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Different wildfire types promoted two-step terrestrial plant community change across the Triassic-Jurassic transition

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Frequent wildfires associated with emplacement of the Central Atlantic Magmatic Province (CAMP) are thought to have been important drivers of two significant changes in terrestrial plant communities and diversity during the Triassic-Jurassic Mass Extinction (TJME, ca. 201.51 Ma). However, it remains to be investigated whether these two changes are potentially related to different wildfire types. To better understand this relationship, we used a new method to reanalyze fossil pollen and spores across the Triassic-Jurassic transition in the Jiyuan Basin from the North China Plate. Results show that two peaks in wildfire frequency experienced different types of wildfires, with each linked to significant changes in plant communities and diversity losses. In the first wildfire peak, canopy fires dominated and are accompanied by significant losses of canopy forming plants, while in the second wildfire peak, ground cover fires dominated accompanied by significant losses of ground cover plants. Changes in atmospheric humidity conditions were an important control on the two different wildfire peaks. Relatively humid climatic conditions corresponded to the prevalence of canopy fires and hindered the spread and development of ground cover fires in wet surface conditions. Conversely, relatively arid climatic conditions corresponded with the prevalence of ground cover fires in dry surface environments. Our results provide a potential relationship between terrestrial plant communities and wildfire types, which is important to further understanding of terrestrial environmental and floral changes driven by Large Igneous Provinces.

KEYWORDS

central Atlantic magmatic province, Triassic-Jurassic transition, terrestrial plant community, wildfire types, charcoal

1 Introduction

The Triassic-Jurassic mass extinction (TJME, *ca.* 201.51Ma) represented one of the most severe biological crises of the Phanerozoic that resulted in the loss of approximately 50% of marine genera and a two-phase decline in plant diversity on land (McElwain et al., 1999; Hallam, 2002; McGhee et al., 2004; Wignall and Bond, 2008; Callegaro et al., 2012; McGhee et al., 2013; Wotzlav et al., 2014; Wignall and Atkinson, 2020; Lindström, 2021; Zhang et al., 2022). Currently available evidence suggests that the TJME can be attributed to the environmental consequences of pulsed eruptions in the Central Atlantic Magmatic Province (CAMP) (Hesselbo et al., 2002; Ruhl and Kürschner, 2011; Callegaro et al., 2012; Greene et al., 2012; Callegaro et al., 2013; Dal Corso et al., 2014; Percival et al., 2017; Lindström et al., 2019; Panfili et al., 2019; Ruhl et al., 2020; Wignall and Atkinson, 2020; Lindström et al., 2021; Shen et al., 2022; Zhang et al., 2022). It is hypothesized that CAMP volcanism released large amounts of isotopically light CO₂ into the atmosphere across Triassic-Jurassic (T-J) transition, through both direct release and indirect action from magmatic intrusion into organic layers, causing globally significant negative carbon isotope excursions (CIEs) in marine and terrestrial strata (e.g., Hesselbo et al., 2002; Dal Corso et al., 2014; Lindström et al., 2019; Ruhl et al., 2020; Wignall and Atkinson, 2020; Lindström et al., 2021; Shen et al., 2022; Zhang et al., 2022), global warming (Shen et al., 2022), ocean anoxia (Jost et al., 2017), and ocean acidification (van de Schootbrugge et al., 2007; Greene et al., 2012), increased chemical weathering (Shen et al., 2022), and frequent wildfires (Song et al., 2020; Zhang et al., 2022).

Frequent wildfires across the T-J transition are thought to be the main cause of changes in terrestrial plant communities and diversity at that time (e.g., Song et al., 2020; Zhang et al., 2022). Studies from the western Tethys (including North America, East Greenland, Poland, Denmark, and Sweden) (Jones et al., 2002; Marynowski and Simoneit, 2009; Belcher et al., 2010; Pole et al., 2018; Lindström et al., 2019; Lindström et al., 2021) and eastern Tethys (including South and North China) (Song et al., 2020; Zhang et al., 2022) have demonstrated that the influence of global warming on wildfires has had a significant impact on altering land vegetation and ecosystems, ultimately resulting in soil erosion after the loss of vegetation (van de Schootbrugge et al., 2020; Lindström et al., 2021). Furthermore, previous investigations on inertinite (charcoal) content and palynology in Sweden and Denmark in the western Tethys have shown that changes in plant communities are closely related to wildfire types, with different types of wildfires including ground and canopy fires causing plant communities changes (Petersen and Lindström, 2012). This relationship may also exist in the eastern Tethys region, but further study is required to evaluate this.

