Article

Evolution of insect diversity in the Permian and Triassic

SHUANG-MAO GUI, YU-CHU LIU & LI TIAN*
State Key Laboratory of Biogeology and Environmental Geology, China University of Geosciences (Wuhan), Wuhan 430074, China
✉ *gsm199902@163.com;* ⬤ *https://orcid.org/0009-0005-8813-1105*
✉ *liuyuchusherry@163.com;* ⬤ *https://orcid.org/0000-0002-0664-825X*
✉ *tianlibgeg@cug.edu.cn;* ⬤ *https://orcid.org/0000-0003-3005-2007*
*Corresponding author

Abstract

The global warming that occurred during the Permo-Triassic transition, following the end of the Late Paleozoic glaciation, and the resulting responses of the biota to the changing environment, are considered important analogs for understanding rapid future warming scenarios. While there has been extensive research on the patterns and extent of diversity in plants, tetrapods, and marine invertebrates during the Permo-Triassic, the study of insect diversity and the evolution of their faunal composition has been relatively limited. The question of whether there were insect extinctions during this period continues to be a subject of debate. Here, we present a statistical study on taxonomic diversity of insects—at specific, generic and familial levels—throughout the Permian and Triassic, with subsampled tests on the reported global occurrences. Our result show that more than one insect extinction events, accompanied by significant diversity drop and turnovers of faunal compositional, occurred in the Permian and Triassic. All the uncovered insect diversity crises exhibit strong correspondence with the well-known marine mass extinction events in the Middle Permian, Permo-Triassic transition, Carnian, and Rhaetian, whilst the marine correspondence with the Early Permian insect crisis is less pronounced. Insects, being a major component of terrestrial ecosystems, demonstrate varied diversity responses to climatic changes in Permian and Triassic. Our study sheds new light on the intricate interplay between insect diversity evolution and the changing environmental conditions during these critical geohistorical periods.

Keywords: Diversity change, subsampling, extinction, terrestrial ecosystem, fossil record

Introduction

Permo-Triassic mass extinction was the most severe extinction event in the Phanerozoic, altering the ecosystem from the Paleozoic type to the modern one (Sepkoski, 1984; Benton, 2016; Benton & Newell, 2014). The eruption of the Siberian flood basalts and arc volcanos (Burgess & Bowring 2015; Fielding *et al*., 2019) triggered rapid global warming and widespread anoxia, significantly limiting the habitable spaces for marine organisms (Bottjer *et al*., 2008; Song *et al*., 2014; Benton, 2018; Dal Corso *et al*., 2022). Unlike the insightful acknowledgments on marine records, how terrestrial organisms and environments were affected is much less understood (Benton & Newell, 2014; Gastaldo, 2019). For examples, terrestrial tetrapods and plants are considered to have been impacted on their faunal composition and biogeographic distribution during the Permo-Triassic transition, resulting in a "tropical tetrapods gap" and severe devegetation (*e.g*., Sun *et al*., 2012; Benton & Newell, 2014; Shu *et al*., 2023). However, ongoing debates persist regarding the exact scale and timing of these events (Gastaldo, 2019; Nowak *et al*., 2019; Allen *et al*., 2020; Romano *et al*., 2020; Viglietti *et al*., 2021).

