



Holocene ecosystem succession and fire regime evolution at Tannersville Bog, northeastern United States

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Abstract

10 Northern peatlands are among the largest long-term terrestrial carbon reservoirs on Earth, with carbon accumulation jointly regulated by climate, hydrological conditions, and vegetation composition. Future climate warming is expected to accelerate the transition from lakes to peatlands while increasing the likelihood of peatland fires, which can rapidly release carbon accumulated for millennia. However, our understanding of how fire and peatland ecosystem development co-evolve over millennial timescales
15 remains poorly understood. Tannersville Bog (TANB), a temperate boreal peatland in northeastern Pennsylvania, provides an ideal natural laboratory for investigating how northern peatlands are shaped and affected by fire, post-glacial ecosystem succession, and climate. Here, we integrate pyrogenic polycyclic aromatic hydrocarbons (pyroPAHs), *n*-alkane biomarkers, and sediment composition analyses to reconstruct the Holocene fire and environmental changes of TANB. The combined proxy
20 records identify four major stages of ecosystem succession, from a shallow lake to a rich fen, a fen–bog transitional system, and ultimately a *Sphagnum*-dominated bog. Correspondingly, multivariate classification of PAH assemblages identifies four distinct fire regimes, which we link to vegetation and peatland-development proxies through ordination analyses. These fire regimes evolved alongside ecosystem succession, reflecting shifts in fuel composition, combustion processes, and fire-source
25 characteristics. The lake-to-peatland transition also reveals that changing depositional and preservation conditions influenced PAH distributions without obscuring major fire-regime transitions. Our results demonstrate that long-term fire-regime evolution was jointly controlled by changes in vegetation composition, peatland hydrology, and basin development, highlighting strong mutual feedback between ecosystem succession and fire over millennial timescales.



30 1. Introduction

Northern peatlands cover only ~3 % of the Earth's land surface yet store nearly one-third of the global soil carbon pool, making them one of the largest long-term terrestrial carbon reservoirs and a key component of the global carbon cycle (Loisel *et al.*, 2014; Le Quéré *et al.*, 2018; Loisel and Bunsen, 2020). Their carbon storage capacity is regulated by primary production and organic matter decomposition (Clymo, 1984; Gorham, 1991), which are influenced by climate, hydrology, and vegetation composition (Rydin and Jeglum, 2013; Yu, Beilman and Jones, 2013). However, this balance can be abruptly disrupted by fire, as highlighted by recent extensive wildfires in Canada (Van Gerrevink *et al.*, 2026), which can release substantial amounts of stored carbon and greenhouse gases, with losses that may require centuries to millennia to recover through peat accumulation (Rodríguez Vázquez *et al.*, 2021; Zheng *et al.*, 2021; Wilkinson *et al.*, 2023; VanderRoest *et al.*, 2024). Under future climate warming, continued peatland development, declining water tables (Salimi and Scholz, 2021; Chaudhary *et al.*, 2026), and increasing lightning activity are expected to elevate peatland fire risk in northern regions (Xiao and Zhuang, 2007). Despite the importance of these interactions, the mechanisms linking ecosystem succession, fire regimes, and carbon dynamics over millennial timescales remain poorly understood.

Most northern peatlands originated from post-glacial lakes and gradually evolved through shallow-lake, marsh, fen, and bog stages as organic matter accumulated and hydrological conditions changed (Tuittila *et al.*, 2013; Brosius *et al.*, 2021). This process of lake ontogeny fundamentally reshapes groundwater influence, vegetation composition, nutrient availability, and carbon accumulation, ultimately determining the long-term carbon sequestration capacity of peatlands (Schuller and Sullivan, 2024; Folhas *et al.*, 2025; Gao *et al.*, 2025). However, peatlands are highly dynamic systems that often undergo nonlinear transitions in both ecosystem structure and function (Belyea and Baird, 2006; Yu, 2006). Understanding these long-term ecological transitions is increasingly important because climate warming is expected to influence peatland hydrology and ecosystem structure, thereby affecting future carbon–climate feedback. Further, fire is not only a response to ecosystem change, but also an important driver of ecosystem succession (Clark-Wolf *et al.*, 2023; Bonk *et al.*, 2026). As peatlands evolve from lakes to fens and bogs, changes in vegetation composition, hydrology, and peat accumulation modify fuel availability, combustion conditions, and ecosystem resilience (Van Bellen *et*



al., 2012; Camill *et al.*, 2017). In turn, fire regulates nutrient cycling, vegetation succession, and peat accumulation, creating long-term feedbacks between ecosystem development and carbon storage (Loisel and Bunsen, 2020; Nelson *et al.*, 2021; Turunen *et al.*, 2025; Piczak *et al.*, 2026). Consequently, few studies have examined how long-term peatland succession regulates fire regimes, and how fire feeds back on ecosystem development and carbon accumulation. Addressing this knowledge gap is essential for improving mechanistic understanding of long-term fire–ecosystem feedback and for strengthening the interpretation of molecular paleofire proxies.

This study aims to reconstruct the Holocene fire history of Tannersville Bog (TANB), Pennsylvania, a temperate–boreal peatland, located near the southern edge of North American boreal peatlands (Watts, 1979). TANB provides an ideal natural laboratory for looking into how northern peatlands may respond to future warming. Moreover, its continuous evolution from a post-glacial lake to a mature peatland provides a rare opportunity to examine how ecosystem succession regulates carbon accumulation and environmental change throughout the Holocene. Using a high-resolution sediment record from TANB, we applied a multi-proxy approach that integrates polycyclic aromatic hydrocarbon (PAH) fire proxies, *n*-alkane indicators of peatland development, and sediment composition analysis to investigate how fire regimes and PAH compositions responded to long-term ecosystem succession (e.g., postglacial vegetation and lacustrine ontogeny). Pyrogenic polycyclic aromatic hydrocarbons (pyroPAHs) have already been widely used as paleofire proxies (Miller *et al.*, 2017; Homann *et al.*, 2023; Smolen *et al.*, 2025), with individual PAH compounds differing in their formation pathways, fuel type, combustion temperatures, transport characteristics, and post-depositional behavior, allowing reconstruction of fire regimes beyond simple changes in aggregate biomass burning (Lima, Farrington and Reddy, 2005a; Karp *et al.*, 2020; Vachula *et al.*, 2022). We hypothesize that changes in vegetation composition and lake ontogenic processes altered fuel availability and combustion conditions, resulting in distinct PAH assemblages and fire characteristics through time. To test this hypothesis, we (1) reconstructed the Holocene environmental succession of TANB using *n*-alkane indices; (2) identified temporal changes in PAH assemblages and inferred systematic fire regime changes; (3) assessed the influence of vegetation dynamics and lake development on fire characteristics; (4) evaluated whether local fire-regime shifts corresponded to broader regional fire patterns inferred from charcoal records across the northeastern Appalachians. Together, these analyses provide new insights into the mechanisms linking



ecosystem succession, fuel composition, and fire dynamics on millennial timescales in temperate peatland ecosystems.

90 2. Study site

Tannersville Bog (TANB; 41°02'N, 75°16'W; 277–290 m a.s.l.) is approximately 3 km² in size and is located in Monroe County, northeastern Pennsylvania, near the eastern edge of the Pocono Plateau in the northeastern Appalachian region (Fig.1). The regional bedrock consists of gently dipping Paleozoic sandstones and shales that were extensively modified by the Pleistocene glaciation and covered by the Laurentide Ice Sheet (Yu, 2006). Following deglaciation, the basin evolved through lake infilling and peat accumulation during the early Holocene (Watts, 1979). Pollen, diatom, and macrofossil records from Cai and Yu (2011) demonstrated that the site underwent major ecological reorganization throughout the Holocene, transitioning from a glacial lake (before 9 ka BP) to a brown moss-dominated rich fen (9–1.4 ka BP), and subsequently to a *Sphagnum*-dominated poor fen after approximately 1.4 ka BP. Reconstructions of apparent carbon accumulation rates over the past 8,000 years further indicated that TANB has maintained relatively high carbon accumulation compared with many northern peatlands, likely reflecting increased primary productivity under the warm and humid regional climate (Cai and Yu, 2011).

The region experiences a humid temperate climate, with a mean annual temperature of approximately 9.3 °C and mean annual precipitation of 1340 mm (National Centers for Environmental Information, 2026). The surrounding uplands are dominated by mixed oak forests (Watts, 1979), whereas the peatland supports a boreal-type vegetation assemblage consisting primarily of *Sphagnum* mosses (mainly *Sphagnum magellanicum*), leatherleaf (*Chamaedaphne calyculata*), bog rosemary (*Andromeda polifolia*), cotton grass (*Eriophorum vaginatum*), and cranberry (*Vaccinium macrocarpon*). The dominant tree species are black spruce (*Picea mariana*) and tamarack (*Larix laricina*). TANB represents one of the southernmost low-elevation *Sphagnum*-dominated peatlands along the eastern coast of North America and is widely regarded as a remnant boreal refugia persisting under temperate climatic conditions.

The significant Holocene shifts in hydrology, vegetation composition, and carbon accumulation during peatland development make TANB an ideal natural archive for investigating how fire regimes evolve



alongside ecosystem succession. The transition from an open-water lake to a peatland, followed by the succession of *Cyperaceae*- to *Sphagnum*-dominated plant communities (Watts, 1979), likely altered fuel composition, moisture availability, and fire behavior through time, though previous research has not directly resolved it. Consequently, TANB provides a unique opportunity to examine the interactions among environmental succession, vegetation change, and fire dynamics in the northeastern Appalachian region throughout the Holocene.

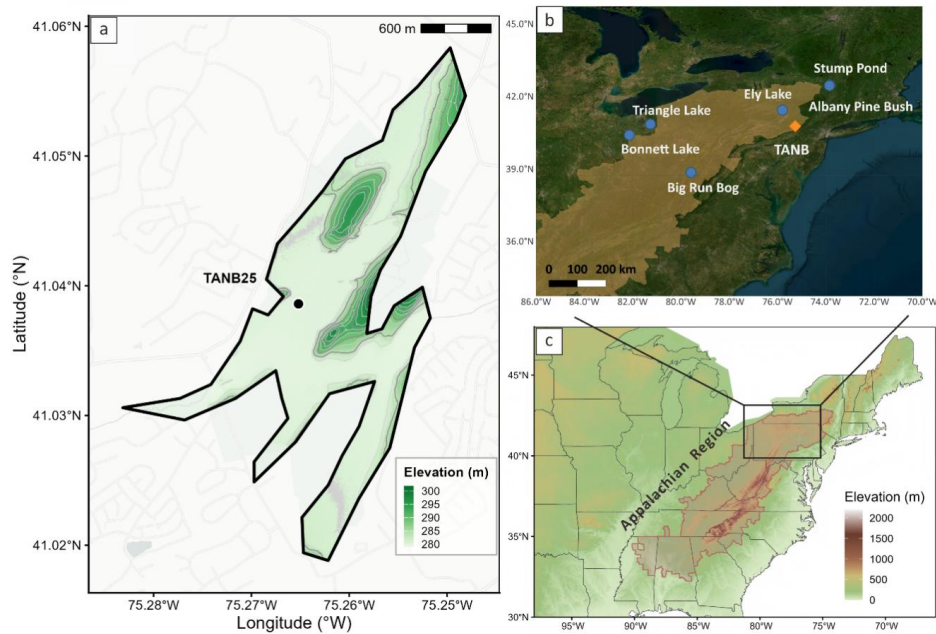


Figure 1. Location of Tannersville Bog (TANB) and other relevant sites in the region. (a) High-resolution topographic map of TANB showing the location of the TANB25 sediment core. The black outline marks the present boundary of TANB, digitized from Google Earth Pro imagery, and elevation is derived from the U.S. Geological Survey (USGS) 3D Elevation Program (3DEP) digital elevation model (DEM). (b) Locations of TANB and six charcoal records used to reconstruct regional Holocene fire activity across the northeastern Appalachians (shaded yellow area; same as in panel c). (c) Regional map showing the position of the study sites within the Appalachian Region (red outline; Appalachian Regional Commission boundary dataset). Terrain shading and elevation colors are based on USGS 3DEP DEM. Basemap sources: Esri World Imagery (b) and Esri Terrain (c). Sources: Esri and its data providers | Powered by Esri. Elevation data: USGS 3DEP. Appalachian Region boundary: Appalachian Regional Commission.

3. Methods

3.1 Sediment core and chronology

In October 2025, we collected an approximately 880-cm-long sediment core from TANB (TANB25; 41°2'17"N, 75°15'57"W; 290 m a.s.l.; Fig. 1a) using a 5 cm diameter Russian peat sampler (Aquatic



Research Instruments). The top 80 cm of the core was sectioned at 5-cm intervals, whereas the remaining 800 cm was subsampled at 2-cm intervals (due to variations in sediment texture).

Considering that *n*-alkane distributions in different vegetation types can vary with environmental
140 conditions, leaf samples from 11 representative plant species surrounding TANB were analyzed to
provide a modern reference for interpreting changes in *n*-alkane within the sediment core records
(Table S2). These species were selected to represent the dominant vegetation types currently occurring
at TANB, based on vegetation descriptions provided by The Nature Conservancy. The sampled taxa
encompass the major vegetation groups in the marsh and its surrounding areas, including conifers,
145 angiosperms, and bryophytes based on modern phylogenetic classification (Morrone, 2023).
The chronological framework of the TANB core was established using accelerator mass spectrometry
(AMS) radiocarbon dating. Woody macrofossils and sediment bulk samples were selected for
radiocarbon analysis (Table 3) and measured at the National Ocean Sciences Accelerator Mass
Spectrometry Facility at the Woods Hole Oceanographic Institution (WHOI). Radiocarbon ages were
150 calibrated to calendar years before present (cal yr BP; present = 1950 CE) using CALIB v8.20 (Stuiver
and Reimer, 1993) and the IntCal20 calibration curve (Reimer *et al.*, 2020). An age-depth model was
subsequently developed using the Bayesian age-modeling software Bacon in R (Blaauw and Christen,
2011).

3.2 Geochemical analysis

155 3.2.1 Organic geochemistry analysis

Sediment samples were freeze-dried prior to extraction of total lipid extracts (TLEs) using an
accelerated solvent extraction (ASE) system with a dichloromethane mixture (9:1, v/v). The resulting
TLEs were dried, weighed, and separated into compound classes by silica gel column chromatography
using eluent solvents of increasing polarity. Three fractions were collected: hexane (F1, containing *n*-
160 alkanes), dichloromethane (F2, containing PAHs), and methanol (F3). In addition, organic compounds
from modern vegetation samples collected at TANB were extracted using the same ASE and silica gel
column chromatography procedure.

Fractions were analyzed using an Agilent 8890 gas chromatograph coupled to a 5977B mass selective
detector (GC–MSD). The instrument was equipped with an HP-5MS UI capillary column (30 m × 0.25



165 mm i.d. $\times$ 0.25 μm film thickness), and helium was used as the carrier gas at a constant flow rate of 1.2
mL min^{-1} . The *n*-alkanes in sediment and modern vegetation samples were measured from the F1
fraction. Samples were injected at 320 $^{\circ}\text{C}$, and the oven temperature was programmed from 80 $^{\circ}\text{C}$ (held
for 5 min) to 310 $^{\circ}\text{C}$ at a rate of 15 $^{\circ}\text{C min}^{-1}$, followed by a final hold to 35.33 min. PAHs were
analyzed from the F2 fraction. Samples were injected at 300 $^{\circ}\text{C}$, and the oven temperature was
170 programmed from 55 $^{\circ}\text{C}$ (held for 2 min) to 110 $^{\circ}\text{C}$ at 50 $^{\circ}\text{C min}^{-1}$, followed by an increase to 320 $^{\circ}\text{C}$
at 12 $^{\circ}\text{C min}^{-1}$ and a final hold to 29.6 min. *N*-alkane and PAH compounds were identified and
analyzed in full-scan mode (m/z 50–550) using electron ionization (EI) at 70 eV, with an emission
current of 34.6 μA and an entrance lens voltage of 22.7 V. The ion source and quadrupole temperatures
were maintained at 230 $^{\circ}\text{C}$ and 150 $^{\circ}\text{C}$, respectively.

