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Refugium amidst ruins: Unearthing the lost flora that escaped the end-Permian mass extinction

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Searching for land refugia becomes imperative for human survival during the hypothetical sixth mass extinction. Studying past comparable crises can offer insights, but there is no fossil evidence of diverse megafloral ecosystems surviving the largest Phanerozoic biodiversity crisis. Here, we investigated palynomorphs, plant, and tetrapod fossils from the Permian-Triassic South Taodonggou Section in Xinjiang, China. Our fossil records, calibrated by a high-resolution age model, reveal the presence of vibrant regional gymnospermous forests and fern fields, while marine organisms experienced mass extinction. This refugial vegetation was crucial for nourishing the substantial influx of surviving animals, thereby establishing a diverse terrestrial ecosystem approximately 75,000 years after the mass extinction. Our findings contradict the widely held belief that restoring terrestrial ecosystem functional diversity to pre-extinction levels would take millions of years. Our research indicates that moderate hydrological fluctuations throughout the crisis sustained this refugium, likely making it one of the sources for the rapid radiation of terrestrial life in the early Mesozoic.

INTRODUCTION

The end-Permian mass extinction (EPME), occurring approximately 251.94 to 251.88 million years (Ma) ago (1), is widely recognized as the most severe among the five major Phanerozoic extinctions (2). This catastrophic event resulted in the extinction of approximately 80% of known species (3), a fact well-supported by marine fossil records (4). Consequently, marine ecosystems experienced a significant reduction in biodiversity, with cosmopolitan disaster or opportunistic taxa dominating for at least 1 Ma after the EPME (5). There is a general agreement among scholars that the EPME has had a detrimental impact on marine ecosystems, but its effects on terrestrial ecosystems are still being explored (6, 7). Many researchers argue that, similar to marine organisms, terrestrial life had also witnessed a significant decrease in biodiversity during the EPME (8, 9). The disappearance of Glossopteris macrofossils, which dominated the late Permian across Gondwanaland and the late Permian tropical Cathaysian Gigantopteris floras in southwest China, exemplifies the profound consequences of the Permian-Triassic biological crisis on terrestrial ecosystems (10, 11). Previous palynological studies have also shown a certain degree of consistency in the global evolutionary trajectory of palynoflora around the EPME. The considerable abundance of freshwater algal fossils (12) and *Reduviasporonites* spp. (13), combined with the trilete spore spike (14, 15) during EPME, has been interpreted as evidence of deforestation events (16, 17) or other environmental disturbances during the EPME (14). Similar to the marine recovery paradigm, extensive palynological evidence from various regions reveals a significant occurrence of cavate trilete spores, such as *Lundbladispora* spp. and *Densoisporites* spp., immediately

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after the EPME (15, 18-20). The sudden and rapid shift in the composition of palynofloral assemblages has been interpreted as a quick takeover of opportunistic species post-EPME, such as quillworts and spike mosses, filling the ecological gap created by deforestation (17, 21). However, other palynological studies, such as those conducted in Pakistan (22), reveal bisaccate pollen-dominated palynological assemblages immediately after the EPME. These findings diverge substantially from the aforementioned evolutionary pattern of palynoflora during the Permian-Triassic biological crisis. Further examination of extensive data from both global macro- and micro-plant fossil records suggests that the decline in plant diversity is largely localized to certain regions and is heavily influenced by the scarcity of fossil-rich non-marine strata during the EPME (7, 23). These contrasting interpretations have sparked debate about how terrestrial plant communities respond to considerable disturbances in Earth's environmental conditions (24), such as intense volcanisms. Moreover, these contrasting interpretations have obscured the understanding of whether iconic Mesozoic plants had experienced a gradual evolutionary process from their Paleozoic ancestors or were reintroduced from refugia (25). Several studies have speculated that mid- and high-latitude hinterland refugia may have served as the origin for the radiation of many Mesozoic plants following the Permian-Triassic biological crises (17, 21). Analysis of extensive macro- and micro-plant fossil data indicates a minor decrease in plant diversity during these crises (7). This suggests that much of the terrestrial vegetation might have survived the EPME in specific terrestrial refugia. Nevertheless, concrete fossil evidence identifying a specific refugium with functional diversity during the Permian-Triassic biological crises remains elusive.

This study presents a combined investigation of palynomorphs, plant, and tetrapod fossils found in the South Taodonggou (STD) Section, located in the Turpan-Hami Basin of Xinjiang Province, northwestern China (Fig. 1B) (26). The chronological sequence of these findings is established using a high-resolution Bayesian age model across the Permian-Triassic boundary (PTB) (26). These findings provide valuable insights into terrestrial refugia at the middle latitudes in the Northern Hemisphere during the EPME.

