoecological research has observed an increase of fire with the rise of hardwood taxa. Notably, the charcoal morphological assemblages from Twin Pond show that the decrease of fire activity contemporaneous with the rise of hardwoods ca. 10 cal kyr BP was associated with a shift in fuel types burned (Fig. 4). Although the MRH evokes the preferential burning of hardwood fuels accumulated with the decline of megafauna populations (Perrotti et al., 2022), none of the paleofire records that form the basis of the MRH have resolved fuel types burned through the characterization of charcoal morphologies. Though the lack of evidence for the MRH in central Appalachia may be incongruent with previous findings in eastern North America, it could be explained by a scarcity of megafauna in the less productive highlands of Appalachia (Johnson et al., 2016; Pym et al., 2023). In sum, the Twin Pond charcoal data do not support the MRH in central Appalachia while also highlighting the potential utility of charcoal morphologies to test the underlying mechanism behind the MRH in regions where paleoecological data support it.

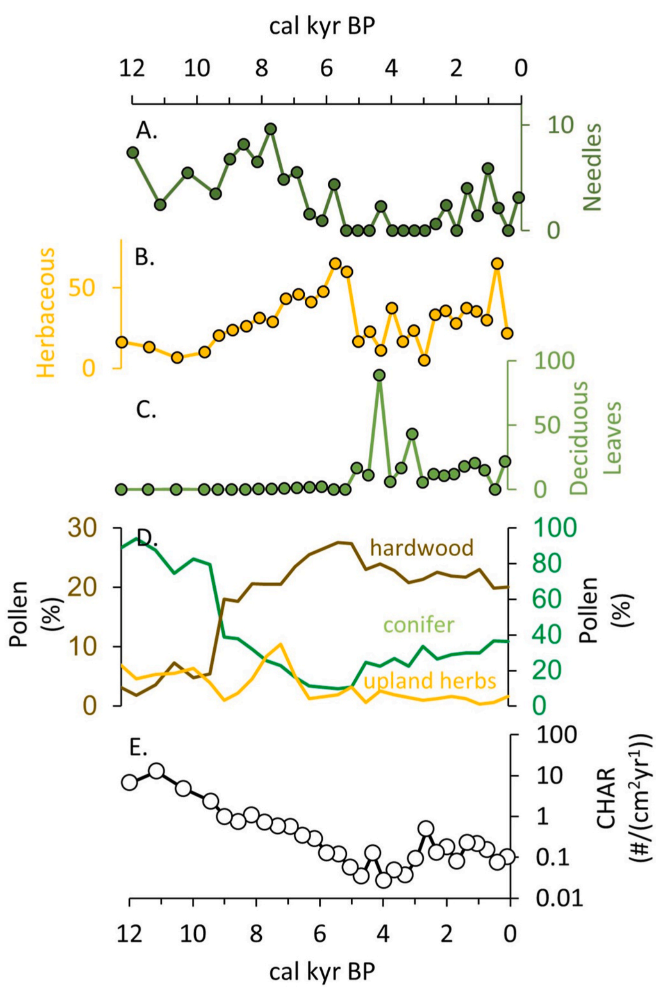

Fig. 6. In contrast to the glacial-interglacial in central Appalachia, fire and fuel types share a clear relationship during the Holocene (11.1 cal kyr BP to present). Over the course of this period, charcoal morphotypes characteristic of needles (A; dark green) declined whereas those characteristic of herbaceous material (B; yellow) and deciduous leaves (C; light green) increased. These changes in charcoal morphotypes broadly mirror the relative shifts of vegetation compositions of these plant types (D), as evident in the Hack Pond pollen record (Craig, 1969). Likewise, the decline of needle charcoal broadly corresponds with overall fire activity (E), indicating the likely link between conifer vegetation and fire during the interglacial period of central Appalachia.

In contrast to the glacial-interglacial transition, fire and vegetation share a close correspondence during the Holocene period (11.1 cal kyr BP to present) in the Twin Pond record. Indeed, during the Holocene, CHAR values broadly correspond with the relative abundance of charcoal morphotypes characteristic of needles, as well as the relative abundance of conifer taxa (Fig. 6). The dichotomy of fire and vegetation relationships between the glacial and deglaciation to interglacial periods is puzzling but could suggest that fire-fuel relationships are more pronounced during interglacial periods in central Appalachia. Likewise, during the deglaciation, temperature and precipitation were changing quickly, which may have overridden fire-vegetation relationships relative to the stable climatic conditions of the Holocene.