175 *N*-alkanes ($\text{C}_{16}\text{--C}_{35}$) and PAHs were quantified for each peak based on Selective Ion Monitoring (SIM)
mass (m/z ; Table. S1) and calibrated against external standards (Sigma-Aldrich 49452-U for *n*-alkanes
and 48953-U for PAHs). Calibration curves were generated from four known dilutions of each standard
($n = 4$), and separate calibration curves were established for each target compound to account for
differences in instrumental response. To minimize instrument drift, calibration curves were re-
180 established after every 25 samples analyzed.

PAH and *n*-alkane abundances were expressed as fluxes ($\text{ng cm g}^{-1} \text{yr}^{-1}$) by incorporating sediment
accumulation rates derived from the age-depth model. Fluxes were used rather than concentrations to
account for changes in sediment and peat accumulation associated with the long-term development and
environmental evolution of TANB, thereby reducing potential biases arising from variations in
185 sedimentation rates. To further account for differences in organic matter preservation, fluxes were
normalized to organic matter content (OM %).

3.2.2 Sediment composition analysis

Organic matter content was determined using loss-on-ignition (LOI) analysis, a widely used method for
estimating the water, organic matter, and carbonate content of sediments (Heiri, Lotter and Lemcke,
190 2001). Volumetric samples (1 cm^3) were collected at 20-cm intervals throughout the TANB core.
Samples were sequentially combusted at 120 $^{\circ}\text{C}$ for 8 h and 550 $^{\circ}\text{C}$ for 2 h to quantify organic matter
and ash-free bulk density (AFBD; Peteet *et al.*, 2020).



3.2.3 Geochemistry indices

Several indices were calculated to characterize the distributions of *n*-alkanes and PAHs within the sediment samples. The definitions, equations, and interpretations of these parameters are summarized below (Table. 1).

Alkane indices:

(1) Average Chain Length (ACL)

ACL describes the weighted mean chain length of long-chain *n*-alkanes (Eglinton and Hamilton, 1967) and is widely used to infer changes in vegetation composition and environmental conditions. ACL typically varies among plant functional groups, with herbaceous vegetation generally exhibiting higher values than woody vegetation (Xiao *et al.*, 2025). In addition, terrestrial plants tend to produce longer-chain homologues under warmer and drier conditions (Castañeda and Schouten, 2011). Thus, variations in ACL may reflect changes in both vegetation composition and environmental conditions and will be interpreted in conjunction with other ecological indicators.

(2) Carbon Preference Index (CPI)

CPI measures the predominance of odd-carbon-numbered long-chain *n*-alkanes relative to even-carbon-numbered homologues (Bray and Evans, 1961) and is widely used as an indicator of organic matter preservation. Fresh higher-plant waxes commonly show high CPI values (4–40), whereas microbial decomposition and diagenetic alteration progressively reduce this odd-over-even predominance, causing CPI values to approach the same values (~1) in mature rocks and oils (Collister *et al.*, 1994). In peatland studies, CPI is frequently used to infer peat humification and organic matter degradation (Lehtonen and Ketola, 1993). However, both microbial activity and bacterial production of long-chain *n*-alkanes tend to increase under warmer conditions, CPI may also provide information on past climatic variability (Zhou *et al.*, 2005; Ortiz *et al.*, 2010).

(3) P_{aq}

The P_{aq} index is commonly used to distinguish inputs from aquatic and emergent macrophytes from those of terrestrial vegetation (Ficken *et al.*, 2000; Nichols *et al.*, 2006; Zhou *et al.*, 2010). Generally, P_{aq} values below 0.1 indicate dominant terrestrial vegetation inputs, values between 0.1 and 0.4 suggest contributions from emergent or floating macrophytes, and values above 0.4 indicate a predominance of submerged or floating aquatic macrophytes (Ficken *et al.*, 2000; Ronkainen *et al.*, 2013a). However, because *Sphagnum* mosses and aquatic macrophytes share similar lipid distributions characterized by abundant C_{23} *n*-alkanes (Baas *et al.*, 2000; Ortiz *et al.*, 2010), P_{aq} in peatland environments may reflect both hydrological changes and shifts in peat-forming vegetation. Therefore, in this study, P_{aq} was interpreted alongside the $C_{23}/(C_{23}+C_{29})$ ratio.

(4) Terrestrial-to-Aquatic Ratio (TAR)

TAR compares the abundance of long-chain terrestrial *n*-alkanes with that of short-chain aquatic-derived *n*-alkanes and is widely used to assess the relative contributions of terrestrial plants versus algal and bacterial organic matter (Bourbonniere and Meyers, 1996a). Higher TAR values (>4) generally indicate stronger inputs from terrestrial vascular plants, whereas lower values (<4) reflect increased contributions from aquatic sources (Wang *et al.*, 2014). Given the limitations of P_{aq} in *Sphagnum*-



dominated peatlands, TAR was used in this study as an additional indicator of terrestrial vegetation inputs and hydrological change.

(5) $C_{23}/(C_{23}+C_{29})$

235 The $C_{23}/(C_{23}+C_{29})$ ratio is commonly used to distinguish inputs from *Sphagnum* mosses and terrestrial vascular plants (McClymont *et al.*, 2008; Bingham *et al.*, 2010). *Sphagnum* species are characterized by abundant mid-chain *n*-alkanes, particularly C_{23} and C_{25} , whereas terrestrial higher plants are typically dominated by long-chain homologues (C_{29} – C_{33}) (Nott *et al.*, 2000; Bingham *et al.*, 2010). As a result, higher $C_{23}/(C_{23}+C_{29})$ values generally indicate greater contributions from *Sphagnum* species.
 240 However, because mid-chain *n*-alkanes are preferentially degraded during early diagenesis relative to long-chain homologues, this ratio may decrease by organic matter degradation through time (Lehtonen and Ketola, 1993; Zhang *et al.*, 2017).

PAH indices:

(1) *LMW/Total PAHs*

245 The LMW/Total PAHs has traditionally been used as an indicator of combustion temperature, with lower values generally associated with higher-temperature combustion processes (Lima, Farrington and Reddy, 2005b; Wang, Wang and Herath, 2017). More recently, Karp *et al.* (2020) proposed that this ratio primarily reflects the physicochemical properties of PAH compounds and can be used to distinguish between PAHs derived from combustion residues (0.35–0.80) and smoke emissions (0.75–
 250 0.95). Building on this interpretation, recent studies have further linked variations in LMW/Total values to differences in vegetation openness, particularly between herbaceous fuel-dominated fires and canopy-closed, woody fuel-dominated fire systems (Karp *et al.*, 2023; Smolen *et al.*, 2025).

(2) *Ret/3-ring PAHs*

The Ret/3-ring PAHs ratio was developed from combustion experiments conducted by Karp *et al.*
 255 (2020) and has been applied to assess the changes in fuel type. Higher values (> 0.1) indicate a greater contribution from gymnosperm-derived fuels, whereas lower values (< 0.1) suggest dominance of angiosperm fuels. This relationship arises because retene is derived from conifer diterpenoid precursors and is recognized as a diagnostic biomarker of conifer combustion (Simoneit, 1977; Disnar and Harouna, 1994).

260 (3) *Ret/(Ret+Chry)*

The Ret/(Ret+Chry) ratio is commonly used to distinguish fuel sources based on the conifer-derived origin of retene. Values of 0.15–0.50 typically indicate fossil-fuel combustion, whereas values > 0.80 suggest dominant biomass burning inputs (Yan *et al.*, 2005; Kuo *et al.*, 2011; Denis *et al.*, 2012; Miller *et al.*, 2017).

265 Apparent carbon accumulation rate (aCAR):

The aCAR was calculated by combining peat accumulation rates derived from the age–depth model with measurements of ash-free bulk density and carbon content (Frolking, Talbot and Subin, 2014). In peatland studies, aCAR is an indicator of carbon sequestration efficiency and long-term peat accumulation dynamics (Young *et al.*, 2021; Zhang *et al.*, 2025).

270 **Table 1.** Definitions and indices used in this study to examine changes in fire and environment.



Indices	Equation	Previous study
Average Chain Length (ACL)	$ACL_{27-33} = \text{odd} \sum_{n=27}^{33} (C_n \times n) / \sum_{n=27}^{33} C_n$	(Eglinton and Hamilton, 1967)
Carbon Preference Index (CPI)	$CPI = \frac{1}{2} \left[\left(\frac{\text{odd} \sum_{n=27}^{33} C_n}{\text{even} \sum_{n=24}^{32} C_n} \right) + \left(\frac{\text{odd} \sum_{n=27}^{33} C_n}{\text{even} \sum_{n=26}^{34} C_n} \right) \right]$	(Bray and Evans, 1961)
P _{aq} index	$P_{aq} = \frac{(C_{23} + C_{25})}{(C_{23} + C_{25} + C_{29} + C_{31})}$	(Ficken <i>et al.</i> , 2000)
Terrigenous/Aquatic Ratio (TAR)	$TAR = \frac{(C_{29} + C_{31} + C_{33})}{(C_{29} + C_{31} + C_{33} + C_{17} + C_{19})}$	(Bourbonniere and Meyers, 1996b)
C ₂₃ Ratio	$C_{23} \text{ Ratio} = \frac{C_{23}}{(C_{23} + C_{29})}$	(Ronkainen <i>et al.</i> , 2013a)
LMW/Total PAHs	$LMW/Total = \frac{(Phen + Ant + Flu + Pyr)}{(Phen + Ant + Flu + Pyr + BaA + Chry + BkFF + BeP + BaP + IP + BghiP)}$	(Stogiannidis and Laane, 2015)
Ret/3-ring	$Ret/3 - ring = \frac{Ret}{(Ret + Ant + Phen)}$	(Karp <i>et al.</i> , 2020)
R/(R+C)	$R/(R + C) = \frac{Ret}{(Ret + Chry)}$	(Yan <i>et al.</i> , 2005)
MMW compounds	<i>Fluoranthene, Pyrene, Benzo[a]anthracene, Chrysene</i>	(Lima,
HMW compounds	<i>Benzo[k]fluoranthene, Benzo[a]pyrene, Indeno[1,2,3-c,d]pyrene, Dibenzo[a,h]anthracene, Benzo[g,h,i]perylene</i>	Farrington and Reddy, 2005a)
Apparent Carbon Accumulation Rate (aCAR)	$aCAR = \frac{Peat \text{ Vertical Accretion}}{Ash - free Bulk Density \times Carbon Content}$	(Frolking, Talbot and Subin, 2014)

3.3 Peatland development analyses

3.3.1 Cumulative carbon accumulation

Apparent carbon accumulation rates (aCAR) were calculated using peat and sediment bulk density, OM % (Talbot *et al.*, 2014), and Bacon-derived age estimates (R. Bacon, . Carbon accumulation was reconstructed throughout the sediment core to evaluate long-term changes in carbon sequestration during lake-peat transition. Cumulative carbon accumulation was subsequently calculated by integrating carbon accumulation through time, providing a measure of total carbon storage and enabling comparison of carbon sequestration dynamics among different stages of environmental development.



280 3.3.2 Cumulative Carbon Accumulation Model

To identify long-term trends in carbon accumulation, generalized additive models (GAMs) were fitted to cumulative carbon accumulation trajectories (R. mgcv, Wood, 2017). GAMs provide a flexible framework for characterizing nonlinear changes in ecosystem development through time without predefining any functional forms (Burkett *et al.*, 2005; Lai *et al.*, 2024). Observed cumulative carbon
 285 accumulation trajectories were subsequently compared with theoretical peat accumulation curves predicted by the Clymo peat growth model (Clymo, 1984). This comparison was used to evaluate deviations from expected peatland developmental pathways and to identify periods of accelerated or reduced carbon accumulation associated with environmental change. To further explain the carbon accumulation change, paleotemperature and paleoprecipitation records for the TANB site were
 290 extracted from the TraCE-21K-II climate simulation (He and Clark, 2022) and used as independent climatic reference data.

3.3.3 Environmental zonation and analysis of published pollen data

Major environmental transitions during the development of TANB were identified using stratigraphically constrained cluster analysis (CONISS; R. rioja, Steve Juggins, 2009). The analysis
 295 incorporated organic matter (OM) content, apparent carbon accumulation rate (aCAR), and *n*-alkane indices (P_{aq} , CPI, and TAR), which reflect changes in hydrology, organic matter sources, and peat accumulation processes. Since CONISS preserves the stratigraphic order of samples (Grimm, 1987), it identifies ecological boundaries and periods of environmental reorganization within sedimentary records. We used the resulting zonation to define the major environmental succession at TANB
 300 throughout Holocene.

Cai and Yu (2011) previously applied CONISS to the TANB pollen record and identified 6 pollen zones. To reduce the influence of individual plant taxa on the clustering results, to provide a more robust analysis of vegetation change, and to further assess the consistency between environmental transitions inferred from *n*-alkane proxies and vegetation succession, we reclassified the pollen
 305 assemblages into five major vegetation groups relevant to ecosystem development: broadleaf trees, conifers, herbs, bog heath shrubs, and wetland taxa (Faber-Langendoen *et al.*, 2012; Neale and



Wheeler, 2019). CONISS was then re-applied to the reclassified pollen dataset.

3.4 Fire reconstruction and statistical analyses

3.4.1. Fire regime classification and PAH assemblage analyses

To investigate long-term changes in fire characteristics, PAH assemblages were analyzed using both individual PAH compounds and PAH indices. Fire regime states were identified using a set of PAH indices, including total PAH flux corrected by OM %, the relative abundances of LMW, MMW, and HMW PAHs, and the ret/3-ring PAH ratio (Table 2 & S1). Principal component analysis (PCA; R. factoextra, Kassambara and Mundt, 2016) was first used to relationships among the fire indicators and identify the major gradients in PAH composition. Hierarchical clustering was used to explore the overall structure of the standardized PAH dataset and identify potential groups, while k-means refined sample assignments into distinct fire regimes (Peterson, Ghosh and Maitra, 2018). PCA was then used to visualize the separation among fire regimes and the contribution of individual PAH indicators. To further study changes in PAH assemblage composition, non-metric multidimensional scaling (NMDS; R. vegan, Oksanen *et al.*, 2001) based on Bray–Curtis dissimilarity (Kruskal, 1964) was used to visualize similarities and differences among samples and identify major gradients in PAH composition. Prior to multivariate analyses, the relative abundances of the 17 PAH compounds (Table. S1) were standardized using z-score transformations to minimize the influence of variations in PAH flux.