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Fig. 1. Geological background of the STD Section. (A) Global paleogeographic map in the Early Triassic approximately 250 Ma, showing the location of the STD Section (red star) at approximately 45°N paleo-latitude. Modified from Blakey (54). (B) Map of northwestern China highlighting the STD Section in NE Xinjiang Uygur Autonomous Region, modified from Yang *et al.* (26). (C) Satellite image of the STD area, showing the two parallel studied intervals, PTB, and sites of three tuff layers producing zircon U-Pb chemical abrasion isotope dilution thermal ionization mass spectrometry (CA-ID-TIMS) dates used in the construction of the Bayesian age model of Yang *et al.* (26). (D) Geological map showing South and Central Taodonggou sections in the Tarlong-Taodonggou half-graben, modified from Yang *et al.* (26), Thomas *et al.* (44), and Yang *et al.* (55).

RESULTS

Age model of the STD Section

The Bayesian age model of Yang et al. (26) (the "U-Pb zircon age dating and age model construction" section in Materials and Methods) provides a high-resolution chronostratigraphy of the Wutonggou low-order cycle (LC) in the STD Section (figs. S1 and S2). The median model ages were used to calibrate the litho- and cyclostratigraphy within intervals A and B in the STD Section (Fig. 1C and figs. S1 and S2). These intervals are 200 m apart, where palynological samples were collected (Fig. 1C and fig. S1). The section spans 0.43 Ma from 252.10 to 251.67 Ma, crossing the PTB (Fig. 1C and figs. S1 and S2). The lithology and thickness of rock beds in individual sedimentary cycles in intervals A and B are correlated by physically tracing volcanic ash beds and cycle boundaries on the superbly exposed outcrop (Fig. 1C and fig. S1). The Bayesian age model from Yang et al. (26) was used for the first time to determine the absolute age of fossil-bearing layers in the STD Section. This allows us to estimate the timing and rate of fossil occurrences and changes and to correlate them with other global paleontological records.

Taxonomic composition of palynomorphs, plants, and tetrapods

Three palynological associations were identified in the upper Wutonggou LC of the STD Section based on cluster analysis of the

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relative abundances of various spore and pollen taxa in 15 samples (Figs. 2 and 3, and data S1). In addition, three other samples (2019STD-78.8, 2019STD-84.9, and 2019STD-94.5) yielded a small amount of poorly preserved spore and pollen fossils (fig. S1). Although the fossil data from these samples were not used for cluster analysis, they provide information on the stratigraphic ranges of various spore and pollen genera.

The lowermost palynological association is the Cyclogranisporites sp.-Lycopodiumsporites reticulumsporites (CR) assemblages. Except for sample 2023STD-6L, which is notably distinguished by its prevalence of bisaccate pollen (63.6%), the CR assemblages are predominantly characterized by a high abundance of trilete spores, which constitute 36.1 to 93.0% of the overall composition (Fig. 3). These trilete spores include Cyclogranisporites sp. (9.3 to 20.6%), Lycopodiumsporites reticulumsporites (0.7 to 13.5%), Anapiculatisporites decorus (0.7 to 11.6%), Calamospora liquida (0 to 21%), Cyclogranisporites cf. aureus (0 to 12.4%), and Lundbladispora communis (0 to 10.9%). In contrast, the bisaccate pollen constitutes a subordinate proportion (mostly less than 35%, except for sample 2023STD-6L), which is characterized by the presence of Alisporites tenuicorpus (0 to 30.7%), Scheuringipollenites sp. (0.3 to 10.6%), Alisporites landianus (0.5 to 10.0%), and A. communis (0 to 7.5%) (Figs. 2 and 3, figs. S3 and S4, and data S1). The CR assemblages were obtained from the lower part of the upper Wutonggou LC in samples 2023STD-1L to