Nearly three-quarters of all named living taxa are insects (Mayhew, 2007; Stork *et al*., 2015; Stork, 2018; Eggleton, 2020: fig. 1), colonizing almost all continental habitats (Grimaldi *et al*., 2005; Montagna *et al*., 2019). Nevertheless, our understanding of the patterns and extent of insect diversity, as well as the evolutionary changes in their faunal compositions during the Permian and Triassic periods, lags behind that of plants, tetrapods, and various marine invertebrates. Whether one or more mass extinction of insects occurred in the Permo-Triassic interval is still controversial (Labandeira & Sepkoski, 1993; Labandeira, 2005; Ponomarenko, 2006; Jouault *et al*., 2022). Existing insect diversity studies were mostly based on the taxa records at genus to family level, and possibly heavily biased by sampling issue (*e.g*., Labandeira, 2005). Here, we present a new study on taxonomic diversity of insects, at species, genus, and family level, throughout the Permian
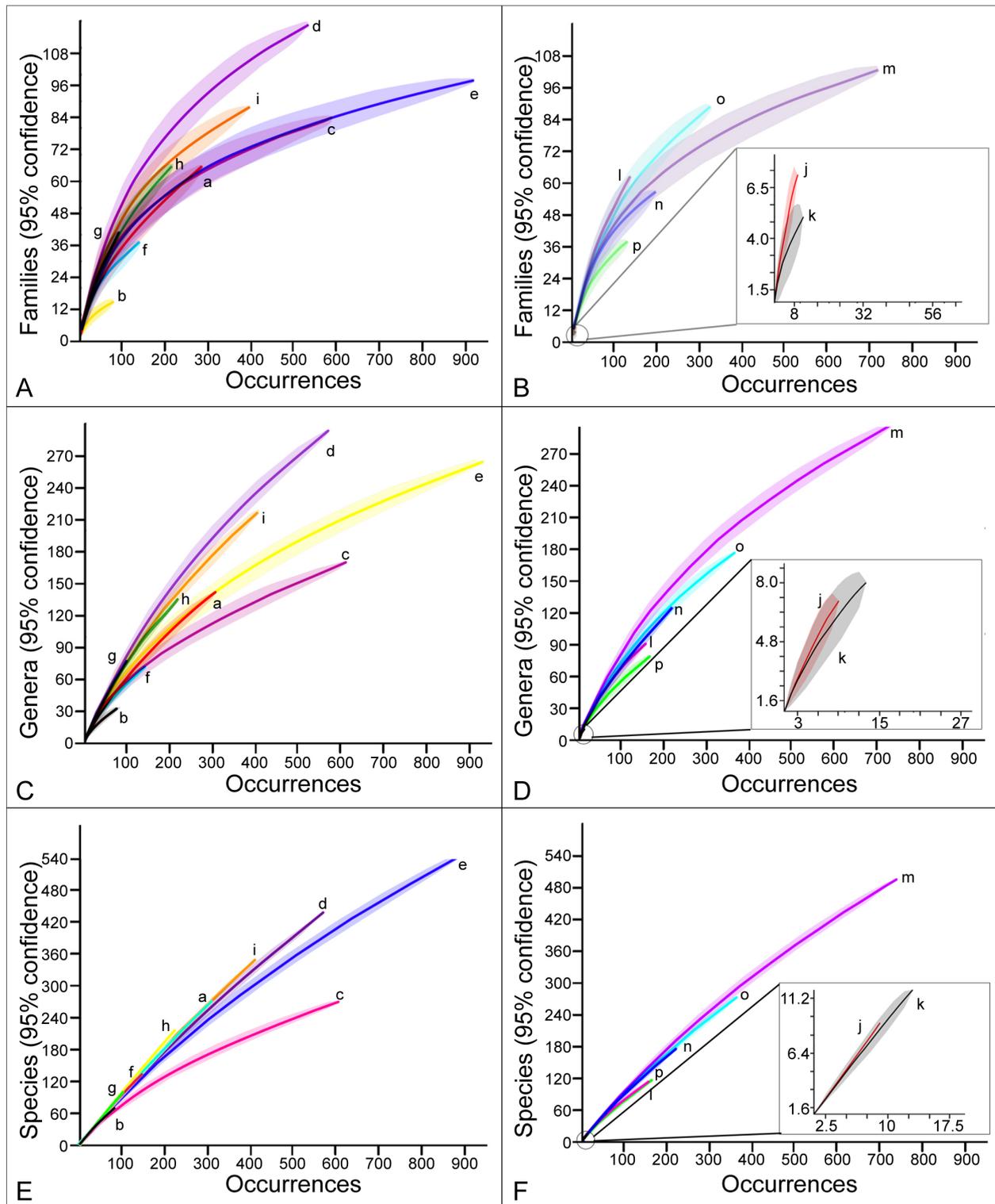
FIGURE 1. Comparative rarefaction curves for the 16-time bins based on analysis of the global occurrences. **A** and **B** at the family level. **C** and **D** at the genus level. **E** and **F** at the species level. a, Asselian; b, Sakmarian; c, Artinskian; d, Kungurian; e, Roadian; f, Wordian; g, Capitanian; h, Wuchiapingian; i, Changhsingian; j, Induan; k, Olenekian; l, Anisian; m, Ladinian; n, Carnian; o, Norian; p, Rhaetian.

and Triassic, with sampling quality context on the global dataset, to provide new insights on mapping the evolution pattern of insect during the transition from the Paleozoic to the Mesozoic era.

Material and methods

Database
To analyze the insect diversity during the Paleozoic-

Mesozoic transition, fossil occurrences were collected from the Permian to the Triassic thoroughly. The raw data were downloaded from the Paleobiology Database (https://paleobiodb.org/#/) on January 7, 2022. Following three criteria, *i.e.*, (1) Indeterminate, unnamed taxa have been excluded, (2) multiple occurrences of the same taxa in a single collection are treated as a single occurrence, (3) collections with uncertain stratigraphic ranges are not included, only occurrences with explicit familial, generic, specific assignments are included in our dataset. A total of 5,110 occurrences derived from 301 collections in 816 literature sources were collected. In total, 3,569 species of 1,749 genera, belonging to 406 families of 40 orders are taken into numerical analyses (online supplementary Table S1).

