Geochemical Perspectives Letters

Impact of wildfires on Gondwanan flora during the Permian–Triassic transition

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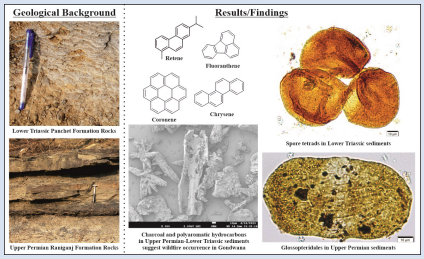
Abstract



The Permian–Triassic (P/T) transition is a critical juncture in Earth's history. Rock sequences from this interval record a significant loss of biodiversity in marine environments, a reduction of terrestrial vertebrates and the initiation of the Lower Triassic coal gap. Despite these records, little is known about the transition's impact on floral diversity and its relation to ecological perturbations. Here, we describe the hydrocarbons and charcoals preserved in Upper Permian–Lower Triassic fluviatile sediments from the East Indian Raniganj sub-basin and link them with potential vegetation shifts in Gondwana. Enrichment of pyrogenic polycyclic aromatic hydrocarbons (PAHs) and charcoalified tracheids reveal the presence of chronic wildfires in this floodplain environment. The pattern of vegetation shifts observed corresponds to a reduction of coal-forming *Glossopteris* Flora, while selective survival and diversification of fire-adapted conifers during the Induan age suggest that wildfires may have exerted an evolutionary pressure. The deficit of coal during the Induan is a clear sign of a decrease in vegetation density. We contend that recolonisation during the Induan occurred in an arid, fire-prone regime which produced charcoal despite scant vegetation cover.

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Introduction

The geological record shows that, for the past 540 Myr, Earth's biosphere experienced a relatively stable rate of background extinction that was occasionally punctuated by mass extinctions followed by biological diversification (Parry, 2021). One such critical event was the end-Permian mass extinction during which around 90 % of marine species and 70 % of terrestrial vertebrates disappeared (Dal Corso *et al.*, 2022 and references therein). A stronger understanding of these crises may be informative in an era of contemporary deforestation, wildfires and climate change. The terrestrial P/T sections in Gondwana, deposited in a wide range of basinal settings, are distributed across South America, South Africa, India, Australia and Antarctica (Benton and Newell, 2014). During most of the Permian, widespread peat-forming depositional environments were largely favoured within 20–80° S palaeolatitude in Gondwana and abruptly perished at the end-Permian as a result of ecosystem collapse (Retallack *et al.*, 1996).

Extinction events also play a role in natural selection through the expansion and creation of new ecological niches (Benton and Newell, 2014 and references therein). Vegetation turnover in Pangea's phytogeographic provinces was evident through the Late Permian–Early Triassic, coincident with widespread occurrences of wildfires (Rees, 2002). Fires may significantly impact ecosystems via the destruction of fauna and vegetation, leading to deforestation, promoting soil erosion and associated deleterious landform effects (Ward *et al.*, 2000), which serve as agents in natural selection (Robinson, 1989; He *et al.*, 2015). Fires can arise across a range of climatic conditions, including humid environments, as long as sufficient flammable biomass is available under high atmospheric pO_2 conditions (Robinson, 1989).

Polycyclic aromatic hydrocarbons (PAHs) and charcoals in geological archives serve as direct evidence of wildfires, while steroids, hopanoids and carotenoids may be associated with ancient biota and palaeoenvironmental conditions (Peters *et al.*, 2007). PAHs are formed through the catagenetic alterations of organic matter and pyrogenic events, such as forest fires, volcanic activity or meteor impacts. For example, a recent study identified centennial scale wildfires with PAHs, and enhanced erosion and marine euxinia indicated by S and Fe concentrations from the Meishan section in China (Saito *et al.*, 2023). Further, carotenoid hydrocarbons are widely associated with anoxic, H_2S-rich waters (Grice *et al.*, 2005; Cui *et al.*, 2020). Combusted morphological remains, *e.g.*, charcoals are also informative such as those sections concurrent with an early terrestrialisation event in the Silurian (Glasspool *et al.*, 2004). This is consistent with the idea that wildfires coevolved with the initial expansion of terrestrial vegetation. Incomplete combustion converts cellular components into highly

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recalcitrant molecular and morphological structures which, when preserved in the geosphere, may offer important insights into past high temperature processes.