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Fig. 2. Selected fossil spores and pollen recovered from the upper part of the Wutonggou LC in the STD Section. Specimens are identified by sample number-slide number-coordinate of England Finder. (A) Leiotriletes sp., 2019STD-63.6-3-39T1. (B) Punctatisporites sp., 2019STD-63.6-1-43L0. (C) Cyclogranisporites sp., 2019STD-58.7-1-40V2. (D) Anapiculatisporites decorus, 2019STD-58.7-2-4104. (E) Apiculatisporis spiniger, 2019STD-58.7-5-35K3. (F) Limatulasporites fossulatus, 2019STD-60.4-2-39Q0. (G) L. limatulus, 2019STD-60.4-4-38N0. (H) L. inaequalais, 2019STD-60.4-3-33N4. (I) Endosporites papillatus, 2019STD-90.5-3-37F3. (J) Lycopodiumsporites reticulumsporites, 2019STD-60.4-5-33R1. (K) Lundbladispora brevicula, 2019STD-58.7-1-33M4. (L) L. foveota, 2019STD-58.7-2-42S0. (M) Klausipollenites schaubergeri, 2019STD-90.5-4-40S1. (N) Lundbladispora brevicula, 2019STD-67.5-3-47P4. (S) Cyclogranisporites cf. aureus, 2019STD-78.8-2-37P0. (T) Scheuringipollenites sp., 2019STD-61.7-5-32P4. (U) Chordasporites brachytus, 2019STD-58.7-5-35V2. (Z) Lueckisporites virkkiae, 2019STD-78.5-2-41T4. (AA) Scutasporites xinjiangensis, 2019STD-58.7-5-36Q2. (AC) Protohaploxypinus regularis, 2019STD-67.5-4-40G4.

2023STD-12L, 2019STD-58.7, 2019STD-60.4, 2019STD-61.7, and 2019STD-63.6 (fig. S1). On the basis of the Bayesian age model (26), it is estimated that the deposition of these samples occurred approximately 59 to 160 thousand years before the EPME, spanning from 252.10 to 252.00 Ma (Fig. 3). It is important to emphasize that a significant quantity of cavate trilete spores, specifically Lundbladispora communis, L. foveota, and Densoisporites spp., which were previously linked to the widespread and adaptable lycopsids-Pleuromeia during the Early Triassic in Xinjiang (data S2) (19, 27), have already appeared in large numbers in the pre-EPME strata of the STD Section (Fig. 3). Hence, it is necessary to re-evaluate the importance of Lundbladispora and Densoisporites as spore genera in the Early Triassic stratigraphy of the Xinjiang region (19). The parent plants specified by the CR assemblages (data S2), along with fossil plants and tetrapods found near these palynological assemblages (Fig. 4), indicate that the lacustrine delta and lakeplain environment in the region were predominantly occupied by lycopsids and Dicynodongrade dicynodontoid Turfanodon before EPME (Fig. 5B) (28). Nevertheless, some horizons in the CR assemblages occasionally exhibit high abundances of gymnosperm pollen, such as sample 2023STD-6L (Fig. 3 and fig. S1). This may represent brief periods of gymnosperm proliferation, potentially associated with regional episodic climate or environmental fluctuations.

The second palynological association, identified in the middle part of the upper Wutonggou LC in the STD Section, is the *Alisporites landianus–Chordasporites australiensis* (LA) assemblages. The assemblages exhibit a notable decrease in the relative abundance of trilete

spores and a substantial increase in bisaccate pollen, comprising 71.2 to 92.9% of the total assemblages. Bisaccate pollen predominantly comprises non-taeniate bisaccate pollen (49.4 to 51.7%) and taeniate bisaccate pollen (20.0 to 40.5%). Within the non-taeniate bisaccate pollen, Alisporites landianus (12.2-22.2%) and A. tenuicorpus (7.1 to 20.0%) constitute a significant proportion. The taeniate bisaccate pollen is predominantly represented by Chordasporites australiensis (2.4 to 12.4%) and C. brachytus (4.1 to 7.6%) (Figs. 2 and 3, figs. S3 and S4, and data S1). The LA assemblages were obtained from samples 2019STD-67.05, 2019STD-67.5, and 2019STD-73.5 (fig. S1). On the basis of the age model (26), it can be determined that these samples were deposited in the period from approximately 251.99 to 251.93 Ma, specifically just before and at the onset of the EPME interval (Fig. 3). It is noteworthy that bisaccate pollen species-such as Lueckisporites virkkiae, Klausipollenites schaubergeri, and Scutasporites xinjiangensis (Figs. 2 and 3, figs. S3 and S4, and data S1)-previously regarded as dominant in the lower portion of the Guodikeng Formation (= lower part of the upper Wutonggou LC) of the Dalongkou Section before the EPME (19, 26), were found to be abundant during the onset of EPME in the STD Section (Fig. 3). The correlation between the composition of LA assemblages and known in situ fossil spore and pollen data indicates a lacustrine deltaic or lakeplain environment densely populated by a gymnospermous or seed-fern forest (Fig. 5A and data S2).