Time bins
We binned the collected data into a series of 16 stage-level time intervals, averaging 6.1 Myr in time duration. These bins are, in sequential order, Asselian, Sakmarian, Artinskian, Kungurian, Roadian, Wordian, Capitanian, Wuchiapingian, Changhsingian, Induan, Olenekian, Anisian, Ladinian, Carnian, Norian and Rhaetian.

Subsampling method
The classic rarefaction is employed to evaluate sample sizes across our time bins. Rarefaction seeks to draw a fixed number of specimens per time interval, either directly or by adopting a proxy based on the number of taxa occurrences or fossil collections (Miller *et al*., 1996; Alroy *et al*., 2001). Rarefaction curves for all time bins are presented in Fig. 1. Diversity data are standardized by repeatedly subsampling from a randomly generated set until a quota of 79, 84, and 84 at the family, genus, and species level respectively (online supplementary Table S2), following the method introduced by Song *et al*. (2018). It worth to note that all the basic terms for further analyses, including taxonomic information, ages (stages) and locations, are all followed the raw records in PBDB. No significant re-elevations were done although there might be few stratigraphic and systematic issues.

Shareholder quorum subsampling (SQS, also known as coverage-based rarefaction) is a method to counter unequal sampling between intervals by randomly drawing from the pool of occurrences, samples and references until a certain quorum of frequency coverage is reached (Alroy, 2010a, b, c; Chao & Jost, 2012; Nowak *et al*., 2019). We generated SQS diversity curves by using a sampling quorum of 0.50 (to keep as many results as possible with as high a Q value as possible). At the family and genus level, we used SQS to account for large variations in the number of insect occurrences over time. However, data on the species level cannot be estimated for SQS subsampling due to insufficient sample size, so do the family subsampling in Induan as well as genus subsampling of Capitanian and Induan, leaving discontinuity in the presented curves (Fig. 1).

Results

Temporal raw diversity changes
The curves of family- (Fig. 2A) and genus-level (Fig. 2B) exhibit similar fates of insect diversity during the Permian and Triassic. The first diversity valley occurred (15 families and 33 genera) in Sakmarian, followed by a large rise from Artinskian (84 families, 169 genera) to Kungurian (119 families, 294 genera). Subsequently, a significant decline (37 families, 72 genera) was shown in Wordian, although a gradual increase occurred in the aftermath until to the peak (88 families, 18 genera) in Changhsingian. Extreme low diversity was found in the late Early Triassic: 5 families, 8 genera in Olenekian. Diversity rebounded in Anisian, then reached a peak (103 families and 299 genera) in Ladinian. During the Middle and Late Triassic, diversity recovered to the Permian level, although small decreases occurred in Carnian (57 families, 125 genera) and Rhaetian (38 families, 78 genera).

Subsampled contexts
Curves of both subsampled and SQS richness of family (Fig. 2A) and genus levels (Fig. 2B) show similar trends with raw records but smaller perturbation amplitude. Furthermore, species richness (Fig. 2C) trends appear to broadly follow genus-level changing pattern but to the Middle Permian: the species-level diversity decreased from Roadian to Capitanian, rather the drop from Kungurian to Wordian in higher taxa level (Fig. 2C). In addition, contrasting to the increased family and genus-level richness, the species-level subsampled diversity (Fig. 2C) decreased in Wordian and Capitanian.