4.3. *Data-model comparison of glacial-deglacial fire history and climate in central Appalachia*

The Twin Pond paleofire record exhibits clear correspondence with the variability of CCSM3-based TraCE-21K-II climate variables across the glacial-interglacial transition. Namely, modelled surface air temperature and precipitation are relatively stable during the glacial (27–17.7 cal kyr BP) and Holocene (11.1 cal kyr BP to present) periods, as compared to the deglaciation (17.7–11.1 cal kyr BP; Fig. 7). Indeed, during the deglaciation, precipitation exhibits several marked multi-millennial-scale oscillations and temperature shows a steady increase

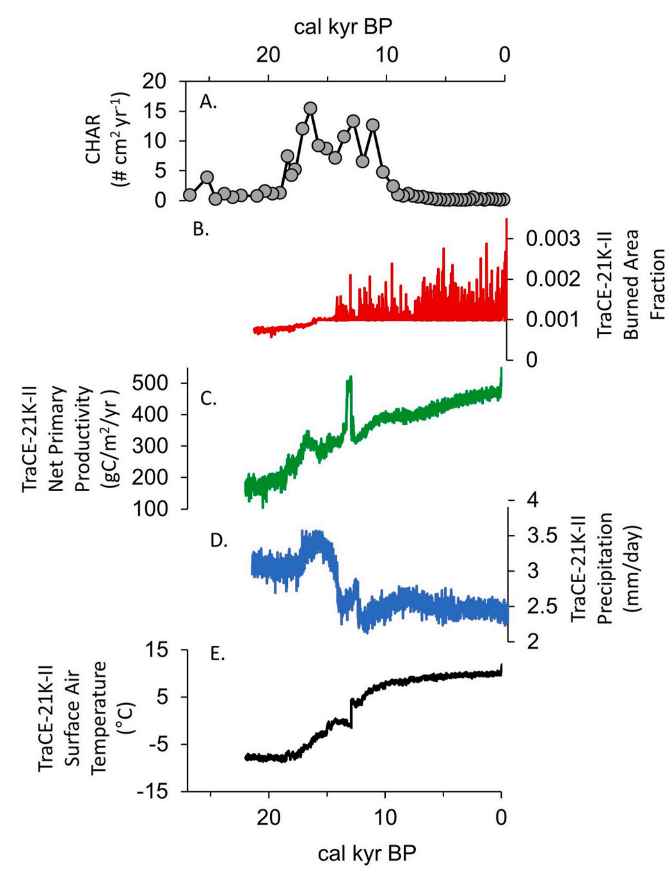

Fig. 7. (A) Paleofire data from Twin Pond and the (B) TraCE-21K-II simulated Burned Area Fraction (BAF; unitless) for the model grid cell containing Twin Pond do not agree with regards to the glacial-interglacial fire history of the region. The model parameterizes fire as a function of fire season length, but that there is a marked increase in BAF when fire season length exceeds half of a year. Comparison of BAF with simulated net primary productivity (C; NPP), precipitation (D) and surface air temperature (E) indicate that this step-wise shift is the likely root of the data-model mismatch. Each TraCE-21K-II dataset is expressed as a decadal mean.

(Fig. 7). Twin Pond charcoal accumulation rates have the highest values during this same period, indicating that long-term climate variability may be an important control of fire activity in central Appalachia.

The modelled fire history in the grid cell containing Twin Pond does not resemble the paleofire data from Twin Pond. Whereas the Twin Pond charcoal data show increased fire activity during the deglaciation (17.7–11.1 cal kyr BP), simulated burned area fraction (BAF) in the TraCE-21K-II experiment supports muted fire activity prior to 15 cal kyr BP and generally elevated fire activity from 15 cal kyr BP to present (Fig. 7). The stark contrast between reconstructed and simulated fire is striking as it suggests that the modelled burned area fraction is not able to reliably characterize paleofire activity in this region and/or on glacial-interglacial timescales.