In this study, we investigate the ZJ-1 borehole in the Jiyuan Basin on the southern North China Plate (NCP) in the eastern Tethys. We use a new method to reanalyze previously published palynological data from Zhang et al. (2022), and combine them with published fossil charcoal and geochemical evidence (also from Zhang et al., 2022), to reveal the potential relationship

between terrestrial floras and wildfire types through the T-J transition.

2 Geological setting

During the Late Triassic, the NCP was situated around 30–40°N in the eastern Tethys (Greene et al., 2012; Zhang et al., 2022) (Figures 1A, B). Prototype basin reconstructions indicate that in the Late Triassic the Jiyuan Basin was located on the southeast part of the Ordos Basin (Liu et al., 2013) (Figure 1B). Provenance of sediment in the Jiyuan Basin was mainly from the northern Qinling-Dabie Orogenic Belt and the southern NCP located to the south (Yang et al., 2012) (Figures 1A, B).

Figure 1C displays the stratigraphic succession of lithological changes and the position of fossil plants assemblages from the Late Triassic to the Middle Jurassic in the Jiyuan Basin. Previous studies have constrained the geological ages of the Tanzhuang and Anyao formations from the Late Triassic to Early Jurassic based on zircon U-Pb dating, $\delta^{13}\text{C}_{\text{org}}$ chemostratigraphic patterns, and palynology biostratigraphy (Lu et al., 2021; Zhang et al., 2022) (Figure 1C).

3 Materials and methods

Palynological and charcoal data (Zhang et al., 2022; sampling locations are shown in Figure 2) were re-analyzed using new method (see below) from the Anyao Formation of the ZJ-1 borehole (35.07001°N, 112.47338°E) in the Jiyuan Basin (Figures 1A, B). Variations in spore and pollen compositions through the studied strata were used to reconstruct climatic conditions based on the climatic preferences of the parent plants (e.g., Li et al., 2020; Zhang et al., 2022; Zhang et al., 2023a; Zhang et al., 2023b; Zhang et al., 2023c). To reveal detailed changes in climatic conditions and plant diversity in the study area, we undertook non-metric multidimensional scaling ordination analysis (nMDS) and Simpson (1-D) Diversity Index analysis based on palynological fossils (e.g., Slater et al., 2019; Zhang et al., 2023b). Spore and pollen data were ordinated using nMDS analysis (at two dimensions) with the Bray-Curtis similarity matrix, a useful ordination method for detecting patterns of co-occurrence among taxa as well as ecological gradients (e.g., Zhang et al., 2023b). Simpson (1-D) values were calculated as $1 - \sum (p_i)^2$, where p is the proportional abundance of species and i is an unbiased measure of evenness, which ranges from zero (one taxon dominates the community completely) to one (all taxa have equal abundance) (e.g., Slater et al., 2019). According to the preferred ecological habits of plants, we reconstructed the vegetation types reflected by the palynological fossils, and identified ground cover, understory, and upper canopy plants (e.g., Petersen and Lindström, 2012). Charcoal abundance was used as a proxy for wildfire (e.g., Scott, 2000; Glasspool and Scott, 2010; Glasspool et al., 2015; Lu et al., 2020; Zhang et al., 2023a). To reveal burning temperatures and type of wildfires, we measured inertinite (charcoal) reflectance values on polished blocks using a Leica DM4500P LED reflected light microscope with a $\times 50$ oil immersion objective. Reflectance values were identified for over 100 points in each sample.