3.4.2. Relationships between fire regimes and environmental variables

To assess the influence of vegetation composition and peatland development on fire regime variability, we performed redundancy analysis (RDA; R. Vegan, Oksanen *et al.*, 2022) and linear discriminant analysis (LDA; R. Mass, Ripley and Venables, 2009) using the fire regime states identified from the PAH data (Liu, 2013). RDA and LDA models were constructed with peatland development indicators (P_{aq} , CPI, ACL, TAR, and aCAR) and pollen-derived vegetation variables (broadleaf taxa, conifers, herbs, bog-heath shrubs, and wetland taxa) (Cai and Yu, 2011). The resulting discriminant functions were used to identify the environmental variables most strongly associated with differences among fire regimes and to evaluate the relative roles of vegetation change and peatland development in shaping



fire characteristics through time.

335 **3.4.3. Regional comparison of fire history**

To evaluate the consistency of the TANB fire record within a broader regional context, we compiled charcoal records from six sites across the northeastern Appalachian region and compared them with the PAH record from TANB (Table. 2). Charcoal datasets were obtained from published records archived in the Neotoma Paleoecology Database (Williams *et al.*, 2018), the Global Paleofire Database (GPD) (Marlon *et al.*, 2016), and The Reading Paleofire Database (Harrison *et al.*, 2022). Site selection was based on two criteria: (1) records had to be located within the northeastern Appalachian region (Fig. 1), and (2) they had to provide a continuous Holocene charcoal record supported by a published age–depth model without major unconstrained age intervals. Records located outside the study region, lacking substantial Holocene coverage, or having inadequate
340 chronological resolution were excluded. To facilitate comparison among records with different sampling resolutions and analytical units, all charcoal records were standardized within each site (z-score; Power *et al.*, 2008) and interpolated to a 250-year temporal grid, with values averaged within each time bin (Tsalickis *et al.*, 2025). Heatmaps were then used to visualize spatiotemporal patterns of fire activity, enabling assessment of regional synchrony, geographic gradients, and long-term
345 trends in Holocene fire activity across the northeastern Appalachian region.

Table 2. Sources of charcoal datasets are used to comparison in this study

Site	Latitude	Longitude	Age (cal BP)	Data source
Ely Lake	41.7	-75.8	22 to 5542	(Clark and Royall, 1996a)
Stump Pond	42.735	-73.828333	7226 to 12947	(Stager, St-Jacques and Tremblay, 2024)
Albany Pine Bush	42.715833	-73.854722	455 to 6426	(St-Jacques, Stager and Tremblay, 2024)
Big Run Bog	39.1162	-79.58082	-72 to 18230	(Chimezie <i>et al.</i> , 2026)
Triangle Lake	41.11906	-81.261335	1698 to 17286	(Jensen <i>et al.</i> , 2021)
Bonnett Lake	40.66667	-82.13718	0 to 18463	(Fastovich <i>et al.</i> , 2020)

4. Results

4.1 Chronology and age model

The TANB core recovered 8.8 m of sediment spanning approximately the last 10,618 years (Fig. 2;



Table 3). One radiocarbon date obtained from a macrofossil plant at 780 cm depth was rejected from inclusion in the model because it yielded an anomalously young age with low confidence (2σ), likely reflecting reintroduction into the core during sampling rather than the depositional age of the surrounding sediments. The resulting age-depth model shows a consistent increase in age with depth, indicating a continuous depositional sequence with no major age reversals or hiatuses. The basal sediments at approximately 880 cm depth are dated to ~ 10.6 ka cal BP. The average sedimentation rate is approximately 0.88mm yr^{-1} with slightly higher accumulation rates in both the top and bottom sediments.

The core comprises three major lithological units (Fig. 2). The basal unit (8.8–7.4 m depth) is composed of dark mud and is overlain by a distinct light-brown transitional layer (7.4–7.0 m). Above this, dark organic-rich mud dominates the interval from 7.0 to 2.0 m, with variable water content and sediment density, and includes isolated sandy mottles between 5.3 and 6.0 m depth. The uppermost 2.0 m is composed of peat that becomes progressively more compact with depth.

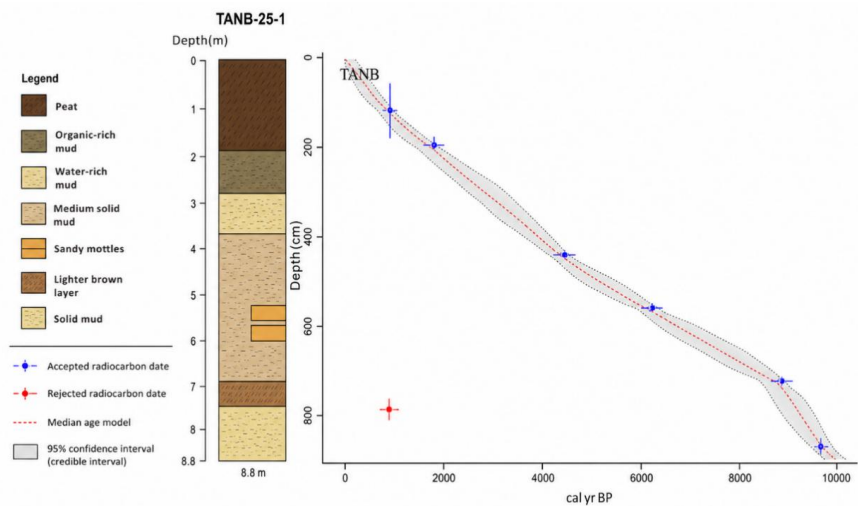


Figure 2. Age-depth model and stratigraphic column for the TANB 25 core. Probability ranges of the radiocarbon dates are shown in purple. The central red dashed line shows the mean values of model iterations. The outer dashed lines denote 95 % confidence levels.

Table 3. Radiocarbon ages informing the TANB age-depth model

Laboratory ID	Depth (cm)	Material dated	¹⁴ C Age (yr BP)	¹⁴ C Age Error	Calibrated Age (cal yr BP)
OS-189667	114–116	wood	750	15	666–690



OS-189668	190–192	wood	1570	15	1399–1478
OS-189669	436–438	wood	3650	20	3895–3998
OS-189599	554–556	Bulk Sediment	5080	20	5749–5829
OS-189600	716–718	Bulk Sediment	7750	30	8446–8593
OS-189694	780–782	wood	980*	15	819–868
OS-191783	854–858	Bulk Sediment	8570	35	9481–9556

*Rejected radiocarbon date

4.2 *N*-alkanes and environmental change

375 The total alkane flux and OM-corrected alkane flux exhibited broadly similar temporal patterns (Fig. 3a). Following normalization to OM %, alkane flux showed an overall increase through the mid-Holocene, reaching a maximum at approximately 5.9 and 10.6 ka cal BP. Additional peaks occurred at around 4.6, 7.3, and 8.5 ka cal BP.

The P_{aq} and $C_{23}/(C_{23}+C_{29})$ records displayed nearly parallel trends (Fig. 3b). Between 0.3 and 2.8 ka cal BP, both indices remained consistently high, generally exceeding 0.9. At approximately 3.1 ka cal BP, both records declined sharply. Thereafter (>3.1 ka cal BP), P_{aq} values fluctuated between 0.2 and 0.4, while $C_{23}/(C_{23}+C_{29})$ values remained between 0.3 and 0.5, exhibiting relatively limited variability. ACL values ranged between 29 and 31 throughout the record (Fig. 3c). The lowest value (~ 27.7) occurred at approximately 1.9 ka cal BP, whereas the highest value (~ 30.9) was observed near 3.6 ka cal BP. After 385 4.0 ka cal BP, ACL varied frequently and significantly, whereas it remained stable (~ 30.3) during the early-mid Holocene. TAR values fluctuated between approximately 1.5 and 3.5 during the early to mid-Holocene, increased sharply to a maximum of 5.4 at approximately 3.2 ka cal BP, and then declined rapidly, remaining close to 0 after approximately 2.8 ka cal BP.

Distinct differences in *n*-alkane distributions were observed among modern vegetation groups (Fig. 390 S3). Conifers were dominated by C_{29} homologues and exhibited intermediate average chain lengths (ACL = 28.5). In contrast, angiosperms, particularly grasses and herbaceous species, were enriched in long-chain *n*-alkanes (C_{33} and C_{35}), resulting in the highest ACL values (32.4). Moss displayed a distribution dominated by mid-chain homologues, with peaks at C_{23} and C_{25} , and the lowest ACL values (25.9).

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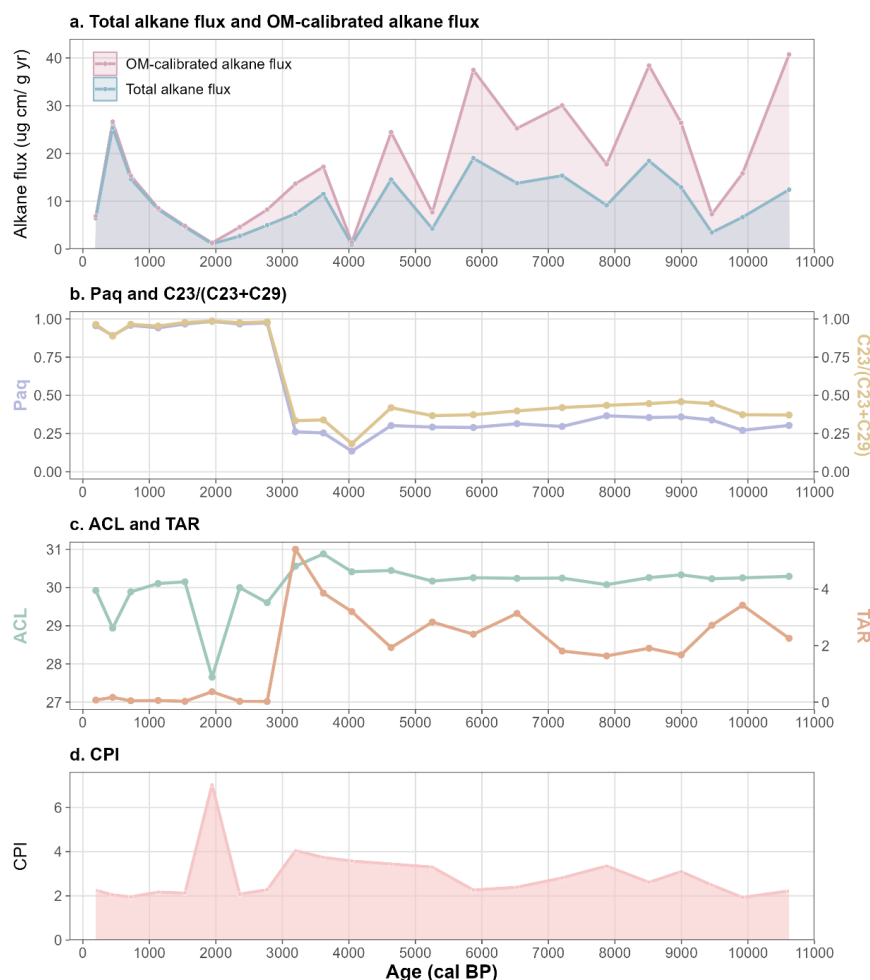


Figure 3. *N*-alkane records from the TANB core. a. OM-corrected total alkane flux (pink) and total alkane flux (blue). b. P_{aq} (purple) and $C_{23}/(C_{23}+C_{29})$ ratio (tan). c. Average chain length (ACL; green) and terrigenous-to-aquatic ratio (TAR; orange). d. carbon preference index (CPI; coral). All records are plotted against calibrated age (cal yr BP).

400

Following the CONISS of OM %, aCAR, P_{aq} , CPI, and TAR, four major zones were identified within the TANB record (Fig. 4). Zone I (>9.2 ka cal BP) shows gradually increasing OM % and CPI values. During this interval, OM % (30–50 %) and aCAR ($\sim 21 \text{ g C m}^{-2} \text{ yr}^{-1}$) remained relatively low, while P_{aq} (~ 0.25 – 0.35) and TAR (1.5–3.5) exhibited only minor fluctuations. Zone II (9.2–3.0 ka cal BP) is defined by higher OM % values (~ 50 – 70 %) and relatively stable aCAR values (~ 13 – $30 \text{ g C m}^{-2} \text{ yr}^{-1}$). P_{aq} gradually declined from ~ 0.35 to 0.20, whereas TAR increased from ~ 2 to 5, both with moderate

405



fluctuations. CPI also displayed a gradual upward trend, although its overall variability remained limited. Zone III (3.0–1.7 ka cal BP) marks a period of significant change, with P_{aq} increasing to approximately 0.98, OM % rising from ~60 % to >90 %, and aCAR increasing from ~20 to 60 g C m⁻² yr⁻¹. CPI exhibited substantial variability and reached its maximum value (~7) within the record, while TAR declined sharply and approached zero. Zone IV (<1.7 ka cal BP) contains consistently high OM % values (>90 %) and high P_{aq} values close to 1.0. aCAR reached its highest values (~150 g C m⁻² yr⁻¹) and remained highly variable, whereas CPI stabilized around 2 and TAR stayed close to 0 throughout the interval.

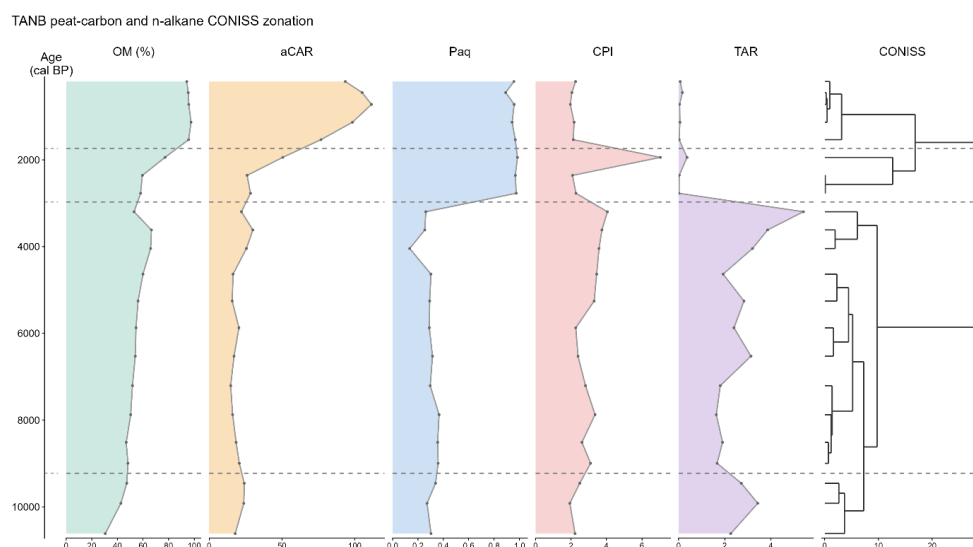


Figure 4. Peat-carbon and *n*-alkane stratigraphy of the TANB core. Profiles show OM %, aCAR, P_{aq} , CPI, and TAR plotted with calibrated age (cal yr BP). The dendrogram on the right presents the results of stratigraphically constrained cluster analysis (CONISS) based on these variables. Dashed horizontal lines indicate the boundaries of the four CONISS zones.

To further evaluate environmental transitions inferred from the *n*-alkane record, we performed a CONISS using pollen data from Cai and Yu (2011), reclassified into five vegetation groups: broadleaf trees, conifers, herbs, bog heath shrubs, and wetland taxa. The pollen-based CONISS analysis identified four major zones that broadly correspond to those defined by the *n*-alkane proxies, although slight differences in the timing of zone boundaries were observed (Fig. S1).