Here, we report the distribution and significance of PAHs, charcoal and select hydrocarbon biomarkers from a stratigraphic section, comprising terrestrial Upper Permian and Lower Triassic rocks to reconstruct past ecosystem changes. While continental sections may potentially be disrupted by stratigraphic gaps, the Raniganj and Panchet formations in the Gondwanan Raniganj sub-basin contain records from the Late Permian and Early Triassic, respectively. In the absence of radiometric age markers, sedimentary formations can be biostratigraphically dated using the first and last appearances of palynotaxa. The *Densipollenites magnicorpus* Assemblage Zone dates the Raniganj as Late Permian (Changhsingian), while the *Lundbladispora-Densoisporites* Assemblage Zone dates the Panchet as Induan (Nowak *et al.*, 2018; Bhattacharya *et al.*, 2021). Data from the present study reveal the palaeoecology of wildfires in relation to the pattern of floral reorganisation during one of the most consequential chapters in the biotic history of the planet.

Methods

A total of 26 drill core samples were collected from a 257 m thick section (Fig. S-1). The geological background is provided in Bhattacharya *et al.* (2021) and details of the samples studied for molecular markers and those studied for palynology are given in Table 1 and Table S-1, respectively. The samples R/M/XX/19 to R/M/XX/55 belong to the Lower Triassic Panchet Formation, while R/M/XX/59 to R/M/XX/69 belong to the Upper Permian Raniganj Formation. The sample R/M/ XX/58, defined by conglomerate-mudstone lithotype, represents the transition from the Permian to Triassic. The methods employed for hydrocarbon and charcoal analyses are provided in the Supplementary Information.

Results and Discussion

Preserved polycyclic aromatic hydrocarbons and micro-charcoal in Upper Permian–Lower Triassic sediments. Unsubstituted high and low molecular weight PAHs in conjunction with micro-charcoals are recorded in the Upper Permian and Lower Triassic sediments in the depth interval between ~257 to 50.5 m (Fig. S-1). The dominant PAHs present are the four-ring compounds fluoranthene (Fl), pyrene (Py), benzo[*a*]anthracene (B[*a*]A) and chrysene (Chy); five-ring aromatics include benzo[*b/j/k*]fluoranthene (B[*b/j/k*]F), benzo[*a*]pyrene (B[*a*]P) and benzo[*e*]pyrene (B[*e*]P). Heavier PAHs with 6 rings, such as indeno[1,2,3-cd]pyrene (InP) and benzo[*ghi*]perylene (B[*ghi*]P) and 7-ringed coronene (Cor) are also recorded (Fig. 1). Retene, usually formed through thermal alteration of conifer resins (Tewari *et al.*, 2019 and references therein), is also detected. The PAHs ratios B[*a*]A/(B[*a*]A + Chy) > 0.35 and Fl/(Fl + Py) > 0.5 correspond to pyrogenic source (Table 1; Fox *et al.*, 2022). The PAHs are

Table 1 A list of selected biomarker and hydrocarbon proxy ratios across the depth of the studied Upper Permian (R/M/XX/69 to R/M/XX/59), transition (R/M/XX/58), and Lower Triassic (R/M/XX/55 to R/M/XX/19) sediments from Raniganj sub-basin, eastern India. Fl: Fluoranthene; Py: Pyrene; B[*a*]A: benzo[*a*]anthracene; Chy: chrysene.