The construction of the fire model within CCSM3 provides some insight into the likely explanation for the data-model disconnect between the Twin Pond paleofire record and TraCE-21K-II. Within CCSM3, vegetation and fire disturbance is simulated by the Lund-Potsdam-Jena Dynamic Vegetation Model (LPJ-DGVM) (Bonan et al., 2003; Sitch et al., 2003). Although the variables within the parameterization of fire in the LPJ-DGVM include fuel load, litter moisture, and plant functional type (Sitch et al., 2003), fire season length is the first order, non-linear control of BAF (Thonicke et al., 2001). Although BAF exhibits a weak positive relationship with fire season length when fire season length is less than half of a year, this relationship increases markedly for fire season lengths exceeding half a year (Thonicke et al., 2001). The empirical basis of this relationship is found in the comparison of fire season length and BAF in several multiannual observational datasets from Portugal, California, and Australia (Minnich, 1998; Russell-Smith et al., 1997; Thonicke et al., 2001; Viegas et al., 1992; Viegas, 1998). When we compare the TraCE-21K-II BAF dataset with simulated precipitation and surface air temperature (Fig. 7), we find no clear correspondences. Rather, BAF seems to have increased markedly ~15 cal kyr BP, during a consistent increase of modelled surface air temperature. We therefore suspect that the increase of BAF reflects the simulated fire season's exceedance of the half year threshold that accompanied warming surface air temperatures. This conclusion is supported by the oscillation of BAF above values of 0.001 after 15 cal kyr BP.

Alternatively, the increase of CHAR values and modelled BAF during the deglaciation could reflect the impact of growing fuel loads available for fire. Indeed, the onset of increased fire activity during this period corresponds to increasing net primary productivity (Fig. 7), which can be considered a proxy of fuel production and availability. At the global scale, in low productivity regions, fuel is a more influential control of fire whereas climate is more important in high productivity areas (Pausas and Ribeiro, 2013). Therefore, increasing net primary productivity during the deglaciation may have increased fuel loads in a relatively low productivity ecosystem and climate state to facilitate increased fire activity. This inference is supported by the unchanged fuel types burned during the deglaciation (Fig. 5).

The variability of climate drivers (temperature and precipitation) and their correspondence to Twin Pond CHAR variations during the deglaciation provide additional perspective on the climate-fire relationships of central Appalachia (Fig. 7). During the deglaciation, modelled temperature consistently increased (except for a sharp step-increase in values ca. 13 cal kyr BP) whereas precipitation varied more, with locally increased values from 17 to 15 and 13 cal kyr, and intervals of decreased values centered at ca. 14 and 11.5 cal kyr BP (Fig. 7). By comparison, Twin Pond CHAR values exhibit three intervals of increased values centered at ca. 16.5, 13, and 11 cal kyr BP (Fig. 7). Notably, the increased CHAR values correspond to intervals of both increased and decreased precipitation, suggesting that the influence of precipitation in fire may be modulated by other factors.

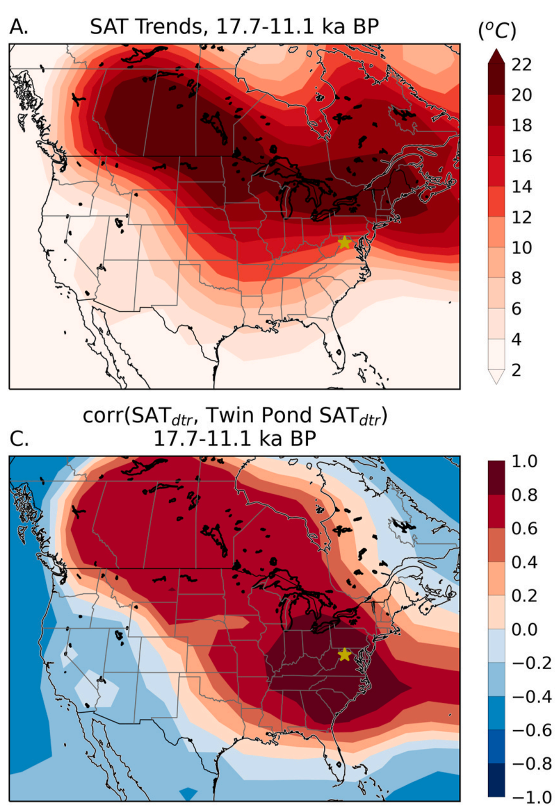

Fig. 8. Climate variability during the deglaciation period (17.7–11.1 ka BP) as simulated in the TraCE-21K-II simulation. Total change in modelled surface air temperature (A; SAT) and precipitation (B; PR) based on linear trends over the deglaciation period. (C) Correlations between the modelled detrended Twin Pond temperature and detrended temperatures across North America over the deglaciation. (D) Same as C but for precipitation. All TraCE analyses are based on decadally averaged temperature and precipitation data.