Zone I (>10.3 ka cal BP) was dominated by conifers, which reached their highest relative abundances in the record (approximately 50–70 %), while broadleaf trees remained comparatively low (20–50 %). Herb, bog heath shrub, and wetland taxa were rare and generally accounted for less than 5 % of the assemblage. Zone II (10.3–2.4 ka cal BP) reflects the expansion and dominance of broadleaf trees, whose percentage increased to 60–75 %. In contrast, conifer percentages declined substantially and fluctuated between approximately 10 % and 35 %. Herbs, bog heath shrubs, and wetland taxa remained relatively scarce, with several temporary increases. Zone III (2.4–0.4 ka cal BP) was marked by increase in herbs and wetland taxa. Herb relative abundances rose to 10–40 %, while wetland taxa increased to approximately 5–14 %. Broadleaf trees remained dominant, whereas conifers persisted at relatively low value and bog heath shrubs continued to show only a minor component of the vegetation. Zone IV (<0.4 ka cal BP) exhibited greater variability in vegetation composition. Herbs remained abundant, and bog heath shrubs increased further, reaching their highest relative abundances in the record (>10 %). Broadleaf trees continued to dominate the assemblage, although their percentage declined as compared with earlier intervals.

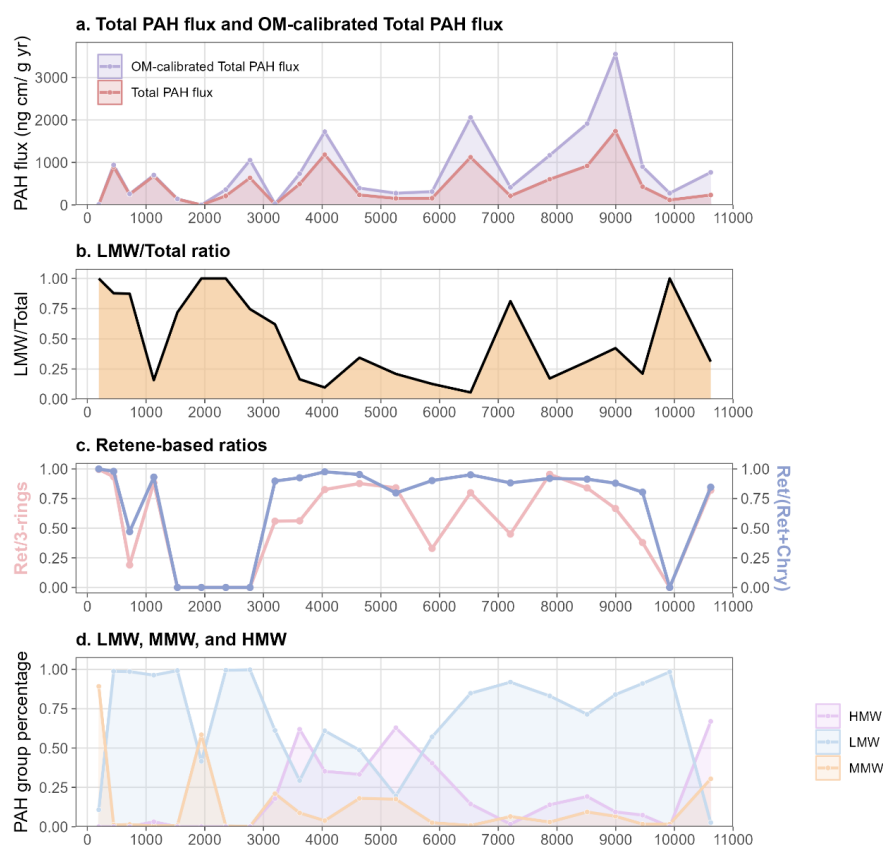
4.3 PAH and Fire History

Total PAH flux and OM-corrected PAH flux exhibited broadly similar temporal patterns (Fig. 5a), characterized by generally low values during the late Holocene and three distinct peaks during the early-mid Holocene. The highest total PAH flux occurred at approximately 9.0 ka cal BP, with additional peaks centered at 2.8, 4.0, and 6.7 ka cal BP.

PAH indices varied substantially through time (Fig. 5b–d). The LMW/Total PAH ratio reached its highest values (approaching 1.0) during late Holocene (<4 ka cal BP), but declined markedly during the middle Holocene, generally remaining below 0.5 except for distinct peaks at around 7.1 and 10.0 ka cal BP (Fig. 5b). The Ret/3-ring ratio remained relatively high (>0.5) throughout most of the early to middle Holocene (2.8–10 ka cal BP), with minimum values occurring at 1.5–2.8 ka cal BP and 10.0 ka cal BP (Fig. 5c). The Ret/(Ret+Chry) ratio displayed a similar pattern with Ret/3-ring ratio (Fig. 5d), showing less variability during the early and middle Holocene and remaining consistently above 0.8. The relative contributions of PAHs with different molecular weights also changed through time (Fig. 5c). LMW PAHs dominated most samples, accounting for more than 70 % of total PAHs during much

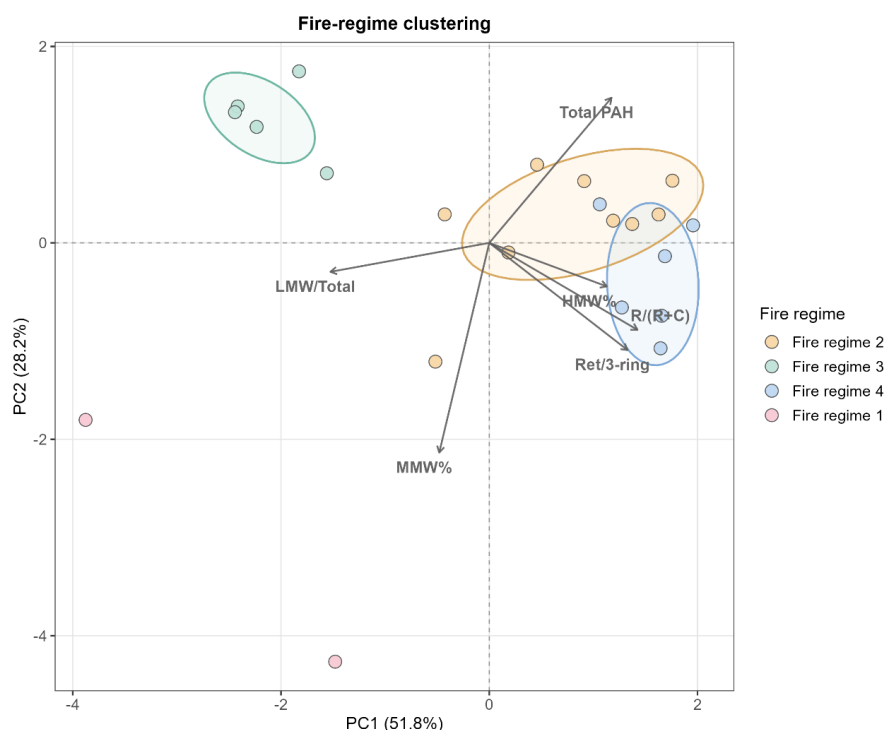


of the early and late Holocene, although their relative abundance decreased during the middle Holocene
 455 (ca. 3.5–6 ka cal BP). MMW and HMW PAHs generally contributed smaller proportions. HMW PAHs
 showed two notable increases between approximately 3.5–4.0 ka cal BP and 4.6–6.0 ka cal BP. MMW
 PAHs reached their highest relative abundance during the late Holocene (ca. 2.0 ka cal BP) but
 otherwise remained a low contribution less than 20 % with minor fluctuations throughout the record.



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Figure 5. PAH records from the TANB peat core. a. OM-corrected total PAH flux (purple) and total PAH flux (red). b. LMW/Total PAH ratio (tan). c. Ret/3-ring PAH ratio (pink) and Ret/(Ret+Chry) ratio (blue). d. low- (blue), medium- (orange), and high-molecular-weight PAH relative abundances (purple). All records are plotted with calibrated age (cal yr BP).



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Figure 6. Principal component analysis (PCA) of PAH data at TANB. Symbols represent individual samples and colors indicate fire-system states identified by clustering analysis. Arrows show the contributions of total PAH flux, LMW/Total PAH ratio, MMW and HMW PAH relative abundances, and retene-based proxies (Ret/3-ring and Ret/(Ret+Chry)). Ellipses indicate the clustering of samples within each fire-system state.

470 Hierarchical and k-means clustering of the standardized PAH indicators identified four distinct fire regimes. PCA was subsequently used to visualize the separation among these cluster-defined fire-system state (fire regimes) and to examine the contributions of individual PAH indicators (Fig. 6). The first two principal components explained 79.5 % of the total variance, with PC1 accounting for 51.8 % and PC2 accounting for 28.2 %. PC1 primarily separated samples characterized by high LMW/Total ratios and MMW % from those associated with higher HMW %, Ret/3-ring ratios, and total PAH flux.

475 PC2 was mainly associated with variation in total PAH flux. Fire regime 3 clustered on the negative side of PC1 and was characterized by relatively high LMW/Total values. Fire regime 4 occupied the positive side of PC1 and was associated with higher HMW % and retene-based indices. Fire regime 2 samples occupied a more central position and appeared to be less strongly influenced by HMW % and

480 retene-related indicators than the other fire-system states. Fire regime 1 samples were more dispersed



within the ordination space and generally corresponded to higher LMW/Total values and MMW %. NMDS analysis further clarified the relationships between fire regime classifications and individual PAH compounds (Fig. S2). The low-stress solution (stress = 0.078) indicates that the two-dimensional ordination preserves the original dissimilarity relationships among samples with minimal distortion and provides a reliable representation of variation in PAH assemblage composition. Fire regime 4 samples were associated with higher relative abundances of HMW PAHs, including benzo[a]anthracene (BaA), chrysene (Chr), dibenz[a,h]anthracene (DahA), indeno[1,2,3-cd]pyrene (IcdP), and benzo[g,h,i]perylene (BghiP). In contrast, fire regime 3 samples were more closely associated with 2-methylnaphthalene and naphthalene. Fire regime 2 samples occupied an intermediate position characterized by greater contributions from phenanthrene (Phe), anthracene (Ant), fluoranthene (Fla), and pyrene (Pyr). Retene was largely separated from the other PAH compounds and aligned primarily with the NMDS2 axis, indicating substantial variation in its contribution among the different fire-system states.

5. Discussion

5.1 Ecohydrological and environmental evolution

5.1.1 Shallow Lake System: 11–9.2 ka BP

In Zone I (>9.2 ka cal BP), P_{aq} values (0.1–0.4) indicate that floating macrophytes were the primary source of *n*-alkanes (Ficken *et al.*, 2000; Ronkainen *et al.*, 2013a), and TAR values (<4) suggest substantial contributions from algal and bacterial organic matter (Wang *et al.*, 2014). Together, these proxies indicate that TANB functioned as a shallow lacustrine system during this interval. CPI values suggest that the preservation state of plant-derived organic matter remained relatively stable throughout this period. The slight increase in CPI may reflect enhanced diagenetic alteration and microbial processing of sediments through time (Collister *et al.*, 1994). It may also be related to the gradual climatic warming (Zhou *et al.*, 2005; Ortiz *et al.*, 2010) simulated by TraCE-21k-II temperature and precipitation (Fig. 7b), as well as regional paleoclimate records that indicate widespread warming during the early Holocene (Axford *et al.*, 2007; Zhao *et al.*, 2010; Moossen *et al.*, 2015; Fastovich *et al.*, 2020; Armstrong *et al.*, 2025). However, the interpretation of CPI remains complex. Previous



studies have shown that CPI is influenced by multiple environmental factors and can vary substantially within individual peatlands (Ronkainen *et al.*, 2013a; Sachse, Dawson and Kahmen, 2015; Feakins *et al.*, 2016; Naafs *et al.*, 2019). Huang *et al.* (2016)'s meta-analysis demonstrated that the relationship between site-averaged CPI values and temperature is generally weak ($r^2 = 0.35$), suggesting that factors other than climate likely contributed to the observed variability.

Despite the inferred climatic warming, ACL values remained relatively stable and did not exhibit a clear warming-related trend. This pattern may reflect the influence of vegetation changes. Pollen records indicate a transition from a sparse, treeless landscape dominated by pioneer herbaceous taxa to conifer-dominated forests between approximately 13 and 9 ka cal BP (Watts, 1979; Cai and Yu, 2011). In addition, Cai and Yu (2011) reported increasing inputs from aquatic vegetation, including brown mosses. Such vegetation changes may have offset any temperature-driven increase in ACL, as pioneer herbaceous plants generally produce higher ACL values (~30-33; Nott *et al.*, 2000; Jeng, 2006), whereas coniferous (Howard *et al.*, 2018) and aquatic vegetation (Liu and Liu, 2016; Aichner *et al.*, 2018) are commonly associated with lower ACL values (~25 and ~22–26, respectively). These patterns are consistent with our modern vegetation *n*-alkane dataset from TANB (Fig. S3). However, the relationship between ACL and vegetation composition remains uncertain, as some studies have reported limited differences among vegetation types (Wang *et al.*, 2014; Wang, Zhang and Hou, 2015).

The relatively stable ACL value (~30.2) with pollen assemblages dominated by coniferous forests and sparse wetland vegetation (Watts, 1979; Cai and Yu, 2011), further supports the interpretation of a shallow-lake environment during this stage.

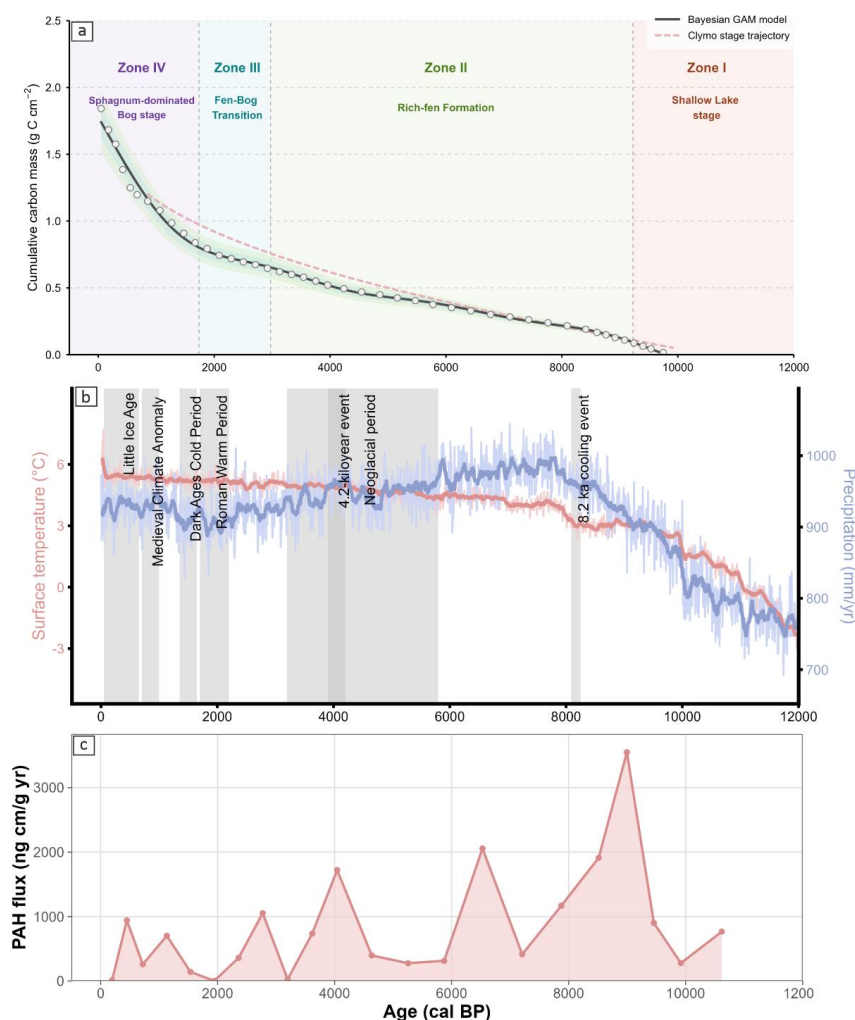


Figure 7. Holocene evolution of ecosystem development, regional climate, and fire activity at TANB. (a) Bayesian GAM reconstruction of cumulative carbon accumulation compared with the theoretical modelled peat accumulation trajectory (Clymo, 1984). (b) Surface air temperature and precipitation in TANB site extracted from the TraCE-21k-II simulation, with major Holocene climatic intervals highlighted. (c) OM-corrected total PAH flux, representing changes in fire activity through time.