Sample no.	Depth (m)	C_{30} βα/(βα+αβ) hopanes	C_{27}/C_{29} steranes	B[*a*]A/(B[*a*]A+Chy)	Fl/(Fl+Py)
R/M/XX/19	50.5	0.05	0.66	0.54	0.53
R/M/XX/24	70.3	0.12	0.27	0.33	0.42
R/M/XX/25	73.5	0.25	1.03	0.06	0.41
R/M/XX/27	85.3	0.11	2.82	0.09	0.46
R/M/XX/28	91.5	0.32	0.87	0.20	0.47
R/M/XX/32	112.1	0.25	0.59	0.16	0.45
R/M/XX/38	147.4	0.31	0.44	0.15	0.42
R/M/XX/41	150.5	0.26	0.47	0.14	0.48
R/M/XX/44	158.0	0.20	0.46	0.20	0.62
R/M/XX/47	178.0	0.32	1.00	0.42	0.68
R/M/XX/48	180.7	-	0.93	0.21	0.55
R/M/XX/51	193.8	0.31	0.20	0.03	0.56
R/M/XX/54	197.5	0.04	0.82	0.23	0.53
R/M/XX/55	199.9	0.33	0.65	0.02	0.50
R/M/XX/58	205.0	0.27	0.09	0.60	0.49
R/M/XX/59	214.3	0.26	0.24	0.52	0.57
R/M/XX/60	220.0	0.22	0.13	0.54	0.52
R/M/XX/61	226.0	0.27	0.03	0.87	0.56
R/M/XX/62	228.5	0.26	0.04	0.85	0.56
R/M/XX/63	231.5	0.23	0.09	0.69	0.51
R/M/XX/64	234.1	0.22	0.14	0.72	0.50
R/M/XX/65	240.3	0.24	0.07	0.74	0.65
R/M/XX/66	242.0	0.19	0.15	0.70	0.49
R/M/XX/67	244.0	0.18	0.05	0.77	0.50
R/M/XX/68	245.7	0.27	0.06	0.83	0.51
R/M/XX/69	257.0	0.28	0.39	0.51	0.51