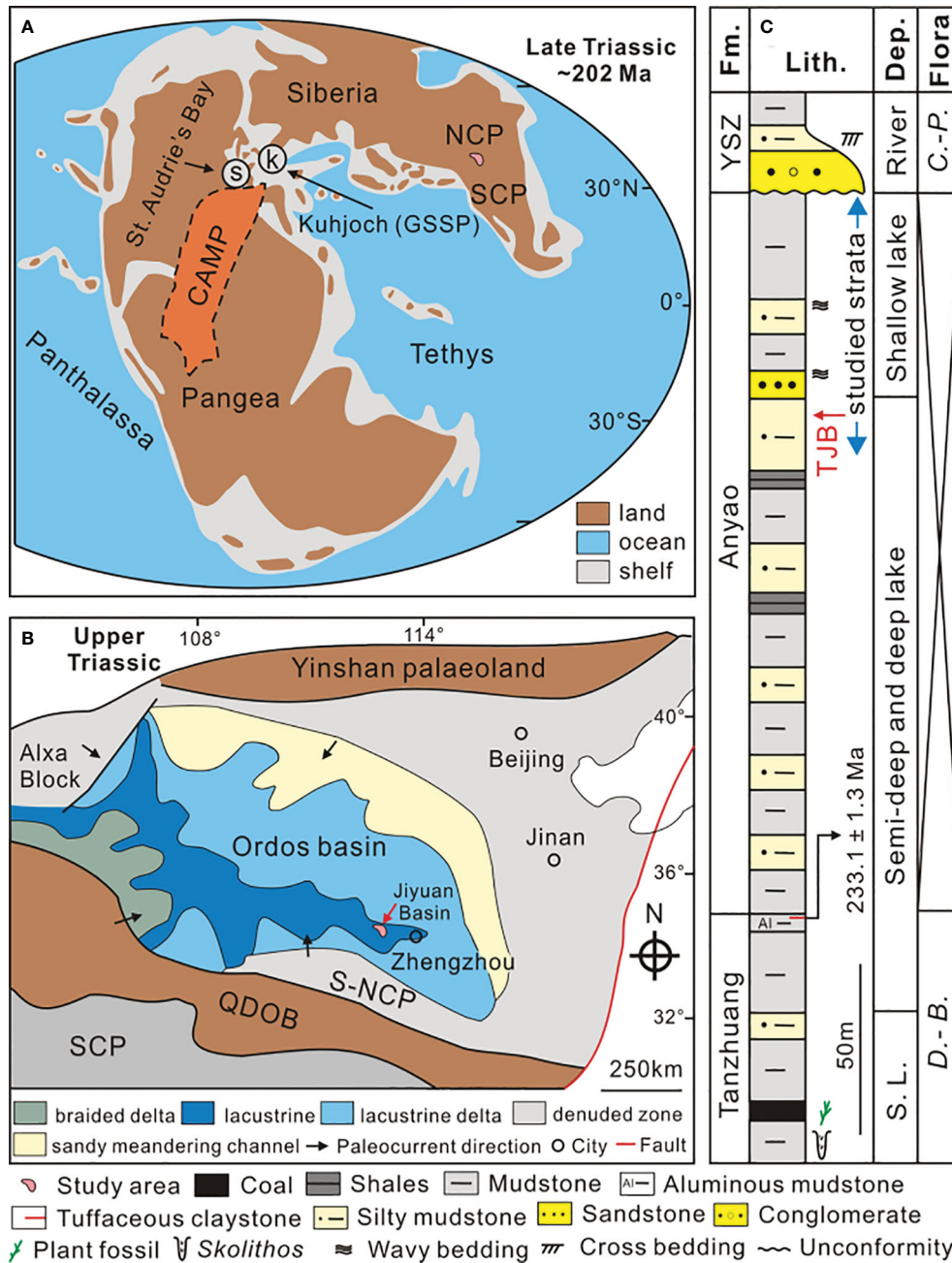


FIGURE 1 Location and geological context for the study area. (A) Palaeogeographic reconstruction for the Late Triassic (~202 Ma) showing location of the NCP and approximate extent of CAMP (revised after [Greene et al., 2012](#)); (B) Simplified tectonic map of the southern NCP during the Late Triassic showing the location of study area (modified from [Liu et al., 2013](#)); (C) Stratigraphic framework of the Tanzhuang Formation to the Lower Yangshuzhuang (YSZ) Formation from the Jiyuan Basin (modified from [Yang et al., 2012](#)). CAMP, Central Atlantic Magmatic Province; NCP, North China Plate; SCP, South China Plate; QDOB, Qinling-Dabie Orogenic Belt; S-NCP, southern North China Plate; SCP, South China Plate; Fm., Formation; m & s, coal, mudstone and silty mudstone; s., sandstone; c., conglomerate; Dep., Depositional environment; C.-P., Coniopteris-Phoenicopsis.

4 Results and analysis

4.1 Palynological assemblages and plant diversity

Thirty-four spore, thirty-two pollen, and eight algae genera have been identified in the study area ([Zhang et al., 2022](#))

([Supplementary Table 1](#)). According to the palynomorph composition, palynomorph abundance variations, and stratigraphically constrained cluster analysis (CONISS) of spore-pollen data, it can be divided into the six palynological assemblage zones ([Zhang et al., 2022](#)) ([Figure 2](#)). In these palynological assemblage zones, two significant plant diversity declines occurred ([Figure 2](#)). In AZ-II, there was a decrease of around 45% in the