The uppermost palynological assemblage consists of only one sample (2019STD-90.5) obtained from the uppermost part of the Wutonggou LC in the STD Section. It is represented by the



Fig. 3. Results of palynological analysis of the upper part of the Wutonggou LC in the STD Section. This figure presents the relative abundances of spore and pollen taxa, spore/pollen ratios, in situ fossil plants and tetrapods, climatic conditions, and their chronological sequence based on the Bayesian age model of Yang *et al.* (*26*) for the STD Section. The figure also highlights the temporal correlation between our findings and the terrestrial palynological events in other regions of the world, which are accurately age-constrained and associated with the EPME. The color dashed line represents an uncertain temporal distribution. P/E, Precipitation/Evaporation; FAD, first appearance datum; EPME, end-Permian mass extinction; TE, terrestrial extinction; STD, South Taodonggou. Age (Ma), (*26*); climate, (*26*); in situ fossil plants, (*31*, *33*); in situ fossil tetrapods, (*28*); recurrent algae spikes in Sydney Basin, (*12*); marine EMPE, (*1*); and TE interval in southwest China, (*34*).

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Fig. 4. In situ fossil plants and tetrapod skeletons recovered from the upper part of the Wutonggou LC in the STD Section before, during, and after the EPME. (A) An upright coniferous trunk preserved in the upper part of the LA assemblages (red arrow). (B) An upright coniferous trunk preserved in the lower part of the LA assemblages, with carbonized roots (red arrow) extending downward from the trunk base into the underlying paleosol. (C) A horsetail axis preserved 9 m below the Ks assemblage (red arrow). (D) A cross-sectional view of *Zhuotingoxylon liaoi* (PB205872) recovered from the upper part of the LA assemblages. (E) A cross-sectional view of *Arthropitys* sp. (PB205873) recovered from the lower part of the LA assemblages. (F) A cross-sectional view of *Septomedullopitys szei* (PB205874) recovered from the upper part of the LA assemblages. (G) A skull of *Lystrosaurus* (field no. XJ12Al and IVPP V 27909), shown in dorsal view recovered from 2 m below the Ks assemblage. (H) An in situ *Lystrosaurus* skull (field no. XJ12C) exposed in lateral view at 7 m below the Ks assemblage.

Klausipollenites schaubergeri (Ks) assemblage and is characterized by a significant increase in the relative abundance of trilete spores (62.9%). Among trilete spores, Punctatisporites sp. (7.1%), Leiotriletes sp. (6.4%), Limatulasporites limatulus (5.7%), and Apiculatisporis spiniger (5%) are dominant. Klausipollenites schaubergeri, on the other hand, stands out as the most prominent pollen type, accounting for 15.7% of the total palynomorph assemblage (Figs. 2 and 3, figs. S3 and S4, and data S1). On the basis of the Bayesian age model (26), this sample was deposited approximately 251.72 Ma, about 160 thousand years after the EPME (Fig. 3). While trilete spores are common in this assemblage, it deviates from the typical contemporary palynological assemblages in Xinjiang due to the limited presence of cavate trilete spores, which typically increase significantly in these assemblages (Fig. 3) (19). On the basis of the greater abundance of trilete spores compared to bisaccate pollen in the Ks assemblage, it is hypothesized that this assemblage indicates the presence of more pteridophyte elements and fewer gymnosperms located on a lacustrine delta (Fig. 5C and data S2). In addition, we found some poorly preserved and sparse spore and pollen fossils in three samples (2019STD-78.8, 2019STD-84.9, and 2019STD-94.5). These samples were located 11.7 and 5.6 m below the Ks assemblage and 4 m above it (fig. S1).

Cyclogranisporites spp., with a few Alisporites spp. and Lunatisporites spp., suggesting a palynological composition similar to that of the Ks assemblage. However, owing to their poor preservation, these fossils are difficult to identify, and their rarity may significantly skew the statistical results. As a result, we excluded them from the Ks assemblage. Nevertheless, these spore and pollen fossils suggest that terrestrial vegetation, represented by the Ks assemblage, may have emerged by the end of the EPME and persisted for 210 thousand years after the EPME (Fig. 3). A total of 55% of the spore and pollen species found in the CR and LA assemblages disappeared in the Ks assemblage (fig. S5). However, this apparent loss might be due to temporary plant withdrawal or taphonomic bias. Our analysis of global and local fossil spore and pollen species occurrence data shows that only 39% of these seemingly vanished species were actually permanently lost in regional or global Triassic deposits (7, 19). Thus, there was no substantial mass extinction at the spore and pollen species level in the STD area throughout the EPME.