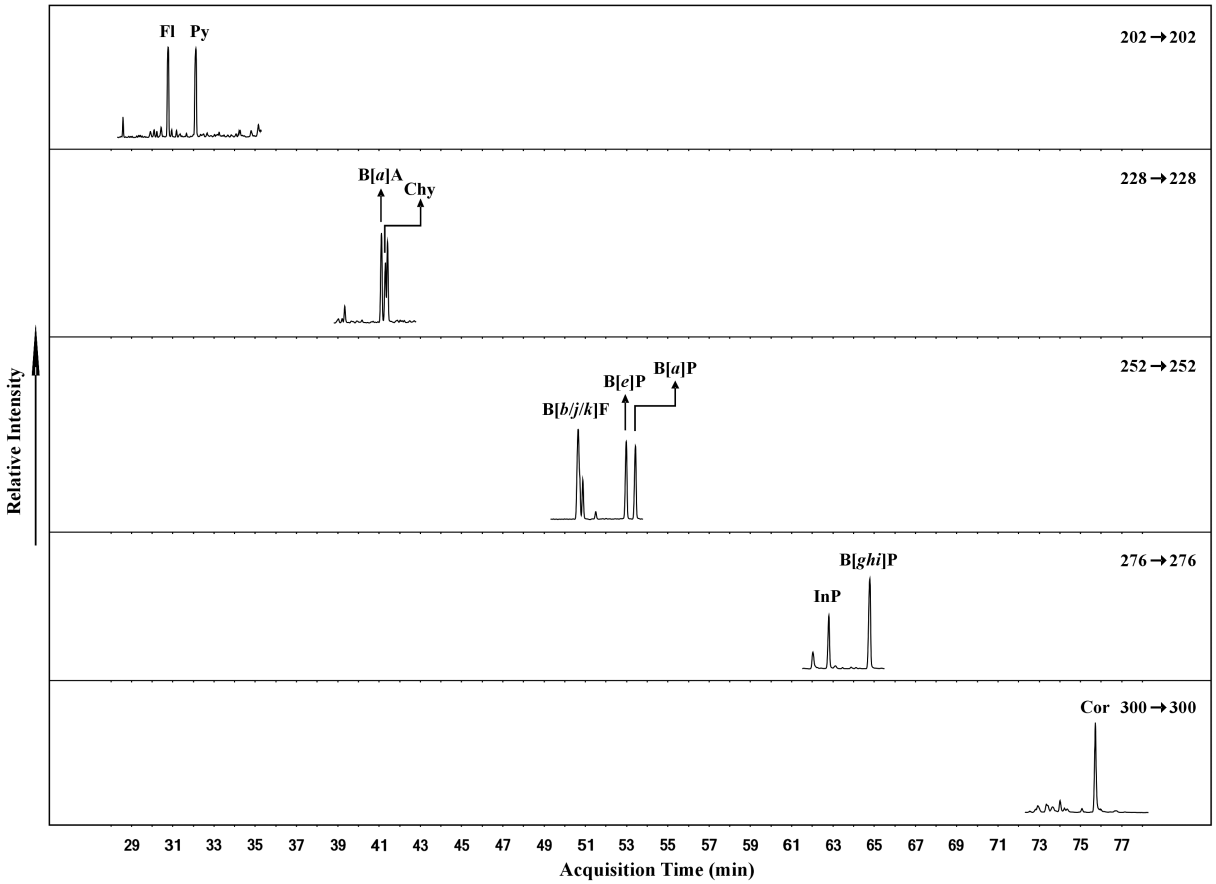

Figure 1 Representative multiple reaction monitoring (MRM) chromatograms obtained from GC-QQQ-MS analyses showing distributions of polycyclic aromatic hydrocarbons in the transition sample (R/M/XX/58), Raniganj sub-basin, eastern India. Fl: Fluoranthene; Py: Pyrene; B[*a*]A: benzo[*a*]anthracene; Chy: chrysene; B[*b*/*j*/*k*]F: benzo[*b*/*j*/*k*]fluoranthene; B[*a*]P: benzo[*a*]pyrene; B[e]P: benzo[e]pyrene; InP: indeno[1,2,3-cd]; B[*ghi*]P: benzo[*ghi*]perylene; Cor: Coronene.

accompanied by well preserved charcoalified tracheids in some samples (Fig. 2a–f) where the homogenised cell walls exhibit circular to oval-shaped uniseriate and biseriate pits, and biseriate alternate pits. The pits serve as evidence of charred woody fragments (Mays and McLoughlin, 2022). A gymnosperm affinity of the charcoalified remains is determined from the anatomical characteristics, although the detailed taxonomy could not be inferred due to fragmentary nature of the remains. Further, detailed palynological inspection reveals the presence of dispersed miospore genera from midcanopy floras, such as *Monosulcites*, and the upper-canopy floras, such as *Chasmatosporites* and *Cycadopites* (Fig. S-2 (1–6)) attributed to Mesozoic gymnosperms (Balme, 1995), in Lower Triassic sediments in the depth interval between 150.5 m and 70.3 m.

Hydrocarbons denoting microbial input into the Upper Permian–Lower Triassic sediments. Derivatives of carotenoid pigments are detected using multiple reaction monitoring (MRM) mass spectrometric analyses. Aliphatic carotenoid compounds such as β-carotane (Fig. S-3) is recorded. These are remnants of cyanobacterial pigments (Lee and Brocks, 2011). The attribution of these biomarkers is buttressed by detection of two peaks for a C_{38} carotenoid (Fig. S-3) sourced from cyanobacteria-specific carotenoid synechoxanthin (Cui *et al.*, 2020). Hopanoids present also denote bacterial contribution, while algal input is indicated by steranes (Summons and Walter, 1990; Peters *et al.*, 2007). Elevated levels (>0.1) of C_{30} βα/(βα+αβ) hopane ratio may indicate contributions from soil bacteria that preferentially produce βα hopanoids (Saito *et al.*, 2023). The C_{27}/C_{29} sterane ratio recorded in Lower Triassic sediments are higher (avg. 0.80) than those in the Upper Permian sediments (avg. 0.12) (Table 1), which along with high abundances of *Reduviasporonites* of presumed algal affinity (Foster *et al.*, 2002; Spina *et al.*, 2015), suggest proliferation of algal biota in the water bodies. The C_{40} monoaromatic β-isorenieratane and diaromatic isorenieratane detected (Fig. S-3) are typically sourced from obligate anaerobic phototrophs, such as brown-pigmented *Chlorobiaceae* adapted to dimly sunlit environments (Summons and Powell, 1986).

From presence of the carotenoids, we infer that both the Changhsingian wetland ecosystem and the Induan waning mire accumulated sufficient sulfate to generate the sulfide necessary for aromatic carotenoid production through reduction and sulfurisation. The β-isorenieratane and isorenieratane offer insights into the redox-stratified conditions where a euxinic bottom layer persists beneath an oxygenated surface. Such a system promotes preservation of both autochthonous and catchment-derived organic matter that is later transformed into coal and carbonaceous shale layers. A build-up of euxinic conditions in the marine realm in Pangea in response to Siberian Trap volcanism is well established (Grice *et al.*, 2005; Saito *et al.*, 2023). Our study suggests development and sustenance of euxinic conditions in a terrestrial ecosystem in Gondwana during P/T.