Discussion

The evolutionary history of insect diversity could be significantly biased by the incomplete fossil records (Shcherbakov, 2008; Schachat & Labandeira, 2021). Béthoux *et al*. (2005) noted that fossil insect records of Permian were not adequate enough to use raw taxonomic richness to represent the diversity. In this study, both the subsampling curves and SQS curves show similar trends with the raw richness at familial and generic levels (Fig. 2). Meanwhile, the rarefaction analyses show that the familial and generic leveled samplings are much more sufficient compared to the species level (Fig. 1).
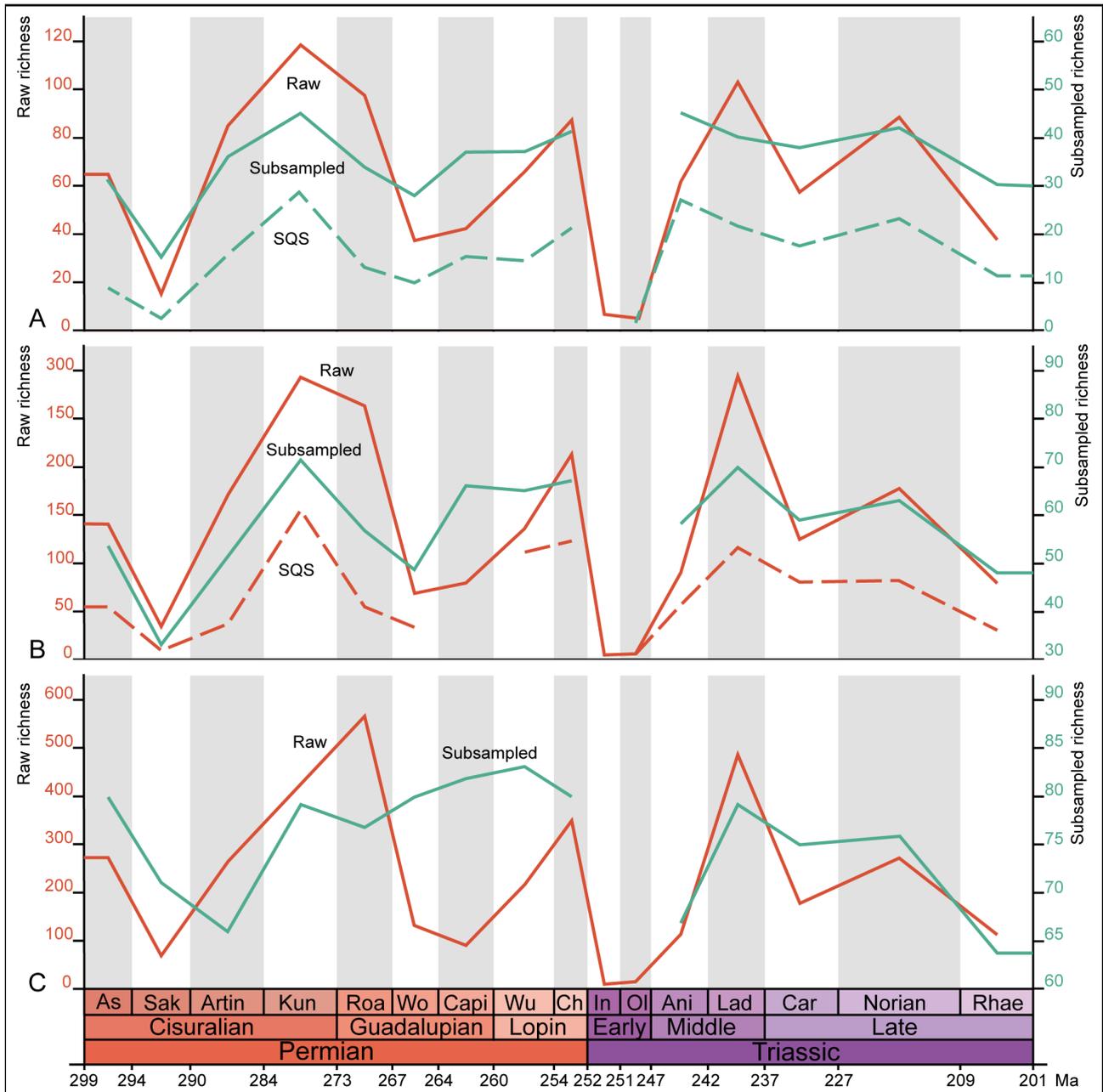
FIGURE 2. Diversity curves of the Permian and Triassic insects. **A**, Counts of all insect families in the full data set (solid red line), estimated counts using the subsampled data (solid green line, data are standardized by repeatedly subsampling from a randomly generated set until a quota of 79 occurrences has been recovered in each bin) and estimated counts using the SQS (dashed green line). **B**, Counts of all insect genera in the full data set (solid red line), estimated counts using the subsampled data (solid green line, data are standardized by repeatedly subsampling from a randomly generated set until a quota of 84 occurrences has been recovered in each bin) and estimated counts using the SQS (dashed red line). **C**, Counts of all insect species in the full data set (solid red line) and estimated counts using the subsampled data (solid green line, data are standardized by repeatedly subsampling from a randomly generated set until a quota of 84 occurrences has been recovered in each bin). As=Asselian; Sak=Sakmarian; Artin=Artinskian; Kun=Kungurian; Roa=Roadian; Wo=Wordian; Capi=Capitanian; Wu=Wuchiapingian; Ch=Changhsingian; In=Induan; Ol=Olenekian; Ani=Anisian; Lad=Ladinian; Car=Carnian; Rhae=Rhaetian. Note: the scales match the curves by color. It worth to note that the subsampled and SQS curves are discontinuous for the extremely small sample size in Early Triassic (Induan and Olenekian) and Capitanian.