The relatively low OM % (30–50 %) and aCAR values ($\sim 20 \text{ g C m}^{-2} \text{ yr}^{-1}$) suggest that sediment accumulation during this stage occurred in an environment characterized by limited biological productivity or substantial inputs of inorganic material, such as sand, silt, and clay (Bruni *et al.*, 2022). This interpretation is consistent with lithological evidence (Fig. 2), which shows relatively high



sedimentation rates during this interval. Combined with the progressively increasing precipitation
 540 simulated by the TraCE-21k-II (Fig. 7b), we infer that enhanced surface runoff likely increased the
 influx of minerogenic material, thereby accelerating basin infilling and promoting the development of
 shallow-lake conditions. The GAM-derived cumulative carbon trajectory closely follows the theoretical
 Clymo curve during this period (Fig. 7a), suggesting that carbon sequestration efficiency was broadly
 comparable to that expected for continuously developing peatlands. This result appears inconsistent
 545 with the generally higher carbon storage capacities of peatlands relative to other terrestrial ecosystems
 (Worrall *et al.*, 2009; Yu, Beilman and Jones, 2013; Lunt, Fyfe and Tappin, 2019). However, previous
 studies have shown that when lake and peatland sediments experience similar climatic conditions,
 vegetation cover, and decomposition regimes, their long-term carbon accumulation rates can be similar
 (Ryabogina *et al.*, 2019). In addition, the relatively high sedimentation rates observed during this stage
 550 may have enhanced carbon burial efficiency.

CONISS analysis (Fig. 3) indicates that TANB had likely already passed through its initial postglacial
 phase before the onset of the sedimentary record examined in this study, as no evidence of a transition
 from a deep postglacial lake to a shallow-lake environment was observed in the sediment sequence.

TraCE-21k-II simulations (Fig. 7b) indicate regional deglaciation prior to 10.6 ka cal BP, while Watts
 555 (1979) documented approximately 120 cm of fossil-bearing silt deposited before 13.3 ka cal BP,
 implying that sediment accumulation began at least by ~14 ka cal BP, which is earlier than findings
 from northern Canada (Miller *et al.*, 2005; Armstrong *et al.*, 2025) and the eastern coastal regions (Zhao
et al., 2010). Furthermore, previous study found that TANB is situated on the outer margin of the
 Laurentide Ice Sheet, a location that may have become ice-free relatively early during glacial retreat
 560 (Watts, 1979). Consequently, the absence of evidence for a deep postglacial lake phase in the sediment
 record likely reflects either an earlier deglaciation history or a basin that was already relatively shallow
 before Zone I.

5.1.2 Rich-Fen Formation: 9.2-3.0 ka BP

Zone II (9.2-3.0 ka cal BP) marks a prolonged period of lake infilling and gradual organic matter
 565 accumulation, ultimately culminating in the establishment of a bog ecosystem. Throughout this
 interval, P_{aq} values fluctuated between 0.1 and 0.4, and TAR values remained mostly below 4,



indicating that aquatic plants, algae, and bacteria continued to contribute substantially to organic matter inputs (Bourbonniere and Meyers, 1996a; Ficken *et al.*, 2000). These results indicate that, although TANB was gradually becoming more terrestrial, it still maintained relatively humid hydrological conditions and a persistently high-water table.

Several temporary hydroclimatic perturbations were overlaid on this long-term trend. The drop in total alkane flux around 8 ka during this period roughly coincides with the timing of the 8.2-ka climate event (Alley and Agustsdottir, 2005), a period characterized by a decline in total biomass due to a sudden cooling. P_{aq} experienced two marked declines at ~7.2 ka and ~4.1 ka cal BP, indicating temporary reductions in aquatic organic matter input. The decline at 7.2 ka occurred during a period of decreasing precipitation in the TraCE-21k-II simulation (8–5 ka; Fig. 7b) and was accompanied by increasing TAR values, suggesting a brief hydrologically driven lowering of water levels. The decrease at 4.1 ka cal BP was more pronounced and coincided with reductions in total *n*-alkane flux and TAR. This interval broadly corresponds to the 4.2 ka climate event, which has been widely recognized as a major Holocene climate perturbation characterized by cooling at high latitudes and drought at lower latitudes (Yang *et al.*, 2015; Walker *et al.*, 2018), although it is not clearly resolved in TraCE-21k-II simulation (Fig. 7b). However, McKay *et al.* (2024) suggest that the magnitude and expression of this event varied considerably among regions, and its significance within the broader context of Holocene climate variability remains debated. Similarly, syntheses of Northern Hemisphere records indicate that although mild drought conditions were widespread, hydrological responses exhibited strong spatial heterogeneity (Nan *et al.*, 2025).

The subsequent increase in P_{aq} between ~4.1 and 3.0 ka cal BP does not appear to reflect expansion of open-water conditions or increasing regional precipitation, as TAR continued to increase and TraCE-21k-II simulations indicate declining precipitation. Instead, this increase is more likely associated with the expansion of *Sphagnum* vegetation. P_{aq} is strongly influenced by C_{23} and C_{25} *n*-alkanes, which are produced not only by aquatic macrophytes but also by *Sphagnum* mosses (Ronkainen *et al.*, 2013b). Consequently, the P_{aq} ratio alone cannot reliably distinguish between these two sources, particularly in the absence of well-preserved macrofossils (Naafs *et al.*, 2019). This interpretation is supported by pollen records from Watts (1979), which show the first appearance of *Cyperaceae* and *Sphagnum* around 4 ka cal BP. Although regional precipitation declined during this interval, *Sphagnum*



establishment was likely driven primarily by autogenic peatland development rather than regional climate. Progressive peat accumulation increased local water retention and promoted the transition from a groundwater-fed fen toward a *Sphagnum*-dominated peatland, creating favorable conditions for *Sphagnum* expansion despite decreasing precipitation. The concurrent increase in ACL, despite relatively stable temperatures, further supports a vegetation-driven rather than climate-driven interpretation.

CPI values remained relatively stable throughout Zone II, suggesting little change in the preservation of plant-derived organic matter. A modest CPI minimum between 7.8 and 5.3 ka cal BP coincided with a relatively wet interval in the TraCE-21k-II precipitation simulation (Fig. 7b) and may reflect enhanced peat humification associated with elevated groundwater levels. Between 9.2-3.8 ka cal BP, OM % increased to more than 70 %, while aCAR steadily rose to approximately 33 g C m⁻² yr⁻¹. In contrast, sedimentation rates declined relative to Zone I (Fig. 2). This pattern suggests that, following an initial period of rapid infilling, the lake gradually shallowed and became increasingly eutrophic as algae and submerged aquatic vegetation decayed and accumulated on the lake floor (Brenner and Escobar, 2009).

Although the expansion of emergent vegetation can enhance sediment trapping and accelerate basin infilling (Beltrán Burgos, 2021), the reduced sedimentation rates observed during this interval may instead reflect enhanced microbial decomposition (Garcin *et al.*, 2022), an increase in lake surface area (Bennett and Buck, 2016), and intensified sediment resuspension within the basin (Luo *et al.*, 2026). The average aCAR during this interval exceeds the mean value reported for northern peatlands by Yu *et al.* (2013), suggesting that a productive rich-fen ecosystem had already become established. Between 3.8 and 3.0 ka cal BP, however, both OM % and aCAR declined slightly, likely reflecting reduced carbon accumulation under drier conditions. Similar drought-driven fen-to-bog transitions have been documented in syntheses of peat records from southern South America (Loisel and Bunsen, 2020), where aridification lowered groundwater levels and enhanced peat decomposition and carbon loss (Garcin *et al.*, 2022).

Despite these fluctuations, cumulative carbon accumulation increased more steadily during Zone II than in Zone I, reflecting enhanced carbon storage within the basin. Nevertheless, the GAM-derived cumulative carbon trajectory remained below the theoretical Clymo curve (Fig. 7a), indicating that carbon sequestration efficiency was still lower than expected for a mature peatland. One possible



625 explanation is that the gradual warming and declining precipitation simulated by the TraCE-21k-II during this interval (Fig. 7b) enhanced microbial activity and organic matter decomposition (Xing *et al.*, 2015; Ratcliffe *et al.*, 2019), thereby reducing net carbon accumulation. This climatic influence may have contributed to the apparent "missing" peat relative to the theoretical accumulation trajectory. Additionally, it should also be noted that the Clymo model was originally developed for *Sphagnum*-
 630 dominated bogs (Clymo, 1984), which generally exhibit greater carbon accumulation potential than those of non-*Sphagnum* peatlands (e.g., median aCAR values of 141 versus 56 kg C m⁻²; Loisel and Bunsen, 2020). Therefore, the discrepancy between the observed and theoretical trajectories likely reflects both climate-enhanced peat decomposition and the incomplete development of a mature *Sphagnum* peatland. Taken together, these results suggest that terrestrialization and organic matter
 635 accumulation progressed during Zone II, but lacustrine influences remained important until peatland conditions became established around 4.1 ka cal BP, when *Sphagnum* and *Cyperaceae* communities began to expand.

5.1.3 Fen-Bog Transition: 3.0-1.7 ka BP

Zone III (3.0–1.7 ka cal BP) highlights a major ecohydrological transition in the evolution of TANB.
 640 The P_{aq} value increased sharply to ~0.98 at ~3.0 ka cal BP, accompanied by nearly parallel trends in the C₂₃/(C₂₃+C₂₉) ratio. We do not interpret this change as evidence of rising water levels or a wetter climate because both proxies are strongly influenced by inputs from *Sphagnum* and brown mosses, which are characterized by abundant mid-chain *n*-alkanes (Nott *et al.*, 2000; Ronkainen *et al.*, 2013a). Instead, these results indicate a marked expansion of moss-dominated vegetation. This interpretation is
 645 consistent with the pollen records of Cai and Yu (2011), which document the dominance of brown mosses and diatoms during this interval. At same time, TAR declined sharply to near zero, while ACL decreased to its lowest values. Together, these changes indicate a reduction in long-chain *n*-alkane inputs from herbaceous plants and an increasing contribution from mosses and aquatic microorganisms. These observations are consistent with the development of a rich-fen environment characterized by
 650 high groundwater levels and persistently wet conditions.

A second major transition occurred between ~2.2 and 1.7 ka cal BP. During this interval, OM % increased to >90 %, and aCAR rose to ~60 g C m⁻² yr⁻¹, indicating a substantial enhancement in



organic matter preservation and carbon accumulation. Cumulative carbon also increased more rapidly than during the preceding interval. Although the GAM-derived trajectory remained below the theoretical Clymo curve (Fig. 7a), this discrepancy is not unexpected because the Clymo model was developed primarily for *Sphagnum*-dominated bogs. Rich fens generally exhibit higher net primary productivity, greater plant diversity, and faster peat decomposition than bogs (Zoltai and Vitt, 1995; Granath, Strengbom and Rydin, 2010), whereas bogs often possess greater long-term carbon accumulation potential because methane production and carbon losses are lower under ombrotrophic conditions (Moore and Roulet, 1993; Whiting and Chanton, 2001). The vegetation changes during this interval are consistent with a classic fen-to-bog transition (FBT). Rich fens are typically dominated by sedges, grasses, rushes, and brown mosses, whereas bogs are characterized by continuous *Sphagnum* carpets accompanied by woody shrubs (Turetsky *et al.*, 2014). The sharp decline in ACL and the rapid expansion of *Sphagnum* inferred from pollen data support such a transition at TANB. Notably, P_{aq} and $C_{23}/(C_{23}+C_{29})$ exhibit little change during this interval, consistent with previous studies showing that brown mosses and *Sphagnum* share similar *n*-alkane distributions dominated by C_{23} , making these indices insensitive to fen-to-bog transitions (Nott *et al.*, 2000; Ronkainen *et al.*, 2013b). Traditionally, fen-to-bog transitions are regarded as an autogenic process driven by long-term peat accumulation, whereby the peat surface gradually rises above the influence of mineral-rich groundwater (Kuhry *et al.*, 1993; Frolking *et al.*, 2010). However, the transition observed at TANB appears relatively abrupt. The pronounced CPI peak and rapid changes in OM % and aCAR suggest a substantial reorganization of organic matter sources and preservation conditions over a relatively short period. Similar nonlinear transitions have been documented in peatlands worldwide, where fen-to-bog transitions may occur over decades to centuries (Hughes and Barber, 2003; Ronkainen *et al.*, 2014). The timing of this transition coincides with a pronounced decrease in precipitation simulated by TraCE-21k-II (Fig. 7b) and broadly overlaps with late-Holocene climatic reorganization in the North Atlantic region, including the Roman Warm Period (Büntgen *et al.*, 2011) and the Dark Ages Cold Period (Geirsdóttir *et al.*, 2009). This correspondence supports the idea that hydroclimatic forcing played an important role in the transition at TANB. Drier conditions may have enhanced peat decomposition, promoted the formation of denser and less permeable peat layers, and gradually isolated the ecosystem from mineral groundwater inputs, thereby accelerating the development of an ombrotrophic bog



(Hughes, 2000; Hughes and Barber, 2004). Although the relative importance of autogenic and allogenic controls on fen-to-bog transitions remains debated (Treat *et al.*, 2016), the evidence from TANB is more consistent with a nonlinear, hydroclimate-driven transition.

685 **5.1.4 *Sphagnum*-dominated Bog: < 1.7 ka BP**

During Zone IV (<1.7 ka cal BP), TANB appears to have reached a mature *Sphagnum*-dominated bog state. OM % remained consistently high (>90 %), although it declined slightly from ~98 % to ~93 %, indicating that peat accumulation and preservation had become relatively stable. as falling water tables can increase oxygen input and accelerate microbial decomposition to some extent (Ratcliffe *et al.*,
 690 2019). At the same time, P_{aq} values remained close to 1.0, and TAR values remained near zero, suggesting that organic matter production was dominated by in situ vegetation, with only minor contributions from terrestrial runoff.

Despite evidence for gradually lowering water tables during this interval, which could increase oxygen availability and stimulate microbial decomposition (Ratcliffe *et al.*, 2019). aCAR increased markedly
 695 and reached its highest value at ~0.7 ka cal BP (~130 g C m⁻² yr⁻¹). Although this pattern appears contradictory, previous studies have shown that total carbon accumulation over the past millennium is strongly and linearly related to growing season length and photosynthetically active radiation, indicating that variations in net primary productivity exert a greater influence on long-term carbon accumulation than decomposition processes (Charman *et al.*, 2013; Xing *et al.*, 2015). This relationship
 700 may partly explain the continued increase in aCAR despite potentially enhanced decomposition.