A succession of ecological changes across Changhsingian–Induan in the Gondwana derived from floodplain environment. In the depth interval from ~257 to ~50.5 m spanning the Changhsingian–Induan, the PAHs ratios and presence of charcoals could be attributed to pyrogenic sources (Table S-1; Fox

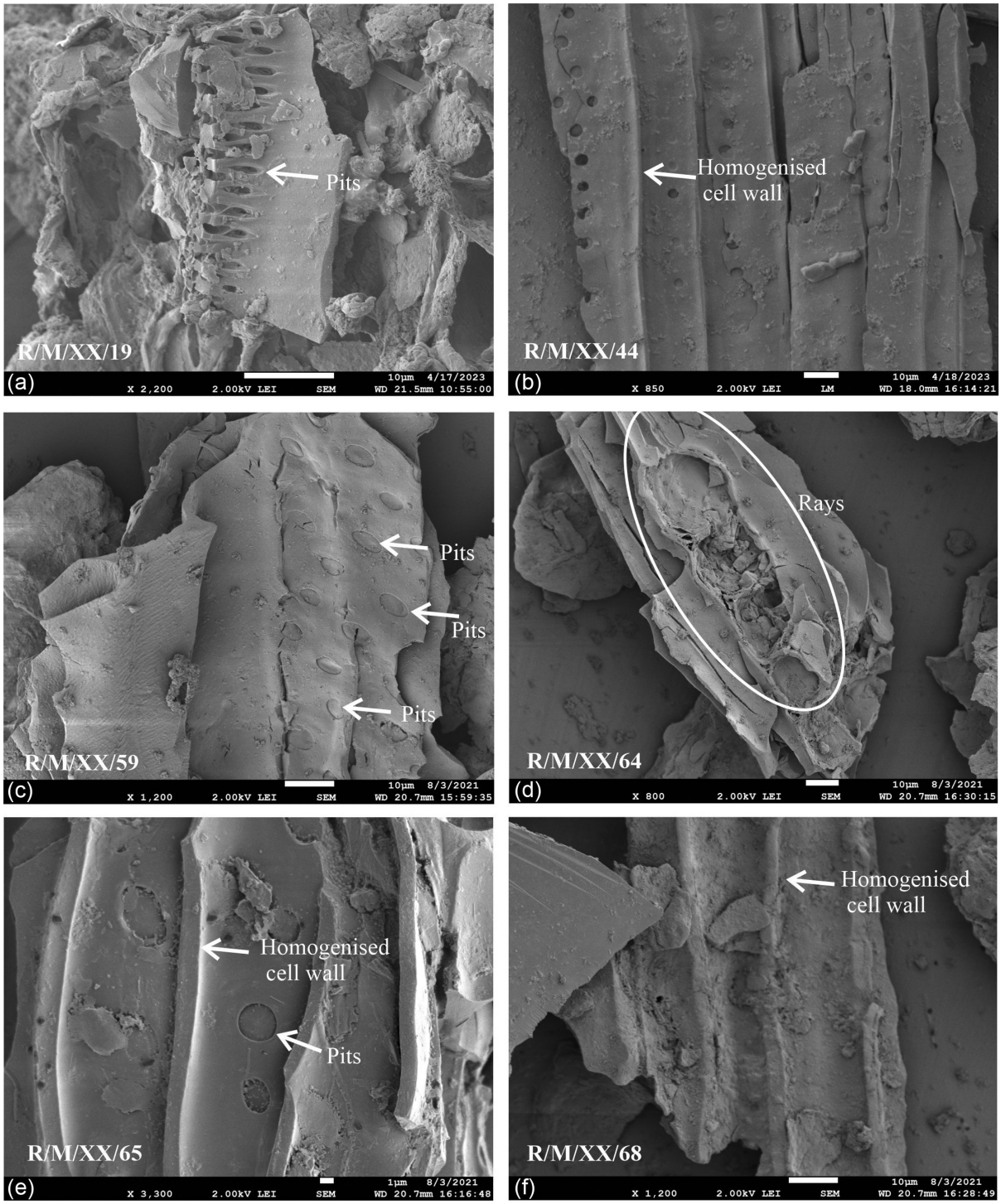

Figure 2 Scanning electron microscope (SEM) images of charcoalified tracheids in selected Upper Permian (R/M/XX/59; R/M/XX/64; R/M/XX/65; R/M/XX/68) and Lower Triassic (R/M/XX/19; R/M/XX/44) sediments, Raniganj sub-basin, eastern India.