Indeed, the low insect diversity in the Early Triassic could be a consequence of lack of specimens (Labandeira & Sepkoski, 1993), there were only less than 30 Early Triassic insect occurrences collected, obviously lower

than the hundreds of occurrences in other time intervals (online supplementary Tabel S1). Indeed, the very limited insect fossils found in the aftermath of the Permo-Triassic extinction would be a hindrance to further study on this mass extinction event (Montagna *et al*., 2019), but the relative long-termed evolutionary analyses are less impacted by the higher sufficient sampling in higher taxonomic levels (Fig. 1).

Our results show that 76.9% of families (65→15), 76.8% of genera (143→33) and 74.1% of species (274→71) decreases occurred from Asselian to Sakmarian (Fig. 2A). This Early Permian insect diversity drop was shown Labandeira & Sepkoski (1993), whereas the diversity curves of few studies (Jarzembowski, 1996; Ponomarenko, 2006; Shcherbakov, 2008) showed continuously increasing from the late Carboniferous to Middle Permian (Fig. 3B, C). In Clapham *et al*. (2016), the insect diversity declined by over 23% from the end-Carboniferous to Sakmarian (Fig. 3C). Moreover, the fauna composition also turned over by this crisis: over 10 orders disappeared whilst Dictyoptera and Palaeodictyoptera raised to be major components.

Our diversity curves show that 68.9% of families (119→37), 75.5% of genera (294→72) and 82.5% of species (565→99) disappeared during the Middle Permian (Fig. 2), basically coinciding with the subsampled family richness drop (about 33% of family extinction) from Kungurian to Wordian in Clapham *et al*. (2016), although the Middle Permian extinction was not recognized in many previous works (Ponomarenko, 2006; Labandeira & Sepkoski, 1993; Labandeira, 2005). In earlier records (Fig. 3B, C), the familial diversity declined from the latest Early Permian or Middle Permian, persisting to the Early Triassic (Labandeira & Sepkoski, 1993; Labandeira, 2005; Shcherbakov, 2008). This was identified as a pre-phase of the Permo-Triassic mass extinction or/and consequence of biased sampling (Labandeira, 2005). In our rarefaction and subsampled analyses, no significant sampling bias is shown in the late Early Permian to Late Permian (Figs 1, 2), supporting this Middle Permian crisis of insect to be a separate extinction, corresponding to the mass extinction of marine organisms and land tetrapods (Bond *et al*., 2010).

From the latest Permian to Early Triassic, Labandeira & Sepkoski's (1993) (Fig. 3B) familial diversity of insects showed about 50% of families potentially disappeared. Jarzembowski's (1996) figures revealed that 18% of orders and 58% of families disappeared from Late Permian to Early Triassic, with an obvious diversity decline at the species level (about 45%). Shcherbakov (2008) (Fig. 3C) noted that during the end-Permian and Induan, 40% of insect families became extinct. This was accepted by the further analysis by Clapham *et al*. (2016), in which SQS was conducted (Fig. 3C). In Condamine *et al*.'s (2016)

research, during the Permian-Triassic transition, the net diversification rate of insects reached its lowest level in the Phanerozoic.

On the contrary, some studies show that there was a decrease in insect diversity during the Late Permian, but they argue that it may not have constituted a catastrophic extinction event: the actual impact was much milder since the background extinction rates were persisting high in deep times (Ponomarenko, 2008; Aristov *et al*., 2013; Ponomarenko, 2016). Nevertheless, many more studies suggest that the Permo-Triassic extinction was there, impacting the macroevolution of marine invertebrates and insects (*e.g*., Signor & Lipps, 1982; Labandeira, 2005; Condamine, 2016; Nel *et al*., 2018). Our results indicate that 92% of families of the latest Permian (88→7) disappeared in the Early Triassic, including 40.9% that went extinct forever. Furthermore, fauna composition also was altered by this event: Schachat & Labandeira (2021) stated that insect assemblages dominated by Hemiptera and Mecoptera prevailed during the Early Triassic. Our results show that the Middle Triassic fauna, characterized by the dominance of Hemiptera, Orthoptera, Coleoptera, and Diptera, replaced the Permian fauna which was mainly composed of Hemiptera, Mecoptera, and the polyneopteran taxa currently put together in set of Eoblattida, although the dominating components were the cosmopolitan Coleoptera and Reculida in Early Triassic temporally (online supplementary Table S2).