If we examine the geography of TraCE-21K-II modelled climate variables for the deglaciation (17.7–11.1 cal kyr BP), we see that long term trends were spatially more broadly coherent for temperature than for precipitation. The grid cell containing Twin Pond experienced warming surface air temperatures that were spatially coherent, albeit with different magnitudes across the North American continent (Fig. 8A). On the other hand, the Twin Pond grid cell exhibits the strongest decreasing trend of precipitation in North America, which is spatially coherent only across southeastern North America (Fig. 8B). Similar to the multimillennial trends, decadal-scale variability of surface air temperature for the Twin Pond grid cell is more spatially coherent with the rest of the North American continent but in the case of precipitation, the spatial coherence is limited to the southeastern North America (Fig. 8C and D).

Our analysis of the spatial variability and correspondence of TraCE-21K-II modelled climate variables with those of the Twin Pond grid cell provides important context for our paleofire analyses. Whereas temperature increased somewhat monotonically across North America, precipitation trends were more spatially and temporally heterogeneous. The spatial variability of precipitation could partly explain discrepancies between paleofire records resolving the deglaciation in eastern North America (as we discuss in the following section). Specifically, the Twin Pond region is characterized by sharp warming gradients and the strongest decrease in precipitation across North America with decreases south of the study site and increases in the north. Additionally, the long term changes in the absolute values of temperature and precipitation (crossing 0 °C at Twin Pond around 14 ka BP for example; see Fig. 7D) may also play an important role in fire activity through shifts in seasonality and vegetation. These data suggest that making continental-scale interpretations of fire-climate relationships on multi-millennial timescales, as is the norm in paleofire research (Power et al., 2008), could oversimplify spatial variability.

4.4. Implications of the Twin Pond paleofire record for future fire in central Appalachia

Twin Pond charcoal data and their relationships to climatic and vegetation changes of the last 27,000 years suggest that central Appalachia may experience increased fire activity in response to anthropogenic climate warming. The deglaciation represents a period of climatic change analogous to the global temperature increase expected in the future (Garelick et al., 2022). If we compare Twin Pond CHAR values with TraCE-21K-II modelled surface air temperatures (Fig. 7), we see that the onset of warming ca. 19 cal kyr BP roughly coincides with the onset of elevated fire activity. Therefore, we conclude that future climate warming is likely to cause increased fire activity in central Appalachia.

A source of uncertainty regarding the meaning of the Twin Pond paleofire record for the future is the role of precipitation. Whereas the deglaciation experienced overall decreasing precipitation, future climate projections for the region forecast increasing precipitation (Fernandez and Zegre, 2019; Marvel et al., 2023). It is important to note, however, that the century-scale outlook for fire activity may still be dominated by temperature increases since the increasing trend in precipitation is more gradual in comparison (Fernandez and Zegre, 2019; Marvel et al., 2023). If we examine fire-climate relationships during the deglaciation in more detail, we see that it provides unique perspective on the dynamic interplay of temperature and precipitation as controls of fire. Namely, during the deglaciation period, increasing temperatures appear to be the direct driver of increased fire activity (Fig. 7), while varying trends in precipitation have complex relationships with fire. Increased precipitation from 17 to 15 and 13 cal kyr coincided with increased CHAR values centered at 16.5 and 13 cal kyr BP (Fig. 7). In contrast, decreased precipitation ca. 11.5 cal kyr BP matched an increased interval of CHAR ca. 11 cal kyr BP. As such, the influence of precipitation on fire during this period appears to have been mixed. Over the course of this period, fuel types and vegetation compositions gradually shifted prior to the onset of broader vegetation change with the start of the Holocene (Figs. 5 and 6). Similarly, net primary productivity and fuel loading steadily increased, suggesting that the role of precipitation may have been modulated by fuel loading rather than fuel composition. Altogether, the deglaciation period demonstrates the complexity of climatic and vegetation relationships controlling fire in central Appalachia as climatic baselines shift.