These fossils predominantly consist of Apiculatisporis spp. and

The palynological assemblages obtained from the STD Section indicate that regional gymnospermous pollen and their parent plants



Fig. 5. Artistic reconstruction of the terrestrial ecological landscape during, before, and after the end of the Permian mass extinction based on fossil palynomorphs, plants, and tetrapods recovered, as well as sedimentological data from the STD Section (illustration by D. H. Yang). (A) Lakeplain (26) was densely populated by a coniferous or seed-fern forest (31) during the EPME, as indicated by the LA assemblages. (B) Lakeplain (26) was dominated by herbaceous lycopsids, as indicated by the CR assemblages. It was inhabited by the *Dicynodon*-grade dicynodontoid, *Turfanodon* (28), before the EPME. (C) Regional vegetation characterized by abundant ferns with fewer gymnosperms and seed ferns (33), as indicated by the Ks assemblage, was located on a lacustrine delta (26). This area was populated by the carnivorous chroniosuchian (37) and the herbivorous *Lystrosaurus* (28) after the EPME.

were not notably affected by the EPME. Gymnospermous pollen, present in a small quantity before the EPME, not only persisted throughout the event but also increased in relative abundance at its onset. They continued to form a crucial part of the palynological assemblages found in the lower Induan deposits in the STD Section (Fig. 3 and data S1). This finding differs substantially from the prevailing wisdom of terrestrial deforestation during the EPME, as evidenced by the abundant presence of freshwater algal fossils and Reduviasporonites spp., coupled with the trilete spore spike (Fig. 3) (13, 15). In addition, our findings contrast with the idea of a transition from gymnospermous forest-dominated landscapes to lands covered by opportunistic or disaster herbaceous lycopsids after the Permian-Triassic biological crises (29), as suggested by the widespread increase in the abundance of cavate trilete spores (17, 21). The discrepancy highlighted in this study raises concerns regarding the potential reworking (30) of gymnosperm pollen during and after the EPME in the STD Section. However, the two sandstone beds sandwiched between samples 2019STD-67.5 and 2019STD-73.5 produce fossilized conifer trunks, specifically Septomedullopitys szei and Zhuotingoxylon liaoi, as well as a small number of calamitalean trunks, such as Arthropitys sp. (Figs. 3 and 4, D to F, and fig. S1) (31, 32). These trunks, notable for their upright orientation, have carbonized roots extending downward from the trunk base into the underlying paleosol (Fig. 4, A and B). This suggests that they were originally buried in their current positions. Therefore, the presence of fossilized conifer trunks in the STD Section provides evidence supporting the existence of a regional riparian coniferous forest coeval with the LA assemblages. The consistent correlation between these findings and the common presence of gymnospermous bisaccate pollen in the LA assemblages (Fig. 3) suggest that most fossil pollen was produced by local parent plants. Last, all fossil pollen recovered from the STD Section consistently displays

a brownish-yellow color, indicating a uniform thermal maturity (Fig. 2 and figs. S3 and S4). This further suggests that it is unlikely that fossil pollen during and after EPME were reworked in the STD Section.

The preservation of palynomorphs in samples above 2019STD-73.5 (2019STD-78.8, 2019STD-84.9, 2019STD-90.5, and 2019STD-94.5) is poor and scarce, with the exception of sample 2019STD-90.5 (fig. S1). However, this preservation status does not imply a prolonged barren period immediately following the EPME (Fig. 3). It is more likely a result of taphonomic biases, stemming from the presence of sandstone and conglomerate above sample 2019STD-73.5 (fig. S1), which are unsuitable for preserving fossil spores and pollen (32). In contrast, the petrified wood and tetrapod skeletons were relatively well preserved in this interval (Fig. 3 and fig. S1). Many in situ horsetail axes (Fig. 4C) and silicified coniferous wood fragments were found in the bed 9 m below the Ks assemblage (26, 33). This finding suggests that regional land vegetation characterized by abundant ferns with fewer gymnosperms and seed ferns (Fig. 5C) might have thrived within 50 thousand years following the EPME (Fig. 3). The fossil spores and pollen recovered in the Ks assemblage and samples 2019STD-78.8 and 2019STD-94.5 suggest that similar land vegetation may have thrived toward the end of the EPME and persisted for 210 thousand years (Fig. 3). The presence of gymnospermous pollen, coniferous fossils, phytoclasts, and root structures in the STD Section (32) throughout the EPME (Fig. 3 and fig. S1) suggests that this area might not have experienced substantial deforestation or prolonged ecological recovery. This contrasts with plant communities in the Sydney basin and southwest China, which underwent these biological crises before and after the EPME (Fig. 3) (11, 34). The STD region may have served as a middle-latitude refugium for terrestrial plants, protecting them from environmental disruptions before, during, and after the EPME (Figs. 1A and 3) (3).