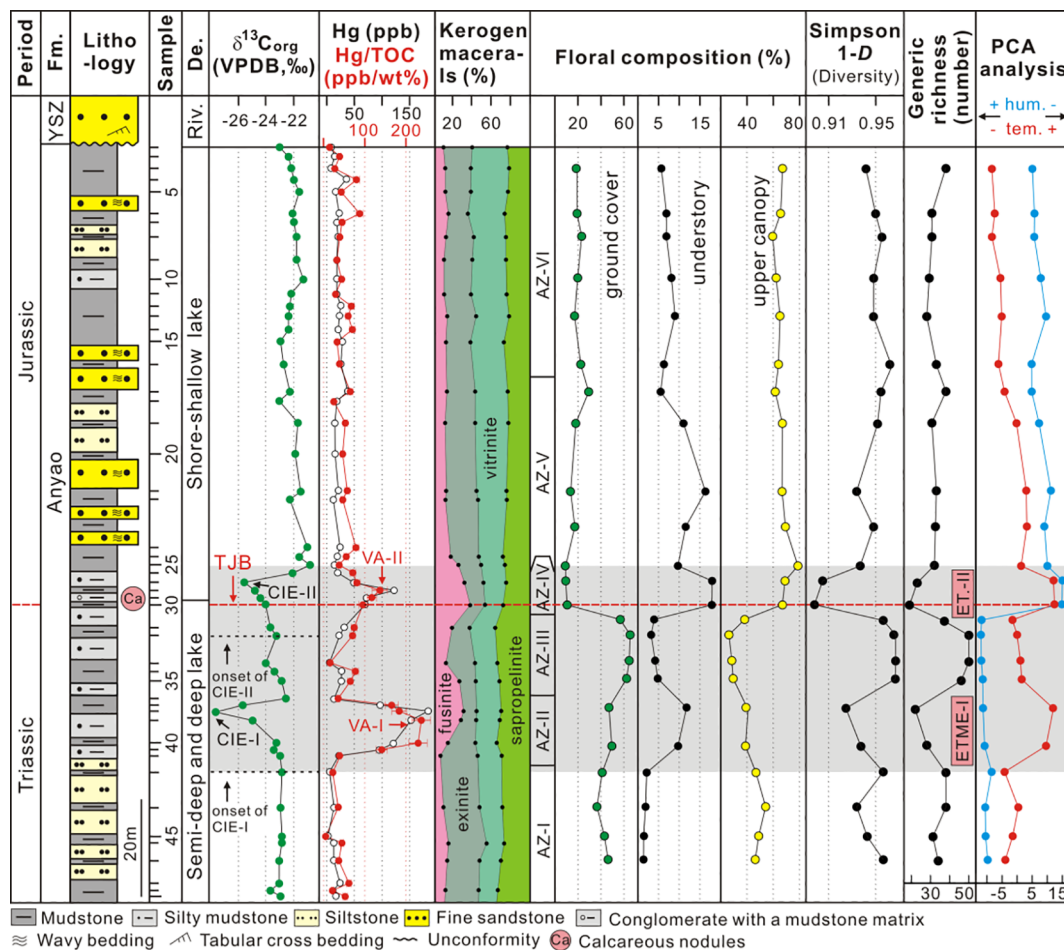


FIGURE 2
 Results of $\delta^{13}\text{C}_{\text{org}}$ values, Hg concentrations, Hg/TOC ratios, kerogen macerals, floral composition, Simpson (1-D) diversity values, generic richness (number of different genera), and principal components analysis (PCA) from the studied borehole in the Jiyuan Basin. $\delta^{13}\text{C}_{\text{org}}$ values, Hg concentrations, Hg/TOC ratios, kerogen macerals, generic richness, and PCA data are from Zhang et al. (2022).

proportion of spores and pollen, with the number of genera decreasing from 38 to 21 (Zhang et al., 2022) (Figure 2). Similarly, in AZ-IV, there was a decrease of approximately 44%, with a reduction from 50 to 28 genera (Zhang et al., 2022) (Figure 2). Moreover, AZ-IV experienced a significant rise in the abundance of *Cyathidites* spores and *Classopollis* pollen, and it marked the first appearance of the *Cerbropollenites* pollen type (Zhang et al., 2022).