However, this significant increase in aCAR is consistent with previous studies showing that apparent carbon accumulation rates are strongly influenced by peat decomposition, such that younger surface peat layers often exhibit higher aCAR values than older, more decomposed layers (Young *et al.*, 2021; Zhang and Välranta, 2024). Although the magnitude of this "ageing effect" remains debated
 705 (Heinemeyer *et al.*, 2018; Young *et al.*, 2021), the comparison with the Clymo model (Fig. 7a) indicates that carbon accumulation accelerated substantially during this interval. Furthermore, studies comparing different peatland vegetation stages have shown that *Sphagnum*-dominated communities generally exhibit higher aCAR values than Sedge-dominated communities (Magnan *et al.*, 2022; Yang, Liu and Bai, 2023) because *Sphagnum* litter decomposes slowly and suppresses microbial decay,



710 thereby enhancing long-term carbon storage (Granath, Strengbom and Rydin, 2010; Zheng, Zhao and Huang, 2026). In addition, climatic variability likely contributed to the observed fluctuations in carbon accumulation. The peak in aCAR around 0.7 ka cal BP broadly coincides with the Medieval Climate Anomaly (MCA; Cerro-Gálvez *et al.*, 2019), whereas the subsequent decline corresponds to the onset of the Little Ice Age (LIA; Ogilvie and Jónsson, 2001). Similar patterns have been reported in northern
 715 peatlands, where carbon sequestration rates decreased during the transition from the MCA to the LIA, likely because lower temperatures and increased cloud cover reduced net primary productivity (Charman *et al.*, 2013; Granlund *et al.*, 2022). However, these climatic fluctuations are not clearly expressed in the TraCE-21k-II simulations (Fig. 7b) for the TANB region. Similar model–proxy discrepancies have been widely reported (Karger *et al.*, 2023; Slattery *et al.*, 2024; Bao *et al.*, 2025).
 720 This may reflect the fact that the CCSM3 model underlying TraCE-21k-II primarily incorporates long-term forcings, such as greenhouse gas concentrations, orbital variations, and ice-sheet boundary conditions (He and Clark, 2022), but does not fully resolve solar and volcanic forcing at centennial timescales that are thought to drive the MCA and LIA (Verkerk *et al.*, 2025). Consequently, TraCE-21k-II simulates long-term Holocene climate trends well but may underestimate short-term late-
 725 Holocene climate variability. Additionally, temperature and precipitation estimates extracted from the nearest model grid cell may introduce spatial uncertainty, as the coarse model resolution and spatial variability in simulated climate patterns may limit their representation of site-specific conditions (Vachula *et al.*, 2024).
 Vegetation composition also changed during this interval. The declines in P_{aq} and ACL after ~0.7 ka cal
 730 BP suggest an increased contribution of long-chain *n*-alkanes, particularly C_{27} and C_{29} , from terrestrial plants. This interpretation is consistent with the pollen record of Cai and Yu (2011), which shows increasing abundances of arboreal taxa such as *Pinus* and *Picea* during the late Holocene. Together, these observations indicate that although TANB had reached a mature peatland stage, its carbon accumulation and vegetation composition remained sensitive to centennial-scale climatic variability.

735 5.2 Fire regime evolution at Tannersville Bog

5.2.1 Holocene fire history reconstructed from PAHs

To minimize the effects of sediment accumulation and organic matter preservation (Stogiannidis and



Laane, 2015), we use OM-corrected pyroPAH fluxes to reconstruct Holocene fire history at TANB. PAH trends do not align with erosion-related signals inferred from *n*-alkanes (Fig. 3d), suggesting that changes in catchment erosion did not drive PAH variability. Degradation is also unlikely to explain the observed patterns. Although LMW PAHs are generally more susceptible to degradation and leaching than HMW PAHs (Lima, Farrington and Reddy, 2005a; Cerro-Gálvez *et al.*, 2019; González-Gaya *et al.*, 2019), no general decrease in LMW abundance with sediment age is observed (Fig. 5d), indicating good preservation of the original fire signal. Furthermore, total PAH flux and OM-corrected PAH flux show nearly identical temporal trends (Fig. 5a), suggesting that changes in depositional conditions exerted only a minor influence on the reconstructed fire history. High PAH abundances in lake sediments are generally interpreted as evidence of increased biomass burning, which may result from larger burned areas, higher fire intensity, more frequent fires, or a combination of these factors (Denis *et al.*, 2017; Zhou *et al.*, 2025). Experimental studies have shown that total PAH emissions vary substantially with combustion temperature (Lima, Farrington and Reddy, 2005a; Zhang *et al.*, 2022), while many paleofire studies interpret changes in PAH molecular-size distributions as indicators of combustion intensity because the aromaticity of combustion products tends to increase with temperature (McGrath, Chan and Hajaligol, 2003; McBeath *et al.*, 2011; Denis *et al.*, 2012). Consequently, both PAH abundance and composition provide important information on past fire regimes, including variations in fire magnitude, combustion conditions, and fuel sources. During the early Holocene (11–8 ka cal BP), fire activity at TANB was relatively frequent and highly variable, reaching a major peak at ~9.0 ka cal BP (Fig. 7c). Although LMW PAHs dominated the assemblage, the LMW/Total PAH ratio fluctuated substantially, accompanied by persistently high retene-related indices (except at ~10 ka cal BP), indicating that both smoke-derived and combustion-residue PAHs contributed to the record. At the peak around 9.0 ka cal BP, the LMW/Total ratio reached ~0.42, which falls within the range characteristic of combustion residues rather than smoke aerosols (Karp *et al.*, 2020), suggesting an important contribution from nearby fires. Correspondingly, this interval was characterized by a mixed fire system involving both extensive biomass burning and relatively high-intensity woody-fuel fires, represented by the comparable occurrence of fire regimes 2 and 4 (Fig. 8a). The overall climate trend during this period was marked by progressive warming and increasing precipitation (Fig. 7b; Kaufman *et al.*, 2004; Axford *et al.*, 2007). Such conditions may have



enhanced fuel production and biomass accumulation, thereby promoting fire activity despite increasing moisture availability (Teckentrup *et al.*, 2019; Bowman *et al.*, 2020; Hu *et al.*, 2025).

During the mid-Holocene (8–3 ka cal BP), total PAH fluxes remained variable, with two prominent
770 peaks at ~6.4 and ~4.0 ka cal BP. Compared with the early Holocene, the LMW/Total PAH ratio
generally decreased, whereas HMW PAHs and retene-related indices increased, indicating a growing
importance of nearby, woody-fuel combustion. These compositional changes indicate that relatively
high-intensity fires involving coniferous or woody vegetation became increasingly important,
corresponding to the predominance of fire regime 4 and reduced occurrence of fire regime 2 (Fig. 8a).
775 This transition broadly coincides with a climate trend of gradually increasing temperature and declining
precipitation. Previous studies have suggested that, on millennial timescales, fire activity is strongly
controlled by moisture-driven fuel availability (Hu *et al.*, 2025), and the combination of abundant
biomass and increasing hydroclimatic stress may have favored more severe local fires during this
period.
780 The late Holocene (3–0 ka cal BP) was characterized by generally lower fire activity and a marked shift
in PAH composition. LMW PAHs became proportionally more abundant, the LMW/Total PAH ratio
remained relatively high (except at ~1.0 ka cal BP), and both HMW PAHs and retene-related indices
declined substantially. Together, these indices indicate a transition toward smoke-dominated or low-
intensity combustion conditions, corresponding to the predominance of fire regimes 1 and 3 (Fig. 8a).
785 Two minor fire peaks occurred at ~1.1 and ~0.45 ka cal BP. The younger event (~0.45 ka cal BP) was
dominated almost exclusively by LMW PAHs, suggesting a predominantly distal smoke source,
whereas the older event (~1.1 ka cal BP) included minor HMW and MMW contributions and a sharp
decline in the LMW/Total ratio (~0.15), implying a temporary return to more local burning and changes
in fuel composition. Although TraCE-21k-II simulates a gradual decline in regional precipitation
790 throughout the late Holocene (Fig. 7b), fire activity remained generally subdued and was characterized
by low-temperature combustion rather than increased burning. This decoupling suggests that fire
regimes became increasingly regulated by vegetation succession and peatland development, with
possible additional influences from human activities during the latest Holocene (Glückler *et al.*, 2022;
Chen *et al.*, 2026). The combustion characteristics represented by these four fire regimes are examined
795 in greater detail below.



5.2.2 Fire-regime shifts inferred from PAH composition

The temporal variations in PAH flux and composition described above can be further resolved into four distinct fire-system state (fire regimes). PCA and NMDS analyses (Fig. 6, S2&S4) independently identify four fire-system state which we interpret to reflect fire regimes that differ in likely combustion temperature, fuel type, and the relative contribution of smoke versus combustion residues, as supported by previous research examining PAHs (Karp *et al.*, 2020).

Fire regime 1 occupies an isolated position in the ordination space and is represented by only a few samples, suggesting that it represents a relatively rare combustion state. PAH abundances are uniformly low across all components (Fig. S4), indicating weak fire signals. Because combustion-derived PAHs are emitted in both gaseous and particulate phases and can be transported over considerable distances before deposition (Czimczik *et al.*, 2002; Collura, Azambre and Weber, 2007), this regime likely reflects distant fire sources or transitional combustion conditions rather than local burning. However, the ecological significance of this regime remains uncertain due to the limited number of observations. Fire regime 2 forms a broad cluster characterized by high total PAH flux, and moderate abundances of HMW PAHs and retene. Experimental studies have shown that PAH concentrations in combustion residues are highest at moderate temperatures (400–500 °C) and decrease under either cooler or hotter conditions (Karp *et al.*, 2020). Given that PAH production is jointly controlled by biomass availability, combustion temperature, and oxygen supply (McGrath, Chan and Hajaligol, 2003; Lu, Zhu and Zhu, 2009; Kappenberg *et al.*, 2019), the relationship between high PAH flux and combustion temperature remains uncertain. The relatively balanced distribution of PAH components in this regime suggests contributions from both local and regional fires. This interpretation is broadly consistent with differences in the transport and depositional behavior of PAHs. LMW compounds are generally more volatile and may undergo greater atmospheric transport (Dachs and Eisenreich, 2000; Shen *et al.*, 2011), whereas HMW PAHs are more strongly associated with soot and black carbon particles (McGrath, Chan and Hajaligol, 2003). However, the spatial source areas represented by individual PAHs are more complex and depend on compound-specific transport, partitioning, and depositional processes, such that PAH records cannot be interpreted using a simple local-versus-regional distinction (Vachula *et al.*, 2022). Higher retene further indicates an important contribution from coniferous fuels (Simoneit, 1977), although the variable retene flux implies mixed gymnosperm and angiosperm fuel



825 sources. Overall, fire regime 2 likely represents relatively extensive biomass burning involving mixed fuel types.

Fire regime 3 is characterized by high abundances of naphthalene and 2-methylnaphthalene, high LMW/Total PAH ratios, and relatively low contributions from HMW PAHs and retene. Because these volatile LMW compounds are enriched in smoke aerosols (Karp *et al.*, 2020), this regime is interpreted
830 as smoke-dominated combustion. However, although the general source area and transport behavior of smoke-derived PAHs can be constrained (Vachula *et al.*, 2022), their exact transport distance and spatial representation are difficult to determine because they are influenced by site-specific factors, including wind conditions, atmospheric circulation, and vegetation canopy structure (Ramya Bala *et al.*, 2025). Previous studies have also associated high LMW/Total ratios with lower combustion
835 temperatures and oxygen-limited burning conditions (Shapchenkova, Loskutov and Kukavskaya, 2023; Wang *et al.*, 2023; Wu *et al.*, 2026). Consequently, fire regime 3 likely reflects regional smoke transport and/or local smoldering fires dominated by herbaceous or peat fuels.

Fire regime 4 differs markedly from the other groups, exhibiting high abundances of HMW PAHs, high retene-based indices, and low LMW/Total PAH ratios. Retene is derived from diterpene precursors
840 abundant in gymnosperm wood (Simoneit, 1977, 2002), indicating a strong contribution from woody, particularly coniferous, fuels. The predominance of HMW PAHs indicates that the fire signal was mainly derived from nearby combustion sources, reflecting the limited transport distance of these compounds (Ma *et al.*, 2013; Han *et al.*, 2015). The low LMW/Total PAH ratio further suggests that combustion residues dominated the PAH assemblage, with little contribution from distant smoke-
845 derived PAHs. HMW PAHs are generally associated with oxygen-rich, high-temperature (>500 °C), and high-efficiency combustion (Zuo *et al.*, 2025), and compounds such as benzo[a]pyrene (BaP) have been proposed as indicators of high-temperature fires (Marynowski *et al.*, 2025). Together, these characteristics indicate that fire regime 4 most likely represents nearby high-intensity fires, such as crown fires or surface fires involving woody vegetation.



850 **5.3 Coupling between environmental transitions and fire regime change**

5.3.1 Fire-ecosystem feedback on millennial timescales

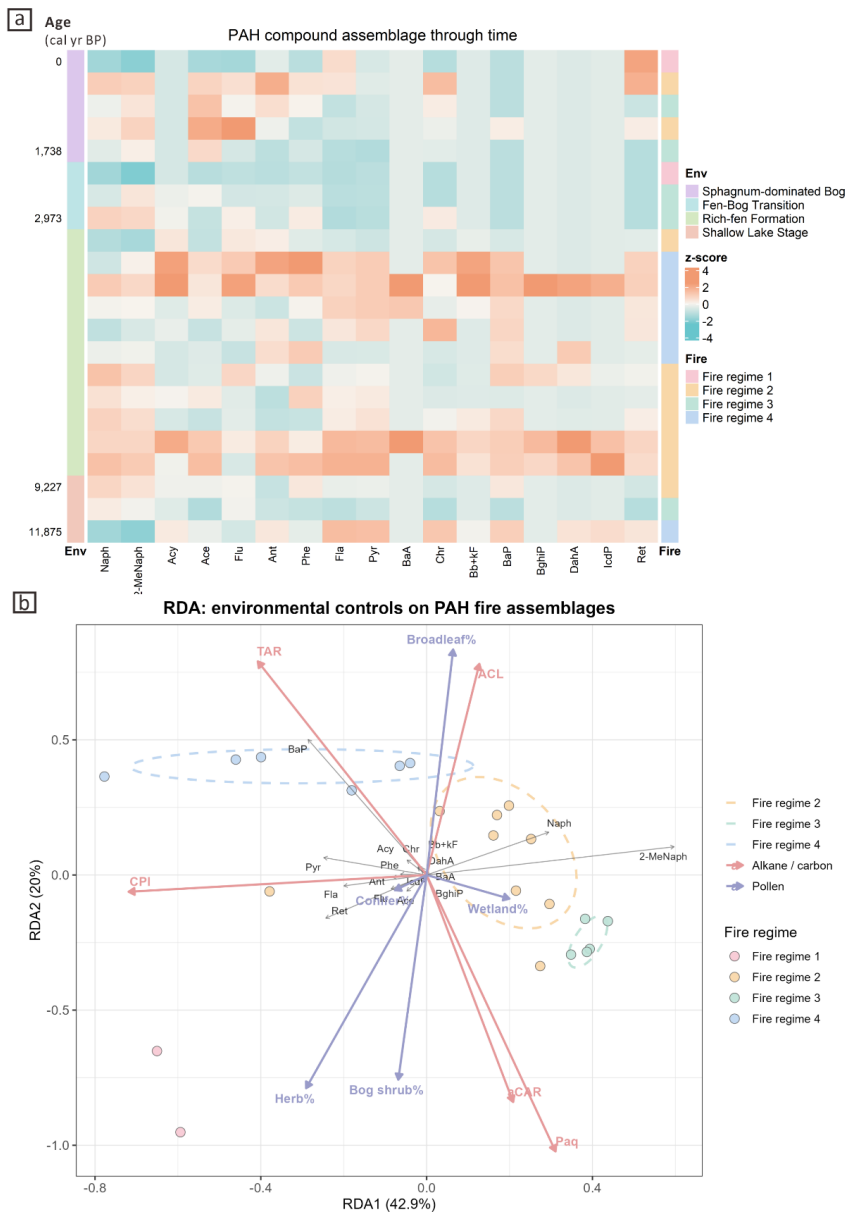


Figure 8. Ecosystem influence on PAH fire assemblages at TANB. (a) Standardized flux (z-scores) of PAH compound assemblages at TANB during the Holocene. The left annotation bar (Env) denotes the four stages of



855 environmental development inferred from *n*-alkane and carbon accumulation proxies. The right annotation bar
 (Fire) indicates the four fire regimes identified from hierarchical clustering of PAH compositional indices. (b)
 RDA showing the relationships among PAH assemblages, lake development indices, and pollen record. Points
 represent individual sediment samples, and colored ellipses denote the four fire regimes identified from PAH
 composition. Red arrows represent *n*-alkane and carbon accumulation variables, and blue arrows indicate pollen-
 860 derived vegetation groups.