et al., 2022). The charcoal particles are generally less abundant in Lower Triassic samples as compared to Upper Permian samples (Table S-1). Well defined phases with characteristic distributions of PAHs and charcoals suggest a distinct fire ecology in the floodplain environment (Fig. 3). The observed PAHs and charcoal in the Upper Permian sediments (~257 to ~214 m) are produced as a result of burning the arborescent *Glossopteris* Flora that flourished on floodplains (Fig. 3a). This depth interval depicts a high charcoal amount in the palynological remains (Table S-1), suggesting frequent wildfire events during the Changhsingian. Seasonal desiccation in Gondwana plausibly incited burning of combustible woody vegetation in an otherwise cool and humid environment. However, independent of strong seasonality, high atmospheric pO_2 would support combustion of such flora by counteracting the dampening effects of the humidity (Robinson, 1989; He *et al.*, 2015; Mays and McLoughlin, 2022). Initially, the Changhsingian *Glossopteris* Flora regenerated after the burning events evident from their palynological distribution (Bhattacharya *et al.*, 2021). In the next phase, between ~205 m (marked by the conglomerate-mudstone lithotype) to ~180 m, the samples are devoid of detectable palynological remains except for the presence of charcoal in two samples

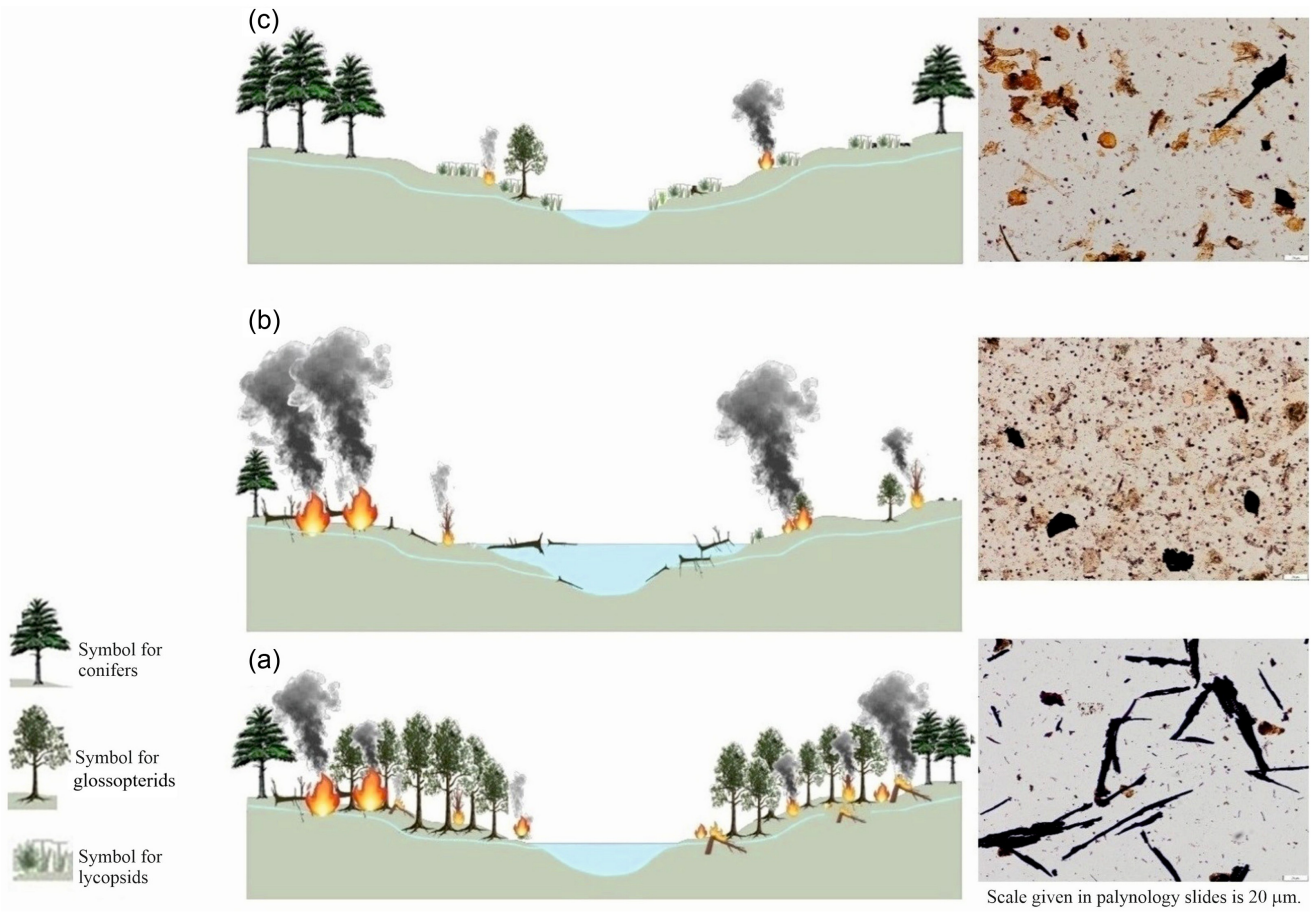

Figure 3 Palaeoecological changes during Changhsingian–Induan transition. This series depicts **(a)** a fire-prone dense mire where *Glossopteris* spp. thrived as the main coal-forming flora and conifers as subordinate flora during Changhsingian, **(b)** an impoverished ecosystem where the mire ceased to exist and fires continued burning the dieback vegetation during the transition, and **(c)** the recolonisation of the floodplains by conifers and the opportunistic lycopsids in a fire-prone ecosystem during Induan. Water table and kerogen matter (samples R/M/XX/61 in **(a)**; R/M/XX/50 in **(b)**; R/M/XX/28 in **(c)**) shown.

(R/M/XX/51 and R/M/XX/50). We interpret this to represent an ecosystem where vegetation density was reduced with continued fire episodes at the end-Permian and the earliest Triassic (Fig. 3b). The pyrogenic PAHs in this interval (Table 1) may correspond to frequent wildfires burning available combustible matter, which was likely comprised of dieback vegetation. At the ~178 m core depth, pronounced differences in the floodplain vegetation suggest a reduction of *Glossopteris* Flora with repopulation of the non-coal forming "clastic swamp" environment by diverse conifer and lycopsid genera (Bhattacharya *et al.