In addition, we propose that there were insect extinctions both in Carnian and Rhaetian, as many other terrestrial and marine animals suffered. Our results show that 44.7% of families (103→57), 58.2% of genera (299→125), 64.5% of species (498→177), and 57.3% of families (89→38), 55.7% of genera (176→78), 57.3% of species (274→117) disappeared in Carnian and Rhaetian, respectively. These two diversity crises had been shown in Clapham's curves (Fig. 3C), although his subsampled familial decreases (~25%, Clapham *et al*., 2016) were much lower than our results. These two events were not recognized in earlier studies, as many of them show continuous diversity decline from the Middle Triassic to the Late Triassic (Labandeira & Sepkoski 1993; Labandeira 2005; Shcherbakov 2008). This might be similar to the known none-insect fossil records: "more than one event in the late Triassic mass extinction", as entitled by Benton (1986).

In the modern biosphere, insects are much more abundant and diversified in the warm and humid low latitudes (McKenna & Farrell, 2006; Novotny *et al*., 2006; Economo *et al*., 2018; Fattorini, 2022). Similarly, the temperature might have played a key role in the insect diversity changes during the Permian and Triassic (Fig. 3A). A slight and brief cooling occurred from Asselian to Sakmarian, associating with the first diversity crisis
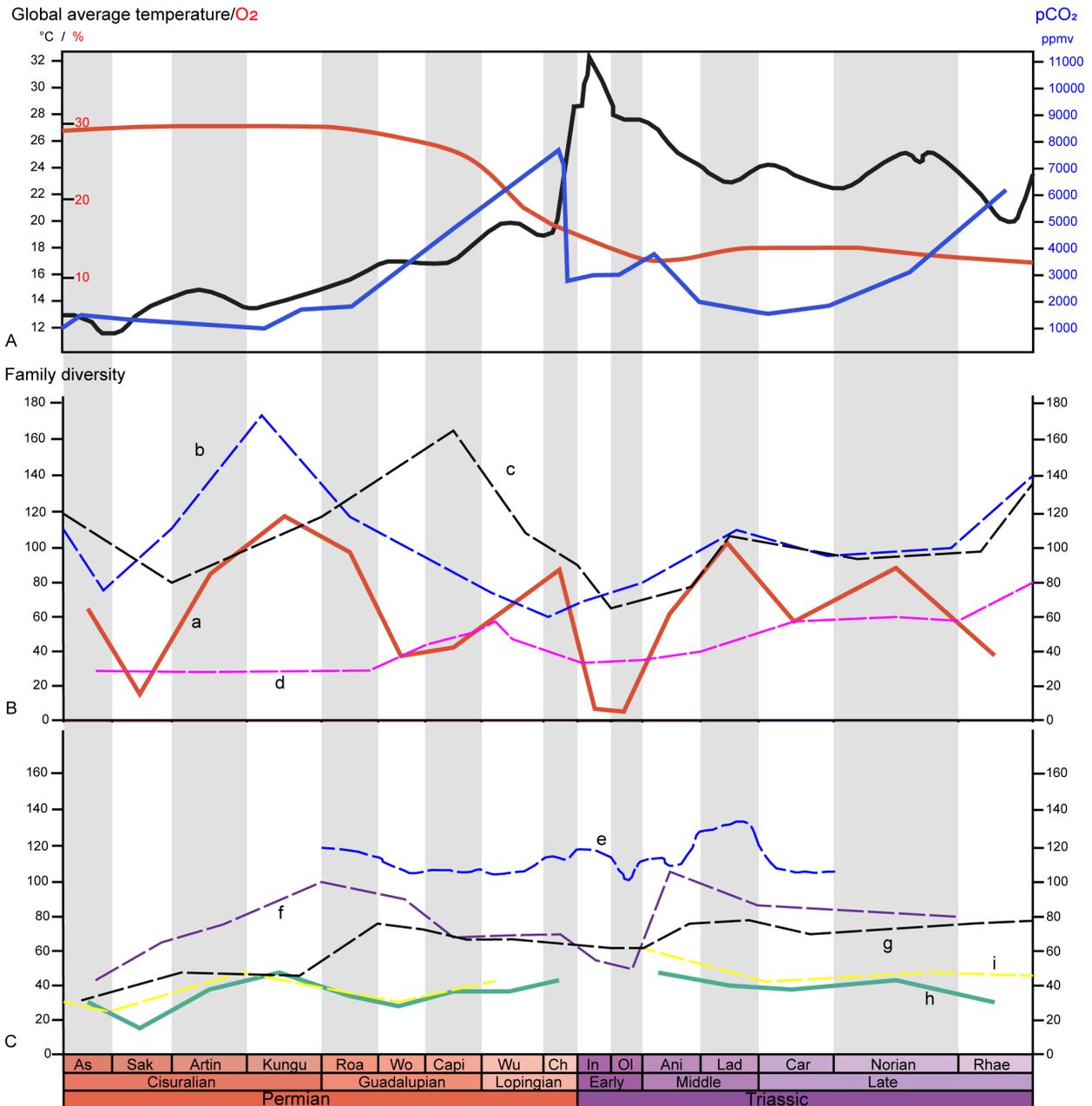
FIGURE 3. Environmental proxies and known insect diversity curves of Permian and Triassic. **A**, Global Average Temperature, O₂ content and *p*CO₂ during Permian and Triassic: the red line is the curve of O₂ content (Uhl *et al*., 2008); the black line is the Paleotemperature (Scotese *et al*., 2021); the blue line is the curve of *p*CO₂ (Retallack, 2013). In the diagrams **B** and **C**, a: red line stands for the diversity curve of insect at family level in this study; b: blue dashed line is the family-level insect diversity by Labandeira (2005); c: black dashed line is the family-level diversity in Labandeira & Sepkoski (1993); d: pink dashed line is the family-level insect diversity by Ponomarenko (2008); e: blue dashed line is family-level insect diversity by Jouault *et al*. (2022); f: purple dashed line is the family-level diversity in Shcherbakov (2008); g: black dashed line is family-level insect diversity by Ponomarenko (2016); h: green line is the diversity curve of insect at the family level using the subsampled data in this study; i: yellow dashed line is the subsampled family richness of all insects by Clapham *et al*. (2016).