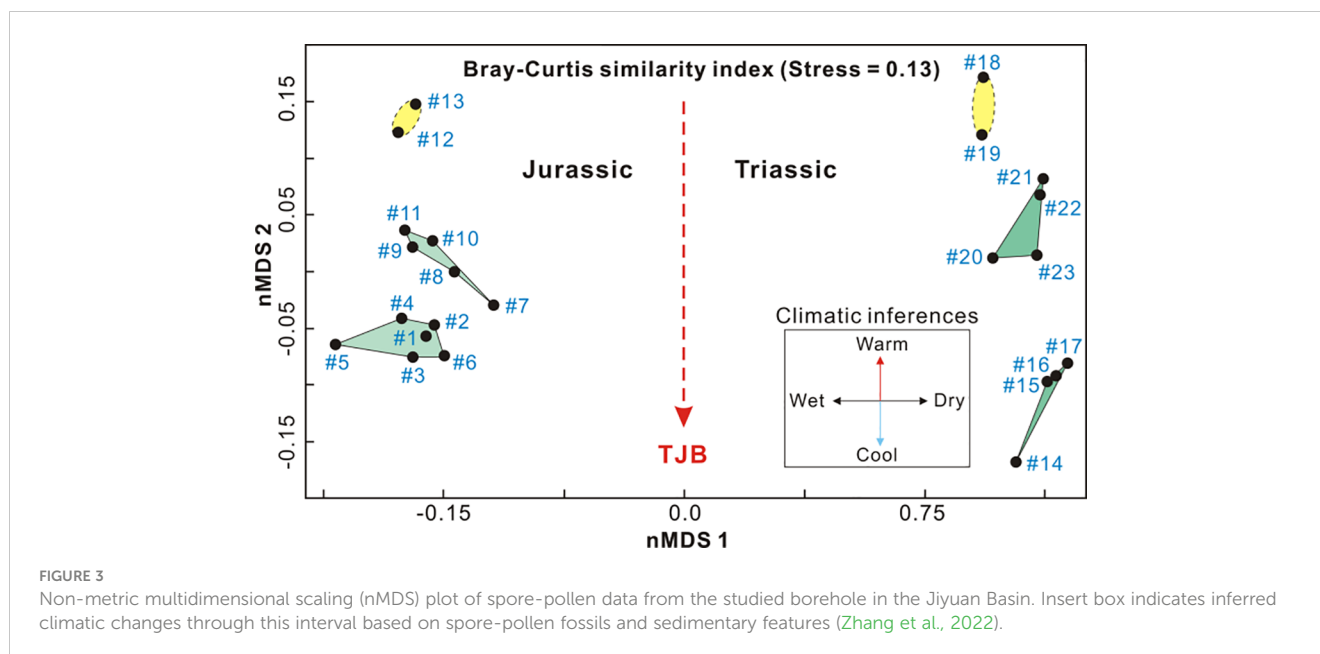
4.2 nMDS and Simpson (1-D) values

In this study, re-analyzing the palynological fossils using nMDS show that AZ-II and AZ-IV were intervals with relatively warm climatic conditions (Figure 3). This is consistent with previous results from principal component analysis (PCA) in the Jiyuan Basin (Zhang et al., 2022) (Figure 2). Results from the Simpson (1-D) analysis also identified two obvious declines in plant diversity during AZ-II and AZ-IV (Figure 2). This is consistent with the vegetation reconstruction results of palynological fossils in the studied Jiyuan Basin (Zhang et al., 2022).

4.3 Changes in terrestrial plant community

In this study, the ecological habits of palynological fossil genera were divided according previous classifications (see Petersen and Lindström, 2012) to include ground cover, understory, and upper canopy plants (Supplementary Table 2). Changes in the plant community structure in the study area are significant and can be divided into six stages that correspond to the changes in the palynological assemblages (Figure 2).

In AZ-I, the relative abundance of upper canopy plants (46.26–54.17%) are slightly more dominant than ground cover plants (36.57–46.26%), with understory plants relatively rare (1.46–2.12%) (Figure 2). In AZ-II, the relative abundance of ground cover plants increases and dominates (47.06–49.51%), with upper canopy plants less abundant (38.84–39.21%) but with an increase in understory plants (9.71–11.76%) (Figure 2). In AZ-III, the relative abundance of ground cover plants develops rapidly and become dominant (56.86–65.38%), followed by a slight reduction in upper canopy plants (26.28–38.24%), while understory plants are significantly less abundant and relatively rare (3.21–4.79%) (Figure 2). AZ-IV sees the relative abundance of canopy plants



becoming dominant (66.96–68.86%), followed by a rapid increase in understory plants (17.85–17.92%), while ground cover plants show a rapid decrease and are relatively sparse (9.43–10.71%) (Figure 2). In AZ-V and AZ-VI, canopy plants are dominant (61.47–78.71%; 59.48–67.01%), followed by ground cover plants (9.03–29.36%; 17.07–23.28%), with understory plants relatively rare (5.50–16.31%; 5.67–8.94%) (Figure 2).

4.4 Inertinite (charcoal) reflectance

In this study, we tested the inertinite reflectance during two peaks in wildfire frequency across the T-J transition in which there are elevated levels of inertinite (Figure 2); results are presented in Supplementary Table 3. During the first wildfire peak, inertinite reflectance values varied between 1.7 and 4.7%Ro, and most (65%) values were between 3.8 and 4.3%Ro. During the second wildfire peak, inertinite reflectance values varied between 0.7 and 3.1%Ro, and most (62%) were between 1.1 and 1.7%Ro.