*, 2021). Fire events intermittently continued until ~50 m, with the reduced charcoal content suggesting a reduction in the density of the recolonising Induan vegetation (Fig. 3c). Palynological results from this section (see Fig. 9 in Bhattacharya *et al.*, 2021) and angular charcoal fragments in Lower Triassic sediments suggest that reworked charcoal from the Upper Permian does not contribute to these Triassic records, although further detailed studies are required from the lowermost Lower Triassic sediments. Despite declining atmospheric pO_2 levels, the growing aridity during the Early Triassic (Macleod *et al.*, 2017) might have played a significant role in prolonging the fire events. The environment was further exacerbated by a rapid warming, as suggested by a study on conodont oxygen isotopes from South China (Chen *et al.*, 2016). This study demonstrates the warming of seawaters, where the temperatures might have risen by ~10 °C; however, this warming event was delayed and asynchronous to the onset of the negative shift in $\delta^{13}C_{carb}$ that has been recognised from multiple Permian–Triassic boundary sections. This suggests that the climate warming may not have been the direct endangering cause of the extinction but rather an accelerating factor in the decline in biodiversity (Chen *et al.*, 2016) demonstratively seen for the *Glossopteris* Flora.

Palaeoecology of wildfires with increasing dominance of conifers in the Triassic. Following the late Palaeozoic deglaciation, the *Glossopteris* Flora became the main coal-forming flora and essentially dominated the Permian period in Gondwana (Rees, 2002). Various traits ensured its rapid colonisation in the southern high latitudes (Mays and McLoughlin, 2022), and there is evidence, from preserved charcoal and fusinite, that the flora was subjected and adapted to wildfires through the Early to Late Permian of India (Murthy *et al.*, 2021 and references therein), as it had been throughout Gondwana (Mays and McLoughlin, 2022). It is possible that a cool, humid Changhsingian afforded climate refugia for elements of the *Glossopteris* Flora through continuous buffering and maintenance of habitat stability (Keppel *et al.*, 2015). However, the strong dependence of *Glossopteris* Flora on facilitative interactions combined with low species diversity inhibited its adaptability to end-Permian and Early Triassic conditions. Additionally, glossopterids largely thrived in lowlands close to water bodies (Prevec *et al.*, 2022), and this might explain the dominant production of the mid-chain *n*-alkanes (Bhattacharya *et al.*, 2021) known to be produced by aquatic

macrophytes. Hence, we posit that such flora failed to adapt and survive in the arid and warmer Induan environment.