Fire, vegetation, hydrology, and peat accumulation at TANB were closely and complexly linked
 throughout the Holocene, yet their relationships were not a one-directional response of fire to
 environmental change. The heatmap analysis shows that fire regimes broadly corresponded to the
 major successional stages of the peatland, transitioning from a shallow-lake stage to rich-fen formation,
 865 followed by a fen–bog transition and finally a *Sphagnum*-dominated bog stage (Fig. 7a). Nevertheless,
 this correspondence was not one-to-one, as individual fire regimes re-occur across different ecosystem
 stages. This indicates that ecosystem succession altered the environmental and fuel conditions favoring
 particular fire regimes rather than directly determining them.

The RDA and LDA provide further statistical support for this relationship. In the RDA, the first two
 870 constrained axes explained 42.9 % and 20.0 % of the total variance, respectively (Fig. 8b). The
 ordination reflects a broad gradient between terrestrial woody input, associated with high ACL, TAR,
 and Broadleaf %, and wetter peatland conditions characterized by high P_{aq} , aCAR, and Wetland %.
 LDA reveals corresponding differences among fire regimes (Figs. S5 and S6): Fire regime 4 is
 associated with the high ACL–TAR value, indicating stronger terrestrial woody inputs; Fire regime 3 is
 875 more closely related to hydrological variables and wetland taxa; Fire regime 2 occupies an intermediate
 position but trends toward the terrestrial-input side; whereas Fire regime 1 remains relatively sparse
 and isolated. Together, these analyses support the interpretation that ecosystem succession modified the
 conditions under which different fire regimes occurred, rather than producing a fixed fire response.

During the shallow lake (11–9.2 ka BP) and rich-fen formation (9.2–3.0 ka BP) stage, fire activity was
 880 dominated by Fire regimes 2 and 4, both of which are associated with higher ACL and TAR values and
 a stronger woody component in the pollen record. This pattern is consistent with pollen records (Watts,
 1979), which indicate that forests began expanding into previously stable tundra landscapes
 surrounding deglacial lakes by ~13.3 ka cal BP. Although broadleaf taxa appeared by ~11.5 ka cal BP,
 pine rapidly became dominant, accounting for nearly 70 % of the pollen assemblage by ~10.0 ka cal
 885 BP. The increasing abundance of coniferous vegetation likely contributed to the prominence of Fire



regime 4 during this interval, as reflected by high retene-based indices. The structure of the early landscape likely further promoted this fire regime. Although open water bodies acted as natural firebreaks that limited the spread of surface fires, the surrounding terrestrial margins provided favorable conditions for the rapid burning of canopy and ground fires (Bonk *et al.*, 2026). At the same time, highly flammable tundra vegetation and open conifer woodlands supplied abundant fuels, which enhanced wind penetration, accelerating fuel drying and fire spread (Blauw *et al.*, 2017; Scordo *et al.*, 2021; Clark-Wolf *et al.*, 2023; Parks *et al.*, 2023). Similar fire behavior has been documented in cold, high-latitude spruce–fir boreal forests, where fire events are generally infrequent but severe (Blauw *et al.*, 2017; Parks *et al.*, 2023). Because these forests develop under cool, moist conditions, they typically accumulate limited fine fuels while maintaining dense canopies. As a result, fires tend to occur during periods of severe drought and often develop into high-intensity crown fires capable of causing widespread tree mortality and major shifts in forest structure (O’Connor *et al.*, 2014; Buma *et al.*, 2022). These characteristics are broadly consistent with the PAH evidence from TANB and may explain the occurrence of fire regime 4 during the early Holocene, followed by a decline in retene concentrations after ~10.6 ka cal BP and an increasing contribution from fire regime 2, which likely reflects a greater influence of lower-intensity or more distant fire signals.

Fire activity during this stage also likely shows important feedback on ecosystem development. Wildfires can remove vegetation cover, destabilize soils, and enhance surface runoff, increasing the delivery of sediment and ash to lakes and thereby altering aquatic habitats and water clarity (Dunnette *et al.*, 2014; Bonk *et al.*, 2026). Such processes may partly explain the relatively high sedimentation rates observed during the shallow-lake phase. In addition, fire can transfer nutrients such as nitrogen and phosphorus from the watershed into aquatic systems (Lewis *et al.*, 2014). High-severity fires may substantially increase nutrient availability, sometimes triggering eutrophication and harmful algal blooms (Piczak *et al.*, 2026). These processes could have accelerated lake infilling and organic matter accumulation at TANB. Consistent with this interpretation, relatively high aCAR values during this interval coincide with enhanced terrestrial inputs from alkane indices and periods of intensified fire activity, suggesting a close coupling between wildfire disturbance, vegetation change and lake ontogeny.

During the late shallow-lake stage and early rich-fen formation, fire activity at TANB was dominated



915 by fire regime 2, characterized by high total PAH fluxes and moderate retene influence compared with
 fire regime 4. This pattern suggests extensive biomass burning involving mixed fuel sources such as
 woody vegetation and herbaceous plants. The transition corresponds closely with pollen records from
 TANB (Watts, 1979), which indicate the expansion of herbaceous vegetation around the lake margins
 after ~8 ka cal BP. Although Cai and Yu (2011) reported the appearance of *Cyperaceae* somewhat
 920 earlier, both records point to increasing importance of herbaceous communities during this interval.
 Herbaceous vegetation typically promotes frequent and rapidly spreading fires because of its high fuel
 continuity and flammability (Coffman, Ambrose and Rundel, 2010; Archibald *et al.*, 2013; Leys,
 Commerford and McLauchlan, 2017; Wragg, Mielke and Tilman, 2018). At the same time, broadleaf
 forests expanded substantially between ~10 and 8 ka cal BP and eventually became an important
 925 component of the regional vegetation (Watts, 1979; Cai and Yu, 2011). Compared with conifer-
 dominated forests, broadleaf forests generally support more diverse ground vegetation and reduce the
 likelihood of extensive crown-fire spread due to greater canopy discontinuity (Boyd *et al.*, 2023;
 Parisien *et al.*, 2023). Broadleaf litter also typically contains higher moisture levels and forms a more
 compact, less flammable forest floor than resin-rich conifer litter (Buma *et al.*, 2022; Bonner *et al.*,
 930 2024). As a result, fires in broadleaf-dominated systems are commonly confined to surface fuels,
 spread more slowly, and generate lower to moderate combustion temperatures. Together, the expansion
 of herbaceous vegetation and mixed forests likely increased overall fuel availability while
 simultaneously reducing fire intensity. These ecological changes occurred during the Holocene
 Climatic Optimum, a period characterized by relatively warm and moist conditions (Fig. 7b, Marcott *et*
 935 *al.*, 2013). Such conditions likely facilitated the transition from open conifer forests to more closed
 complex mixed forests in TANB (Watts, 1979; Cai and Yu, 2011) while also shaping fire behavior.
 Consequently, this interval was characterized by relatively frequent burning, moderate combustion
 temperatures, and mixed fuel sources. From an ecosystem perspective, TANB remained in a transitional
 state between lake and peatland, with fire primarily operating within a fuel system dominated by forest
 940 biomass and wetland-edge vegetation rather than peatland communities. Wildfires therefore mainly
 influenced erosion and nutrient transport to the basin (Piczak *et al.*, 2026), consistent with the high
 carbon accumulation rates observed in the GAM model (Fig. 7a).

Around 6 ka cal BP, the dominant fire regime shifted back to fire regime 4, indicating a transition from



mixed-fuel burning toward higher-temperature fires with a stronger conifer contribution. This shift
 945 coincided with major vegetation changes. Pollen records revealed (Watts, 1979; Cai and Yu, 2011) an
 expansion of coniferous forests during the mid-Holocene, accompanied by a decline in broadleaf
 abundance. These changes likely reflect post-Holocene Climatic Optimum environmental conditions,
 characterized by continued warming and decreasing precipitation (Fig. 7b, Marcott *et al.*, 2013). Drier
 conditions not only favored conifer expansion but also reduced the moisture limitation on fire behavior,
 950 increasing the likelihood of high-intensity burning (Halofsky, Peterson and Harvey, 2020; Hagemann *et al.*, 2021). In addition, previous studies have further shown that areas with repeated fire occurrence
 often experience higher subsequent fire intensity, suggesting the presence of positive fire–fuel
 feedbacks (Taylor, Harris and Drury, 2021). Together, these climatic and ecological changes likely
 promoted the emergence of fire regime 4. The ecological role of fire also likely changed during this
 955 interval. As lake infilling progressed and rich-fen communities became established, wildfires
 increasingly functioned as regulators of peatland succession rather than an external factor of watershed
 disturbance. Fen ecosystems depend on the gradual accumulation of peat and plant biomass (Kuhry *et al.*, 1993; Frolking *et al.*, 2010). However, severe local fires under dry conditions can ignite and
 consume accumulated peat deposits (Ackley *et al.*, 2021; Liu *et al.*, 2023; Liu, Han and Wang, 2024).
 960 By removing vegetation and peat, fires effectively reset successional processes, maintain open habitats,
 and promote the persistence of sedges and other fen taxa (Andersen *et al.*, 2024). In addition, peat
 combustion and ash deposition can temporarily enrich wetland waters with nutrients, altering water
 chemistry, and stimulating the growth of wetland plants and algae (Waters, Smoak and Vachula, 2023).
 These processes may partly explain the increased abundance of wetland taxa observed in the pollen
 965 record (Watts, 1979; Cai and Yu, 2011). Consistent with this interpretation, the comparison between the
 GAM model and Clymo curve indicates a marked gap in carbon accumulation rates between ~6 and 3
 ka cal BP (Fig. 7a), suggesting that fire may become an increasingly important regulator of peat
 accumulation and ecosystem development during the rich-fen stage.
 As TANB entered the Fen–Bog Transition (3.0–1.7 ka BP) and ultimately developed into a *Sphagnum*-
 970 dominated bog, fire regimes shifted markedly from fire regimes 2 & 4, characterized by relatively high
 proportions of HMW PAHs, toward fire regime 3, dominated by LMW compounds, with occasional
 occurrences of fire regime 1. This transition is consistent with the RDA and LDA results. In the RDA,



fire regime 3 clusters toward the P_{aq} -aCAR-Wetland % side (Fig. 8b), while the pollen-based LDA shows greater overlap between fire regime 3 and wetland taxa, herbs, and bog-heath shrubs than with the more terrestrially oriented fire regime 4 (Fig. S6). Fire regime 1 occurs infrequently and exhibits weak compositional characteristics, likely representing periods when local burning was limited and sedimentary PAH assemblages were dominated by weak, long-range transported, or transitional fire signals. These changes suggest that as the peatland surface became increasingly self-regulated and dominated by ombrotrophic or near-ombrotrophic vegetation, local fire signals were progressively modulated by wetter peatland conditions. Unlike forest fires, peatland fires are commonly characterized by low-temperature smoldering combustion that consumes carbon-rich organic soils rather than above ground biomass (Lara *et al.*, 2025). Such fires can persist for extended periods, generate substantial smoke, and are strongly controlled by drought and declining water tables (Bourgeau-Chavez *et al.*, 2020; Ackley *et al.*, 2021). Consistent with this interpretation, intervals of stronger PAH signals (Fig. 7c) broadly correspond to drier phases in the TraCE-21k-II precipitation simulation (Fig. 7b). Pollen records indicate that after ~3 ka cal BP, TANB became increasingly dominated by brown mosses and sedges, followed by the expansion of *Sphagnum* during the completion of the Fen-Bog Transition (Watts, 1979; Cai and Yu, 2011). Sedges provide highly flammable fine fuels, whereas *Sphagnum*'s high moisture-retention capacity limits ignition under wet conditions, but prolonged drying can facilitate slow smoldering combustion and low-temperature surface fires (Feurdean, 2021; Prior *et al.*, 2023). These fuel properties help explain the increasing dominance of LMW PAHs and the reduced contribution of HMW compounds in fire regime 3. Although higher LMW/Total PAH ratios are commonly interpreted as reflecting long-range atmospheric transport because LMW PAHs are more volatile than HMW compounds (Wild and Jones, 1995), this interpretation is less applicable in mature peatland environments. Smoldering peat fires generate abundant ground-level smoke enriched in LMW PAHs while producing relatively few HMW compounds. Therefore, the high LMW/Total PAH ratios observed during this stage more likely reflect local, low-temperature, smoke-dominated peat combustion than enhanced long-range atmospheric transport. Although such peat fires may consume accumulated peat, there is little evidence that such burning produced major stratigraphic discontinuities at TANB. The age-depth model remains continuous throughout Zone III & IV (Fig. 3), and no abrupt changes in sedimentation rate or OM % indicate substantial peat removal. Instead, the gradual



transitions observed in *n*-alkane, and PAH records suggest that peat fires likely burned to limited depths, modifying only the upper peat layers while leaving the long-term sedimentary archive mostly intact.

1005 Following the transition to the *Sphagnum*-dominated bog stage (< 1.7 ka BP), the fire record became increasingly dominated by fire regime 2 relative to the preceding Fen–Bog Transition stage (Fig. 8a). Because fire regime 2 likely represents relatively extensive mixed-fuel biomass burning, this shift suggests a change in combustion characteristics associated with peatland development rather than simply greater fire activity. The concurrent increase in aCAR variability (Fig. 4) further indicates
 1010 strengthened interactions among fire, peatland hydrology, and carbon accumulation. This pattern is consistent with the different fire behavior of fen and bog ecosystems. During the fen stage, relatively high water tables maintained by precipitation, groundwater, and surface runoff would have limited peat combustion, with fires occurring primarily in surface vegetation (Liu *et al.*, 2020; Nelson *et al.*, 2021). After developing into an ombrotrophic bog, lower moisture in surface peat promoted peat ignition and
 1015 prolonged smoldering combustion, producing greater smoke emissions and larger subsurface carbon losses (Sulwiński *et al.*, 2020; Andersen *et al.*, 2024; Naszarkowski *et al.*, 2025), which likely contributed to the stronger PAH signals and more variable carbon accumulation observed at TANB. Together, the evidence suggests that as TANB transitioned from a minerotrophic fen to an ombrotrophic bog, fire increasingly acted as an internal regulator of peatland development by
 1020 influencing carbon storage and peat accumulation.