While the STD region shielded most land vegetation from detrimental impacts, a few elements that bypassed this protection may have led to the extinction of the Dicynodon-grade dicynodontoid Turfanodon after EPME (28). Nevertheless, these sheltered land plants were instrumental in enhancing the stability of food chain (35). They drew a considerable influx of surviving land animals seeking refuge in the STD area (36), which expedited the development of a diverse regional terrestrial ecosystem following the EPME. Numerous well-preserved tetrapod skeleton fossils, identified as remains of the carnivorous chroniosuchian and herbivorous Lystrosaurus (Fig. 4G) (28, 37), were found at sites 1, 2, and 7 m below the Ks assemblage (Figs. 3 and 4H and fig. S1). These results indicate the presence of a localized riparian ecosystem on land with an increased functional diversity soon after the EPME, including primary producers as well as primary and secondary consumers. On the basis of the Bayesian age model (26), this diverse terrestrial ecosystem developed within 75 thousand years after the EPME, marking it the earliest recorded example of a diverse terrestrial ecosystem following the EPME (Fig. 3). Recent research on the terrestrial ecosystem model during mass extinction indicates that the restoration of terrestrial ecosystem diversity to pre-extinction levels, especially when primary producers were affected, generally took millions of years (35, 38). In contrast, the emergence of a diverse terrestrial ecosystem in the STD region a mere 75,000 years after the EPME indicates that the terrestrial ecosystems and plant community in this area remained functioning and were not decimated during the EPME.

Refugium sustained under moderate regional hydrological fluctuations

The unique palynofloral pattern in the STD Section deviates from those in both most contemporaneous sections and the nearby Dalongkou Section (11, 15, 17, 19, 22, 39, 40). This is evident in the early appearance of the cavate trilete spore-dominating palynological assemblages before the EPME, the dominance of gymnospermous pollen at the beginning of the EPME, and the scarcity of cavate trilete spores after the EPME in the STD Section. Neither substantial local drought nor excessive rainfall, typically linked with the rebalancing of the hydrological cycle during a global hyperthermal event in the EPME, can sufficiently explain this discrepancy (24, 41, 42). In contrast, a comparison of regional climate proxy data obtained from the paleosol type and elemental composition of the paleosol matrix in Central Taodonggou, situated approximately 2.5 km north of the STD Section (Fig. 1D), with palynological data in the STD Section revealed that alterations in terrestrial palynoflora during the EPME were primarily driven by regional hydrological conditions. The presence of cavate trilete spores in the CR assemblages, which indicates a substantial abundance of lycopsids, suggests a regional climate that was either humid or sub-humid before the EPME (Fig. 3). This inference is based on the fact that pteridophytes, such as lycopsids, rely on the availability of liquid water for their reproductive cycle (data S2) (18, 43). A regional humid climate before the EPME is also substantiated by the consistently elevated levels of the chemical index of alteration minus potassium (CIA-K) observed in the upper portion of the Wutonggou LC in the Central Taodonggou Section. These values indicate an estimated regional average paleoprecipitation of approximately 1000 mm/year (44). In contrast, conifers and pteridosperms typically showed a remarkable ability to adapt to drought, with only a few exceptions (data S2). As a result, the low spore/pollen ratios in the LA assemblages indicate a shift

toward a seasonally dry climate starting from the onset of the EPME (Fig. 3). This climate change is also evident in the increased occurrence of mature Calcisols with Bk horizons (fig. S1), observed from the EPME onward in the Permian-Triassic transitional STD, Central Taodonggou, Dalongkou, and Zhaobishan sections, covering an area of approximately 10,000 km² in the greater Turpan-Junggar Basin (Fig. 1B) (26). The collective evidence strongly suggests that regional seasonal drought coincided with the onset of the EPME. Nevertheless, this drying trend is temporary and exhibits a moderate magnitude, lacking a lasting effect on indigenous terrestrial ecosystems. The fossil spores and pollen recovered from sample 2019STD-78.8, characterized by the abundance of trilete spores and the subordinate occurrence of bisaccate pollen, indicate a regional climate rebound to a subhumid condition at the end of EPME (Fig. 3). This is further corroborated by the relatively elevated CIA-K value of the paleosol matrix located in the uppermost part of the Wutonggou LC in the Central Taodonggou Section (Fig. 1D) (44).