The presence of conifers in Induan suggests that this flora had a different response in the stressed environment. Conifers are known to be equipped with mechanisms to endure fires and arid environments and have a long history of such resilience (Robinson, 1989; He *et al.*, 2015). For example, multiple lines of evidence support the serotinous character of Late-Carboniferous protoconifers, suggesting a long history of fire-adapted traits (for example serotiny) in coniferous gymnosperms (He *et al.*, 2015). Remnants of conifer wood that are found in the form of burnt tracheid remains in our studied samples are consistent with the higher tolerance of conifers to fires. Tracheid cells offer greater resistance to fires since these largely constitute lignified xylem tissues that are less susceptible to complete combustion (Robinson, 1989). The presence of lignin in plants of the *Glossopteris* Flora is noteworthy (Tewari *et al.*, 2019), though conifers contain higher concentrations in comparison (Robinson, 1989). Thus, the conifers that grew through the Changhsingian and Induan were likely already adapted to water and heat stressed environments. Hence, our observations suggest that fires may have fostered the diversification of conifers by creating a new niche through the deforestation of *Glossopteris*. Notably, Bennettitales, recorded in some Lower Triassic sediments, is also known to contain structures analogous to fire-adapted features in modern plants (Bond and Scott, 2010). Moreover, studies have observed the expansion of angiosperm flora during the Cretaceous in different fire regimes (Bond and Scott, 2010), connoting a strong link between plant evolution and fires.

Late Permian floras from each of the five distinct phytogeographic provinces across Pangea experienced episodes of wildfires (Rees, 2002; Mays and McLoughlin, 2022 and references therein). Evidence (mainly charcoal) of Late Permian wildfires in the Pangea are known, both from high and low latitudes—Gröden Formation, northern Italy; the Zechstein (Upper Permian), northwestern Hesse, Germany; Um Irna Formation, Jordan; Junggar Basin, northwestern China; Lambert Graben, East Antarctica; and Sydney and Bowen Basins, eastern Australia (Mays and McLoughlin, 2022 and references therein). The Pangean coal-forming flora collapsed while opportunistic biota colonised during the Early Triassic. These lines of evidence strongly suggest that wildfires were pervasive in Pangea and may have played a role in natural selection, ultimately shaping Early Triassic biodiversity. Fire may have acted as an evolutionary vector, selectively removing the typical coal-forming Pangean seed ferns, but it is unlikely to be the sole factor driving large-scale terrestrial plant extinction. Direct impacts of wildfires probably accelerated soil erosion during the Early Triassic through removal of the binding vegetation and by causing significant changes in fluvial geomorphology (Ward *et al.*, 2000). However, whether fires critically endangered plant floral biodiversity across the extinction boundary is still not clear. Our study reveals sufficiently rapid recolonisation and an increase in diversity of conifers and lycopsids during the Induan, although pre-boundary levels of vegetation density was not attained (Retallack *et al.*, 1996).

Conclusions

Coeval pyrogenic PAHs and micro-charcoals in conjunction with vegetation shifts during the Changhsingian–Induan transition in a Gondwanan floodplain environment reveal a complex palaeoecology influenced by wildfires. The pyrogenic markers, sharp decline of the *Glossopteris* Flora in the Induan and continuation of some early conifers suggest that wildfires may have significantly impacted the floodplain flora in the Raniganj subbasin. We posit that the *Glossopteris* Flora died out as a result of loss of swamp habitat, whereas the conifers might have had an advantage in the fire-prone environment and repopulated the vacated spaces. Understanding the links between abiotic forces and responses of biota during mass extinctions is particularly important in contemporary environments increasingly challenged by wildfires and widespread aridification.

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Additional Information

Supplementary Information accompanies this letter at https://www.geochemicalperspectivesletters.org/article2532.

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