Fire-vegetation relationships in our analyses provide an ambiguous perspective for future fire activity in central Appalachia. Species ranges are expected to shift in eastern North America in response to future climate warming (Morin et al., 2008; Morin and Thuiller, 2009) and the role of fire disturbance in driving these ecosystem shifts is unclear (Liu et al., 2013). Although our analysis of the Holocene period suggests that increases of coniferous taxa may be accompanied by increased fire activity (Fig. 6), fire activity during the deglaciation did not share a clear relationship with vegetation composition and fuel types (Fig. 6). In contrast, the onset of fire activity during the deglaciation is concomitant with steady increases of net primary productivity and potential fuel loads (Fig. 7). We interpret these conflicting perspectives to show that fire-fuel-type relationships in central Appalachia do not hold during periods of shifting climate baseline conditions as a function of fuel loading. Since future anthropogenic climate change is expected to manifest as rapidly changing conditions, we expect that the increased fire activity driven by warming temperatures and increased fuel loading may occur regardless of vegetation composition shifts or vegetation-focused mitigation steps.

The disconnect between TraCE-21K-II modelled BAF and central Appalachian fire history highlights a potential mismatch of climate scenarios of the two datasets. Namely, CCSM3 was built and calibrated to simulate modern fires due to the availability of observational fire history data. In contrast, the Twin Pond paleofire dataset experienced a wide range of Earth System climatic conditions. However, because the climate system may experience changing climatic baselines that mimic those of the future (consistent warming), our comparison echoes calls to improve fire's resolution in ESMs (Hantson et al., 2016; van Marle et al., 2017). In this way, the Twin Pond charcoal reconstruction serves as a case-in-point of the utility of paleoclimate data-model approaches (Kageyama et al., 2018; Liu et al., 2009; Otto-Bliesner et al., 2017).

5. Conclusion

Our charcoal data from the Twin Pond paleofire record provide the first perspective on central Appalachia's fire history across the glacial-interglacial transition. Broadly, we observe that the last 27,000 years of fire history was characterized by three distinct periods: (1) the glacial (27–17.7 cal kyr BP) when fire activity was relatively low and charcoal morphotypes were characteristic of wood and needle fuels, (2) the deglaciation (17.7–11.1 cal kyr BP) when fire activity increased markedly but fuel types were unchanged from the glacial, and (3) the interglacial Holocene (11.1 cal kyr BP to present) when fire activity decreased and charcoal fuels shifted towards more twigs, deciduous leaves, herbaceous material, and rootlets, with fire activity in close association with vegetation changes. The timing of fire and vegetation changes evident in the Twin Pond record contrasts with other published paleoecological transitions identified in eastern North America. Namely, the Twin Pond record shows a decline of fire activity coincident with increases in hardwood taxa, whereas the inverse relationship has been found in other eastern North America paleoecological records.

We compare the Twin Pond paleofire record to CCSM3-based TraCE-21K-II variables and find that although there is clear correspondence between the charcoal data and climate variables (precipitation, temperature), there is little agreement between the charcoal and modelled burned area fraction. The cause of this disagreement could be due to the construction of the fire model within CCSM3 or a potential mismatch of the climate scenarios of the two datasets. When we examine the geography of TraCE-21K-II modelled climate variables (precipitation, temperature), we find that long term trends were spatially more broadly coherent for temperature than for precipitation. The relative spatial heterogeneity of precipitation could explain some of this disagreement between the Twin Pond charcoal record and previously published paleofire records from other parts of eastern North America.

Overall, the Twin Pond charcoal datasets and their relationships to climatic and vegetation changes of the last 27,000 years suggest that central Appalachia may experience increased fire activity in response to anthropogenic climate warming. In contrast, the Twin Pond paleofire record's relationships with precipitation and vegetation provide ambiguous perspective for future fire activity in central Appalachia.

Credit author statement

All authors have made substantial contributions to the manuscript and have approved the final version. N. Balascio and R. Vachula designed the study. J Stockton, B Landolt, N. Balascio and R. Vachula collected and analyzed samples. A. Karmalkar undertook data-model comparison analyses. All authors participated in writing and editing the manuscript. All authors have approved the final version of this manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data supporting this manuscript are included as a supplementary file and have been uploaded to the NOAA NCEI Paleoclimatology Database (https://www.ncei.noaa.gov/access/paleo-search/).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quascirev.2024.108805.

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