DISCUSSION

Overall, the palynological succession observed in the STD Section does not indicate any substantial local drought or excessive rainfall before, during, or after the EPME. Instead, it appears to be primarily influenced by moderate regional hydrological fluctuations. This environment might have served as a refugium for the iconic Mesozoic flora that emerged in the late Permian (25), potentially contributing to the stability of the food chain and attracting numerous terrestrial animals that survived the EPME. These findings suggest that the STD region may have played a crucial role as one of the source regions for the diversification of terrestrial life following the EPME in the early Mesozoic.

The complex nature of the terrestrial ecosystem recovered from the STD Section necessitates a reevaluation of the significance of refugia in the evolutionary processes of terrestrial ecosystems, which may have existed but have been underappreciated because of the unfavorable conditions for fossil preservation and imprecise age determination in terrestrial deposits.

MATERIALS AND METHODS

Geologic setting

The STD Section is located approximately 80 km south of the renowned non-marine Permian-Triassic transitional Dalongkou Section (Fig. 1B), which has previously been suggested as a possible global reference section for non-marine PTB (45). The STD Section is situated on the southern periphery of the Bogda giant anticline and was deposited in the Tarlong-Taodonggou half-graben, displaying notable variations in lateral facies and thickness (Fig. 1D). During the Permian-Triassic transition, the Turpan-Hami Basin was positioned on the easternmost margin of the Kazakhstan Plate at approximately a latitude of 45°N in the northeastern region of Pangea (Fig. 1, A and B). The Wutonggou LC in the STD Section spans from the late Wuchiapingian to early Induan (26). Our investigation confirms the productivity of the upper 38.7 m of the Wutonggou LC for palynomorphs. This interval consists of conglomerates, sandstones, shales, bentonites, and various paleosols, such as Protosol and Calcisol (fig. S1) (26), which were deposited in alternating fluvial and lacustrine lakeplain, littoral, and deltaic environments.

Palynology

A comprehensive collection of 129 palynological samples was obtained from the upper part of the Wutonggou LC, specifically from intervals A and B of the STD Section in the Turpan-Hami Basin (fig. S1). Interval B is located 200 m west of interval A (Fig. 1C). All samples were subjected to crushing and weighing (30 to 50 g per sample) and treated with the standard HCl-HF-HCl palynological maceration method (46). The resulting organic residues were filtered through a 10-µm mesh to separate palynomorphs and other organic particles. The palynomorphs and other organic particles were affixed onto permanent microscope slides using glycerin jelly and sealed with wax. The slides were examined using a Leica DM2500 microscope and a Nikon D800E camera connected to a computer equipped with Nikon Camera Control Pro 2 microscope software (version 2.4.1). A minimum of 300 grains were designated for enumeration in each palynological sample for statistical analysis. Following the initial examination, 12 samples exhibited palynomorph productivity and achieved the desired count of 300 palynomorphs. In addition, samples 2023STD-5L, 2019STD-63.6, and 2019STD-90.5 yielded observations of 185, 283, and 140 grains, respectively (fig. S1 and data S1). Furthermore, three other samples (2019STD-78.8, 2019STD-84.9, and 2019STD-94.5) produced a small quantity of poorly preserved spore and pollen fossils. Because of the poor preservation of fossils in these samples, only a few can be identified to genera, which could lead to significant deviations in the statistical results. Thus, the count of spore and pollen fossils from these samples was not included in the statistical analysis (Fig. 3 and fig. S1). The slides are housed in the State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China. Each slide is designated a specimen number, spanning from 2019STD-58.7 to 2019STD-94.5, as well as from 2023STD-1L to 2023STD-12L. All fossil spores and pollen in the figures are located using the England Finder Slide.

Constrained incremental sum of squares (CONISS) cluster analysis, using Euclidean distance as the dissimilarity measure, identified three distinct palynological associations based on the relative abundances of different palynomorph taxa in each sample (fig. S6 and data S1) (47). To interpret these associations, it was essential to consider the paleoclimatic and paleoenvironmental preferences of the plants that produced the most prominent types of spores and pollen. These types included lycopsid spores (cavate trilete spores), fern spores (mostly trilete spores), and conifer and pteridosperm pollen (bisaccate pollen) (18, 27, 48–50).