we identified in this study, while a 5°C global averaged temperature decline occurred from late- Norian to middle- Rhaetian in association with the diversity drop in Rhaetian (Fig. 3). Controversially, the severe insect extinction in the Permo-Triassic transition and persisting low diversity

in Early Triassic were accompanied by the rapid warming (Fig. 3). Although the greenhouse had been hypothesized as a major environmental factor to the Permo-Triassic mass extinction for decades (Benton & Twitchett, 2003; Sun *et al*., 2012), the significant O₂ decline in the end-Permian

may also contribute to the massive insect diversity decline (Benton & Newell, 2014; Dal Corso *et al*., 2022).

Considering that plants play crucial role in insect evolution evolutions and fauna compositions (Nel *et al*., 2018) and the close relationship between insects and plants during Permo-Triassic has been evidenced by many fossil records and numerical analyses (Labandeira, 2006, 2013; Wappler *et al*., 2012, 2015; Pinheiro *et al*., 2016; Liu *et al*., 2020), the vegetation distribution and changing history may also contribute to the insect evolution during Permian and Triassic. The "coal gap" during the Early and early Middle Triassic indicates that vegetation was sparse or possibly absent during that time (Retallack *et al*., 1996, 2011). Xiong & Wang (2011) showed that plant diversity in South China persist decrease from the early Late Permian (Wuchiapingian) to the early Middle Triassic (Anisian). Although at the global scale, the taxa richness of plants might be not significantly reduced in the Permian-Triassic mass extinction, as Nowak *et al*. (2019) argued, the devegetation of low-high latitudes peatlands and forests did occur, showed by many recent studies from Sydney Basin, South China and North China (*e.g*., Vajda *et al*., 2020; Feng *et al*., 2020; Shu *et al*., 2023). The loss and recovery of the insect-favorable-habitats is highly possible key to the insect evolution in Permian and Triassic, impacting the diversity changes and feeding ecology adaptions (Nel *et al*., 2018; Jouault *et al*., 2022; Dal Corso *et al*., 2022).