5.3.2 PAH preservation biases in environmental transition

The succession from a shallow lake to a peatland at TANB provides a valuable opportunity to evaluate how changes in depositional environment may influence PAH preservation, and, consequently, the interpretation of fire histories. Because PAH deposition and preservation differ fundamentally between
 1025 lake and peat environments (Pastukhov, Loiko and Kaverin, 2021), these processes should be considered when interpreting early Holocene fire records. In lakes, PAHs are supplied through both atmospheric deposition and catchment runoff, with surface runoff and riverine transport often representing the dominant pathways (Adams *et al.*, 2018). After entering the water column, PAHs associate with suspended particles and dissolved organic matter before deposition, where they may



1030 subsequently be modified by bioturbation, sediment focusing, and sediment resuspension (Colby,
 2019). Moreover, because LMW PAHs are more water-soluble and more susceptible to microbial
 degradation than HMW compounds, preferential loss of LMW PAHs may reduce the LMW/Total PAH
 ratio in lacustrine sediments (Lima, Farrington and Reddy, 2005a; Cerro-Gálvez *et al.*, 2019; González-
 Gaya *et al.*, 2019). Similar signals are also observed in the TANB sediment records, which suggest that
 1035 the relatively low abundance of LMW PAHs during the shallow-lake and early rich-fen stages may
 partly reflect preferential degradation and loss during lake deposition, rather than changes in fire
 behavior alone. However, high LMW PAH concentrations remain preserved within these intervals, total
 PAH flux and OM-corrected PAH flux exhibit nearly identical temporal trends, and LMW PAHs show
 no systematic decline with sediment age (Fig. 7c) to some extent limits the magnitude of such
 1040 influences. In contrast, PAHs preserved in peatlands are derived almost entirely from atmospheric
 deposition (Dreyer *et al.*, 2005) and become strongly adsorbed in organic matter, greatly limiting post-
 depositional mobility (Thuens, Blodau and Radke, 2013; Pastukhov, Loiko and Kaverin, 2021; GeLe *et*
al., 2026). The acidic, nutrient-poor, and largely anaerobic conditions that characterize the later
Sphagnum-dominated bog further suppress microbial degradation, promoting better preservation of the
 1045 original fire signal than other stages in TANB core. Together, these observations suggest that
 depositional and preservation biases modified the magnitude of the PAH signal but did not
 fundamentally obscure the fire-regime reconstruction at TANB. For PAH records spanning major
 ecosystem transitions, future studies should explicitly consider how changes in ecosystem state may
 influence PAH deposition, preservation, and decomposition before attributing variations in the
 1050 sedimentary PAH record solely to changes in fire activity.

5.4 Regional comparison across NE Appalachia during the Holocene

Comparison with published charcoal records and regional TraCE-21k-II indicates that the Holocene fire
 history reconstructed from TANB broadly follows regional fire trends across the northeastern
 Appalachians (Table 2), particularly during the early to mid-Holocene, but diverges following peatland
 1055 development during the late Holocene (Fig. 9 & S7). Regional climate reconstructions show that all
 three climate trajectories (all-sites mean, Coastal Atlantic, and Interior Appalachian means)
 experienced similar long-term Holocene evolution, with relatively warm and increasingly moist



conditions during the middle Holocene followed by gradual cooling and declining precipitation during the late Holocene (Fig. 9c). The close agreement among these regional climate records suggests that broad-scale climatic forcing influenced fire activity throughout the northeastern Appalachians, whereas local ecosystem development increasingly controlled fire behavior at individual sites.

The strongest correspondence is observed between TANB and the Coastal Atlantic sites (Fig. 9b). Both the regional mean and several Coastal Atlantic records exhibit generally elevated fire activity during the early to middle Holocene, consistent with warm climatic conditions that promoted vegetation productivity and fuel availability (Clark and Royall, 1996b; Oswald and Foster, 2011). Previous studies attribute this pattern to the widespread occurrence of fire-adapted pine–oak vegetation growing on well-drained sandy soils, particularly *Pinus rigida* and *Quercus* (Clark and Royall, 1996b). New charcoal records from Albany Pine Bush and Stump Pond further indicate that these pine barrens ecosystems have experienced frequent burning since approximately 11 ka cal BP (Tremblay *et al.*, 2024). TANB exhibits a comparable long-term fire history during this interval despite differences in sedimentary proxy, suggesting that regional climate and pine expansion together exerted a common control on fire activity across the Coastal Atlantic region. Following the transition from a lake to a peatland, however, TANB increasingly diverges from the Coastal Atlantic regional fire trend. This local shift in hydrology and fire behavior may also provide a mechanism contributing to the persistence of Tannersville's isolated vegetation refugia, by buffering these communities from the more intense surface-fire regimes characteristic of the surrounding landscape (Nelson *et al.*, 2021; Davies *et al.*, 2023). Although regional climate continued to follow the same long-term cooling and drying trends (Fig. 9c), fire regimes at TANB shifted toward low-temperature, smoke-dominated combustion associated with peatland development rather than the high-intensity surface fires characteristic of pine barrens. The establishment of fen and subsequently bog hydrology fundamentally altered fuel composition, moisture availability, and combustion processes, causing local hydrological conditions to become increasingly important in regulating fire behavior. Consequently, late-Holocene fire variability at TANB reflects ecosystem succession and peatland hydrology more strongly than regional climatic forcing alone.

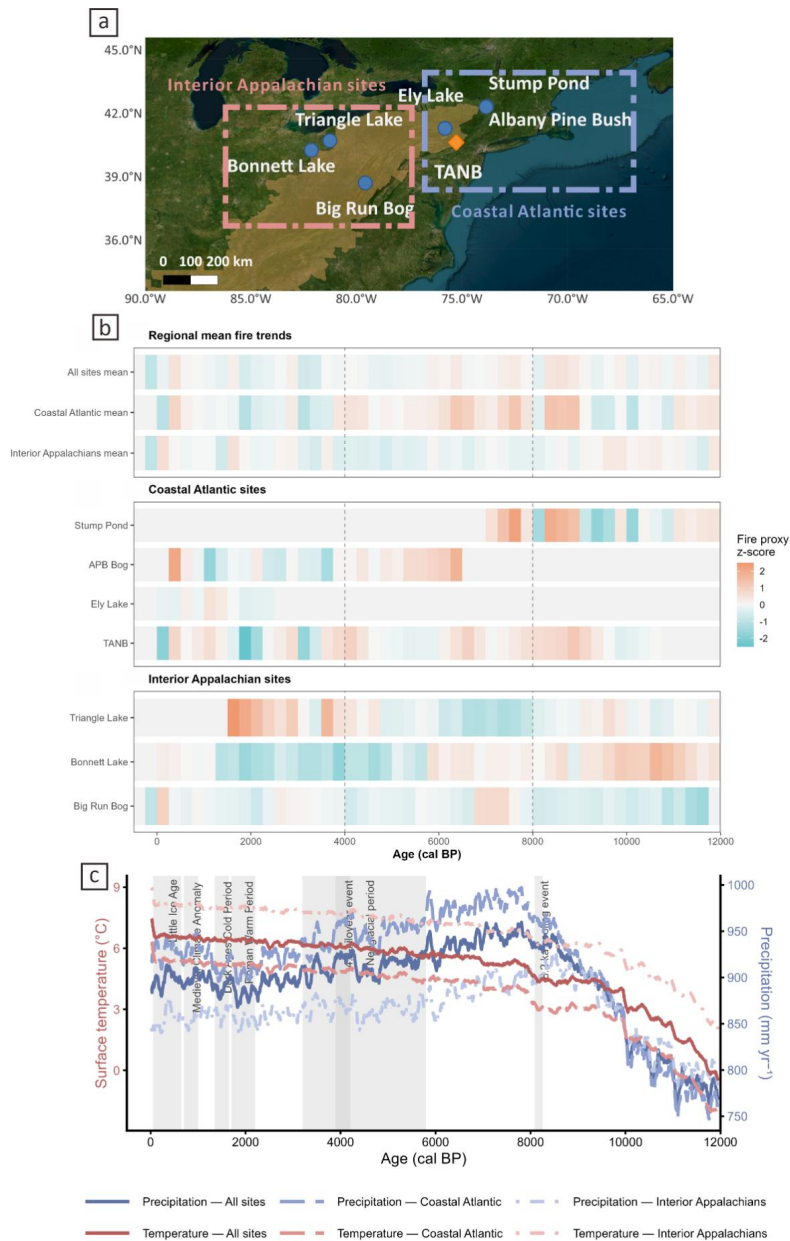


Figure 9. Regional Holocene fire and climate patterns across the northeastern Appalachians. (a) Locations of TANB and six published charcoal records, grouped into Coastal Atlantic and Interior Appalachian regions. Basemap source: Esri World Imagery (a). Sources: Esri and its data providers | Powered by Esri. (b) Heatmap of standardized fire-proxy records (z-scores), showing the all-sites mean, regional-group means, and individual site records. Dashed vertical lines divide the early (12–8 ka cal BP), middle (8–4 ka cal BP), and late Holocene (4–0 ka cal BP).



cal BP). (c) TraCE-21k-II regional mean surface temperature and precipitation reconstructions for all sites and for the Coastal Atlantic and Interior Appalachian groups.

Compared with the Coastal Atlantic sites, Interior Appalachian records display more spatially
 1095 heterogeneous and episodic fire histories (Fig. 9b). Individual sites such as Triangle Lake, Bonnett
 Lake, and Big Run Bog experienced fire peaks at different times despite sharing similar long-term
 climatic trends (Fig. 9c). Previous studies suggest that after spruce declined during the early Holocene,
 expansion of mesic hemlock–beech–hardwood forests under increasingly humid conditions reduced
 regional burning, with fire occurring primarily during episodic droughts (Jensen *et al.*, 2021; Chimezie
 1100 *et al.*, 2026) or ecological reorganizations (Coop *et al.*, 2020; Robbins *et al.*, 2024). Although several
 Interior Appalachian peatlands also underwent ecological succession, differences in the timing and
 trajectory of these transitions likely contributed to the heterogeneous fire histories among sites
 (Robbins *et al.*, 2024; Chimezie *et al.*, 2026). TANB similarly shows a temporal shift in dominant fire
 controls: during the early to middle Holocene, its fire history more closely resembled Coastal Atlantic
 1105 records, likely reflecting shared climatic forcing and fire-prone vegetation. As lake infilling and
 peatland development progressed, however, local hydrology and changing fuel composition
 increasingly regulated fire behavior. Thus, TANB reflects a transition from stronger regional climate–
 vegetation control to greater local ecosystem and hydrological regulation during the late Holocene.
 Finally, differences among fire records may also reflect differences in the spatial and process
 1110 sensitivities of the proxies themselves. The source area represented by sedimentary charcoal varies with
 particle size, with larger charcoal particles generally reflecting more proximal burning and smaller
 fractions integrating fire activity over broader spatial scales (Vachula *et al.*, 2018). Similarly, individual
 PAHs differ in their spatial fidelity to area burned, with some compounds primarily reflecting relatively
 local burning and others integrating fire activity over broader source areas (Vachula *et al.*, 2022). PAH
 1115 assemblages are also sensitive to combustion conditions, fuel characteristics, physicochemical
 properties, and transport and depositional processes (Lima, Farrington and Reddy, 2005a; Zuo *et al.*,
 2025). Consequently, the apparent asynchrony between TANB and charcoal-based records does not
 necessarily indicate contrasting fire histories under similar climatic conditions, but may reflect
 differences in the spatial scales and fire features. These relationships remain complex, however, and the
 1120 specific fire characteristics represented by charcoal and PAH records remain uncertain (Vachula *et al.*,



2024; Zuo *et al.*, 2025). Similarly, the TraCE-21K-II simulations are better suited to characterizing broad, long-term climatic trends than short-term or site-specific variability. The internally consistent TraCE-21k-II temperature and precipitation estimates provide a standardized framework for regional comparison, within which the greater coherent among Coastal Atlantic fire records suggests stronger regional climatic and vegetation controls, whereas the heterogeneity among Interior Appalachian records indicates greater local ecological and hydrological influence. Collectively, these patterns suggest that regional climate established broad constraints on Holocene fire activity, while vegetation succession, lake ontogeny, and hydrological development increasingly shaped its local expression, with potential anthropogenic influences during the late Holocene remaining difficult to distinguish from natural variability.

5. Conclusions

This multi-proxy reconstruction from TANB provides new insight into the long-term interactions among ecosystem succession, and fire-regime evolution in the northeastern Appalachian region during the Holocene. By integrating PAH molecular compositions with *n*-alkane biomarkers, and sediment composition analysis, we illustrate that changes in fire regimes were closely coupled to ecosystem succession rather than responding directly to climate alone.

- Four major stages of ecosystem development were identified, representing the transition from a shallow lake to a rich fen, a fen–bog transitional stage, and finally a *Sphagnum*-dominated bog. Progressive changes in vegetation composition, hydrology, and terrestrial organic matter input fundamentally altered fuel availability and combustion environments throughout the Holocene.
- PAH assemblages reveal four distinct fire regimes characterized by different combustion conditions, fuel composition, and fire source areas rather than simply variations in fire magnitude. High-temperature, woody-fuel combustion dominated the early Holocene under conifer-rich landscapes, whereas mixed-fuel burning became increasingly important during rich-fen development. Following peatland establishment, fire regimes shifted toward low-temperature smoldering combustion associated with wetland vegetation and peat fuels.
- Ordination analyses (RDA and LDA) further demonstrate that fire-regime variability was



1150 jointly controlled by vegetation composition, terrestrial organic matter input, and peatland
hydrology. Fire therefore functioned not only as a response to ecosystem change but also as
an ecological regulator. During the lake and rich-fen stages, burning likely accelerated
sediment delivery, nutrient input, and organic matter accumulation within the basin.
Following peatland establishment, wildfire increasingly regulated vegetation succession and
maintained open fen and bog communities. At the same time, differences in PAH transport,
1155 deposition, and preservation between lacustrine and peatland environments highlight the
importance of considering ecosystem evolution when interpreting molecular paleofire
records.

- Comparison with charcoal records from the northeastern Appalachians further support that
the fire histories were influenced by common climatic forcing but strongly modified by
1160 regional vegetation, hydrology, and landscape setting.

Appendix A. Supplementary Material

Supplementary Material includes additional figures and tables presenting the PAH compounds
analyzed, modern vegetation *n*-alkane distributions, supplementary multivariate analyses of PAH
assemblages and fire regimes, and supporting data for the reconstruction of Holocene ecosystem
1165 succession and fire-regime evolution at Tannersville Bog. The supplementary link is available at:
<https://doi.org/10.35099/h445-qa12>.

Data availability

All data analyzed in this study were obtained from previously published sources, as cited in the
manuscript. More detailed data information is available at: <https://doi.org/10.35099/n58b-bh05>.

1170 Authorship contributions

Yufan Feng: Conceptualization, Methodology, Software, Formal analysis, Investigation, Data curation,
Writing – original draft, Writing – review & editing, Visualization. **Richard S. Vachula**: Methodology,
Investigation, Formal analysis, Writing – review & editing, Project administration, Funding acquisition.



Ambarish V. Karmalkar: Methodology, Resources, Investigation, Data curation, Writing – review & editing, Visualization, Funding acquisition. **Alexandra Tsalickis:** Investigation, Methodology, Writing – review & editing. **Nicholas L. Balascio:** Methodology, Investigation, Formal analysis, Writing – review & editing, Funding acquisition.

Competing interests

The contact author has declared that none of the authors has any competing interests.

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