Fossil tetrapod

J.L.'s team conducted fieldwork in 2012 and 2019, searching for and collecting fossil vertebrates from the STD Section. They documented more than 20 fossil occurrences during these times. Only some of these occurrences preserved the skull and could be identified as *Lystrosaurus* based on the downward-sloping snout. Examples of these specimens include XJ12C and XJ12AI (IVPP V 27909) (Fig. 4, G and H). The lowest level where *Lystrosaurus* has been found is approximately 6 m above the PTB (fig. S1). A bystrowianid specimen (IVPP V 26541) was also discovered at a higher level, about 12 m above the PTB (28). In the lower part of this section (28), which is 3 m below the CR palynological zone, *Turfanodon* and *Vigilosaurus* were also recorded (51). These samples are housed in the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China.

Fossil plants

There are 39 in situ fossil trunks that have been found and excavated from the layer between samples 2019STD-67.5 and 2019STD-73.5 (Fig. 3 and fig. S1). Among them, two trunks belong to the calamitaleans, and the rest are of coniferous affinities (*31, 32*). In the layer 4 m above the PTB, we found hundreds of petrified woody fragments (Fig. 3 and fig. S1). These include 1 in situ coniferous trunk, 30 unidentified in situ small horsetail branches with a diameter less than 3 cm, and the rest are coniferous roots (*32, 33*). The fossil trunks and roots from the STD Section were examined using thin sections, following the method described by Hass and Rowe (*52*). These fossils and thin sections are currently kept in the Palaeobotanical Collection of the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China. Each thin section was assigned a specimen number, ranging from PB205872 to PB205874.

U-Pb zircon age dating and age model construction

The Bayesian age model for the STD Section has already been published in (26). Readers are referred to (26) for detailed descriptions of laboratory procedures, analytical data, and age interpretations. However, we briefly describe it here to validate the age calibration of each fossil-bearing horizon.

Zircons were extracted from seven tuffs and bentonites. Six of these are from the Wutonggou LC in the northern and southern Tarlong sections, as well as the STD Section, which are approximately 4 km apart (Fig. 1C and figs. S7 and S8) (26). One is from the Shaofanggou LC in the STD Section (Fig. 1C and fig. S8) (26). The Radiometric dating analyses were conducted in the Isotope Geology Laboratory of Boise State University, Boise, ID, USA. The zircons were first analyzed by laser ablation inductively coupled plasma mass spectrometry (LA-ICPMS) to obtain ²⁰⁶Pb/²³⁸U dates spanning a wide range with relatively large 2σ errors of several million years. These dates and the cathodoluminescent images of analyzed zircon grains were used to screen and select zircon grains that produced LA-ICPMS dates in the range of estimated geologic ages for further analysis using the chemical abrasion isotope dilution thermal ionization mass spectrometry (CA-ID-TIMS) method. The U-Pb dates of single zircon grains of a sample obtained by the CA-ID-TIMS method were used to calculate the weighted mean $^{206}\text{Pb}/^{238}\text{U}$ dates with small 2σ errors in the range of 0.01 Ma. These dates were interpreted as either the depositional or maximum depositional age for the sample.

The interpreted high-resolution CA-ID-TIMS ages of seven tuffs and bentonites were used to construct a Bayesian age model of a composite upper Permian-Lower Triassic section in the study area to convert the cyclostratigraphy into chronostratigraphy. Eight dates are from the Wutonggou LC in the north and south Tarlong sections and the STD Section; one is from the Shaofanggou LC in the STD Section (Fig. 1C and figs. S2, S7, and S8). The thickness of the composite section is normalized with respect to that of the South Tarlong and STD sections (fig. S8), which are ~4 km apart (fig. S7) (26). The three sections are situated within the same half-graben (fig. S7) and were correlated by using a prominent and persistent coal bed located in the upper part of the Wutonggou LC as the datum, which is positioned 52.7 m below the base of the study interval in the STD Section (figs. S1 and S8). The algorithm of Trayler et al. (53) was used in the calculation of the Bayesian age model. The results are reported as the median age and the lower and upper limits of the 95% high-density interval. The median age of the studied interval in the STD Section ranges from 252.10 to 251.67 Ma. The corresponding lower limit ranges upsection from 0.16 to 0.65 Ma and the upper limit from 0.18 to 0.24 Ma (fig. S2) (*26*).

Supplementary Materials

The PDF file includes: Figs. S1 to S8 Legends for data S1 and S2 References

Other Supplementary Material for this manuscript includes the following: Data S1 and S2

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