5 Discussion

5.1 Changes in terrestrial plant communities and wildfire styles

Recent studies based on chemostratigraphy ($\delta^{13}\text{C}_{\text{org}}$ patterns) and palynological biostratigraphy have constrained the geological age of the target strata in the studied Jiyuan Basin and indicate that the T-J boundary is located in the upper part of Anyao Formation; this position roughly corresponds to palynological sample #JY-6 in the JZ-1 core (Zhang et al., 2022) and is consistent with our nMDS analysis (Figure 3). In this study, nMDS analysis showed that there were significant differences between Late Triassic and Early Jurassic plant types accompanied by a significant decline in plant diversity

inferred from the Simpson (1-D) value (Figure 2). Similar phenomena have been observed in the United Kingdom (Bonis et al., 2010), Germany (van de Schootbrugge et al., 2009; Lindström et al., 2019; Lindström et al., 2021), Denmark (Lindström et al., 2019; Lindström et al., 2021), Austria (Bonis et al., 2009), North America (Olsen et al., 2002), Australia (De Jersey and McKellar, 2013), and New Zealand (De Jersey and McKellar, 2013) and appears to represent a global signal (Wignall and Atkinson, 2020).

Changes in terrestrial plant types and diversity across the T-J transition were greatly influenced by the occurrence of frequent wildfires (Song et al., 2020; Zhang et al., 2022). In the study area, there were two significant peaks in the abundance of fusinite content and charcoal fossils across the T-J transition, indicating that there were two intervals with more frequent wildfires (Zhang et al., 2022). Frequent wildfires seem to be a global phenomenon across the T-J transition, with similar records recorded in North America, East Greenland, Poland, Denmark, Sweden, and South and North China (Jones et al., 2002; Belcher and McElwain, 2008; Marynowski and Simoneit, 2009; Pole et al., 2018; Lindström et al., 2019; Song et al., 2020; Lindström et al., 2021; Zhang et al., 2022). The two wildfire peaks in the study area were accompanied by significant changes in plant types and diversity, suggesting that frequent wildfires are the primary cause of significant changes in terrestrial plant ecosystems (Zhang et al., 2022). In this study, ground cover plants flourished during the first wildfire peak across AZ-II and AZ-III, while the abundance of understory and upper canopy plants decreased (Figure 2). During the second wildfire peak across AZ-III and AZ-IV, upper canopy plants flourished and ground cover plant significantly decreased (Figure 2).

Different types of wildfires may be responsible for changes in different plant types across the T-J transition. Previous studies have shown that ground, surface, and canopy wildfires are characterized by significant differences in burning temperature (Jones, 1997; Scott, 2000). Ground fires have a maximum burning temperature

of 400°C during ground litter burns (Scott and Jones, 1994; Scott, 2000), while surface fires burn litter, herbs, and shrubs and attain a maximum temperature of 600°C (Scott and Jones, 1994; Scott, 2000). However, canopy fires burn larger trees and shrubs and can reach higher maximum temperatures of 800°C (Scott and Jones, 1994; Scott, 2000). Extensive experimental data in previous studies have shown that changes in inertinite reflectance values can reflect burning temperatures and type of wildfires (e.g., Jones et al., 1991; Scott, 2000; Scott and Glasspool, 2007; Petersen and Lindström, 2012; Xu et al., 2022). The burning temperature, denoted as T , can be represented by the linear regression equation $T = 184.10 + 117.76\%Ro$ ($r^2 = 0.91$) (Jones, 1997), where %Ro corresponds to the measurable inertinite reflectance. In this study, changes in inertinite reflectance values provide evidence for wildfire types across the T-J transition. According to the above equation, burning temperature of the two wildfire peaks in the study area vary from 631.59–690.47°C and 313.64–384.29°C respectively. The first wildfire peak had higher burn temperatures and was likely dominated by canopy type wildfire, while the second wildfire peak had lower temperatures and was dominated by ground cover type wildfire (Figure 2). We consider that in the first wildfire peak canopy fires promoted significant change in plant community composition marked by the disappearance of canopy plants, whereas in the second peak ground cover fires promoted significant changes in plant community composition marked by the disappearance of surface plants. Similar changes in terrestrial wildfire patterns have been observed in Sweden and Denmark (Petersen and Lindström, 2012).

5.2 CAMP as a potential driver of the Triassic-Jurassic transition changes

Recent studies have shown that CAMP emplacement was an important driver of global environment, climate, and floral change across the T-J transition (e.g., Hesselbo et al., 2002; Ruhl and Kürschner, 2011; Greene et al., 2012; Percival et al., 2017; Lindström et al., 2019; Ruhl et al., 2020; Shen et al., 2022; Zhang et al., 2022). CAMP released massive amounts of isotopically light CO_2 into the reservoir of the exogenic carbon cycle and drove major global warming (Ruhl and Kürschner, 2011; Ruhl et al., 2020; Zhang et al., 2022). Warming climatic conditions at this time are supported by oxygen isotopes from Lavernock Point (United Kingdom) in the northwest Tethys (Korte et al., 2009), pCO_2 increases in pedogenic carbonates from the Newark Basin and the stomatal index (plant fossil cuticles) from Greenland, Sweden, and Northern Ireland (McElwain et al., 1999; Bonis et al., 2010; Schaller et al., 2011; Steinthorsdottir et al., 2011; Schaller et al., 2012; Lindström et al., 2021), and PCA analysis and sedimentological evidence (increased calcareous nodules) in North China (Zhang et al., 2022).

In the context of global warming climatic conditions, in higher temperatures lightning becomes more frequent and wildfires can be more destructive (Glasspool et al., 2015; Miller and Baranyi, 2021). As lightning is the main cause of wildfire, higher temperatures associated with CAMP volcanism would be expected to have

increased the frequency and destructiveness of wildfire events (e.g., van de Schootbrugge et al., 2008; Belcher et al., 2010; Glasspool et al., 2015; Lu et al., 2020; Lu et al., 2022; Zhang et al., 2022; Zhang et al., 2023a; Zhang et al., 2023c). Wildfires are influenced by a variety of factors, including the supply of combustible material, oxygen concentration required for combustion, a conducive climate with low moisture, and an ignition mechanism (Scott, 2000; Glasspool et al., 2015; Lu et al., 2020; Zhang et al., 2022). During the T-J transition, the abundant terrestrial vegetation in the Jiyuan Basin provided ample fuel for wildfires (Zhang et al., 2022). Widespread wildfires across the globe provide evidence for the presence of atmospheric oxygen concentrations suitable for wildfires during this time (see Section 5.1). Global warming climatic conditions during the T-J transition also promoted frequent lightning activity (the primary ignition mechanism) (Scott, 2000; Glasspool et al., 2015; Miller et al., 2017; Lu et al., 2020; Zhang et al., 2022; Zhang et al., 2023a). However, the two periods of warming climatic conditions across the T-J transition that saw significant changes in plant communities and diversity in the study area were accompanied by different types of wildfires (see Section 5.1) (Figure 2). Different atmospheric humidity conditions in the study area under global warming may be the main reason for the different types of wildfires.

In the study area, changes in vegetation types, PCA analysis results, and the widespread occurrence of calcareous nodules indicate that there are differences in atmospheric humidity conditions during the two pulses of plant diversity collapse across the T-J transition (Zhang et al., 2022) (Figure 2). During the first pulse of plant diversity collapse and its subsequent recovery phase, relatively humid climatic conditions prevailed in the study area indicated by an increase in hygrophytes (Zhang et al., 2022). Similar phenomena are also seen in the western Tethys (including Hungary, Great Britain, Denmark, Greenland, and Canada) and the southern Pangaea supercontinent (New Zealand and Australia) (van de Schootbrugge et al., 2009; Lindström, 2016). During the second pulse of plant diversity collapse, relatively arid climatic conditions prevailed in the study area inferred from increases in xerophytes and calcareous nodules (Zhang et al., 2022). Similar climatic conditions have been observed in South China (Huang, 2001; Zhou et al., 2021). In this study, during the first decline in plant diversity (TJME-I) that accompanied by the prevalence of canopy fires, relatively humid conditions caused an increase in the humidity of near-surface plants (including herbaceous plants and shrubs) and plant litter (fuel), which was detrimental to wildfires burning near-surface plants and development of ground cover fires (Figure 4). During the second plant diversity decline (TJME-II), the relatively arid conditions during TJME-II also promoted the decrease in humidity of near-surface plants and plant litter, which was conducive to their burning by ground cover fire, leading to the rapid spread and development of ground cover fires (Figure 4). Therefore, we consider that the different atmospheric humidity conditions in the context of global warming are the main cause of the different types of wildfires in the study area across the T-J transition. Furthermore, we also consider that the combined effect of the variable eruption intensity of the bimodal CAMP, and the southward migration of the tropical pressure convergence zone, may

6 Conclusions

1. Through the Triassic-Jurassic transition in the Jiyuan Basin, two intervals with peaks in wildfire frequency are identified. Inertinite reflectance values, serving as a proxy for burn temperature, records different types of wildfires for the two peaks. In the first peak, wildfires had high burn temperatures indicative of canopy fires and were accompanied by the loss of canopy plants, while in the second peak, wildfires had lower burn temperatures characteristic of ground cover fires and were accompanied by the loss of ground cover plants. The different types of wildfire resulted in significant but different changes in plant community composition, and each included a significant loss in plant diversity. Wildfire was important through the T-J transition in the Jiyuan Basin in shaping plant community composition and was a major factor contributing to the Triassic-Jurassic boundary terrestrial diversity loss and mass extinction.
2. Changes in atmospheric humidity conditions were a significant driver of the two different wildfire peaks. In the study area, atmospheric humidity was significantly different during the two intervals of plant community change. Relatively humid climatic conditions corresponded first to the prevalence of the canopy fires with very humid conditions and surface environments hindering the development and spread of ground cover fires. Relatively arid climatic conditions corresponded with the second peak in wildfire with the prevalence of ground cover fires, with arid conditions promoting the development and spread of ground cover fires.

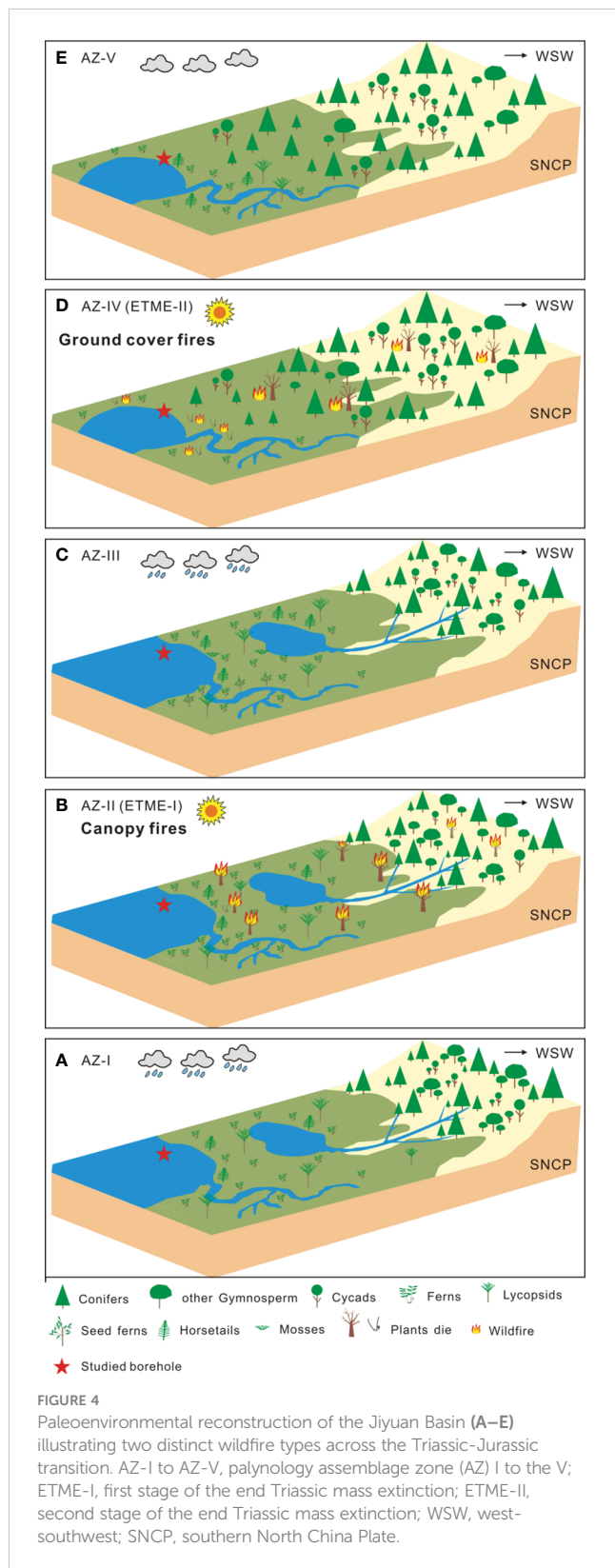
Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material, further inquiries can be directed to the corresponding authors.

Author contributions

PZ: Writing – original draft, Writing – review & editing. MY: Writing – review & editing. JL: Writing – original draft, Writing – review & editing. ZJ: Writing – review & editing. KZ: Writing – review & editing. XX: Writing – review & editing. LeW: Writing – review & editing, Validation. LW: Writing – review & editing. YZ: Writing – review & editing. HC: Writing – review & editing. XZ: Writing – review & editing. YG: Writing – review & editing. HY: Writing – review & editing. LS: Writing – review & editing. JH: Writing – original draft, Writing – review & editing.

have played a role in promoting different wildfires types through driving climate change (Song et al., 2020; Zhang et al., 2022).



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Conflict of interest

MY is employed by PetroChina, XX is employed by China National Administration of Coal Geology, and LW is employed by PetroChina Coalbed Methane Company Limited.

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Supplementary material

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