Limitation: Although our results are in agreement with previous and recent works (*e.g*., Clapham *et al*., 2016; Jouault *et al*., 2022) by showing multiple biodiversity crises of Insecta during Permian and Triassic, there are some important issues limiting the quality of our results: 1) the families and genera are supposed to become extinct but for the vast majority and the phylogenetic analysis is yet done currently, invaliding corroborating the monophyly of their higher taxa and further study on fauna composition and their temporal changes. We attempted to rule out the fauna composition dynamics but failed to get any reliable results for the systematic issues on higher taxonomic levels. The lineage- and guild- based analyses proposed by Jouault *et al*. (2022) might be a practical solution; 2) only about 200 new Permo-Triassic insect records have been added into PDBD for the past 20 months (since we first download in January of 2022), which is far less than the latest new dataset collected in Jouault *et al*. (2022); 3) there seems to be "turning point" in most familiar and some generic rarefaction curves, the increasing trends are still obvious, yet reaching the stable horizontality for the sufficient sampling. Sampling issue is common in the numerical analyses of terrestrial fossils, including plants, tetrapods and insects. The plant diversity change during Permian and Triassic was potentially significant biased for the sampling issue (Nowak *et al*.,

2019), so does our results on Permian and Triassic insect fossils. Since terrestrial settings are the main habitats of most modern taxa (humankind inclusive), fossil data of tetrapods, plants and insects in deep time are to be further updated for deciphering the biotic responses to climatic and environmental changes, as lessons for the present and future.

References

Allen, B.J., Wignall, P.B., Hill, D.J., Saupe, E.E. & Dunhill, A.M. (2020) The latitudinal diversity gradient of tetrapods across the Permo-Triassic mass extinction and recovery interval. *Proceedings of the Royal Society B*, 287 (1929), 20201125. https://doi.org/10.1098/rspb.2020.1125

Alroy, J. (2010a) Geographic, environmental and intrinsic biotic controls on Phanerozoic marine diversification. *Palaeontology*, 53 (6), 1211–1235. https://doi.org/10.1111/j.1475-4983.2010.01011.x

Alroy, J. (2010b) The shifting balance of diversity among major marine animal groups. *Science*, 329 (5996), 1191–1194. https://doi.org/10.1126/science.1189910

Alroy, J. (2010c) Fair sampling of taxonomic richness and unbiased estimation of origination and extinction rates. *The Paleontological Society Papers*, 16, 55–80. https://doi.org/10.1017/S1089332600001819

Alroy, J., Marshall, C.R., Bambach, R.K., Bezusko, K., Foote, M., Fürsich, F.T., Hansen, T.A., Holland, S.M., Ivany, L.C., Jablonski, D., Jacobs, D.K., Jones, D.C., Kosnik, M.A., Lidgard, S., Low, S., Miller, A.I., Novack-Gottshall, P.M., Olszewski, T.D., Patzkowsky, M.E., Raup, D.M., Roy, K., Sepkoski, J.J., Jr., Sommers, M.G., Wagner, P.J. & Webber, A. (2001) Effects of sampling standardization on estimates of Phanerozoic marine diversification. *Proceedings of the National Academy of Sciences*, 98 (11), 6261–6266. https://doi.org/10.1073/pnas.111144698

Aristov, D.S., Bashkuev, A.S., Golubev, V.K., Gorochov, A.V., Karasev, E.V., Kopylov, D.S., Ponomarenko, A.G., Rasnitsyn, A.P., Rasnitsyn, D.A., Sinitshenkova, N.D., Sukatsheva, I.D. & Vassilenko, D.V. (2013) Fossil insects of the middle and

upper Permian of European Russia. *Paleontological Journal*, 47, 641–832.
https://doi.org/10.1134/S0031030113070010

Benton, M.J. (1986) More than one event in the late Triassic mass extinction. *Nature*, 321 (6073), 857–861.
https://doi.org/10.1038/321857a0

Benton, M.J. (2016) The Triassic. *Current Biology*, 26 (23), R1214–R1218.
https://doi.org/10.1016/j.cub.2016.10.060

Benton, M.J. (2018) Hyperthermal-driven mass extinctions: killing models during the Permian–Triassic mass extinction. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, 376 (2130), 20170076.
https://doi.org/10.1098/rsta.2017.0076

Benton, M.J. & Newell, A.J. (2014) Impacts of global warming on Permo-Triassic terrestrial ecosystems. *Gondwana Research*, 25 (4), 1308–1337.
https://doi.org/10.1016/j.gr.2012.12.010

Benton, M.J. & Twitchett, R.J. (2003) How to kill (almost) all life: the end-Permian extinction event. *Trends in Ecology & Evolution*, 18 (7), 358–365.
https://doi.org/10.1016/S0169-5347(03)00093-4

Béthoux, O., Papier, F. & Nel, A. (2005) The Triassic radiation of the entomofauna. *Comptes Rendus Palevol*, 4 (6–7), 609–621.
https://doi.org/10.1016/j.crpv.2005.06.005

Burgess S.D., Burgess, S.D. & Bowring, S.A. (2015) High-precision geochronology confirms voluminous magmatism before, during, and after Earth's most severe extinction. *Science Advances*, 1 (7), e1500470.
https://doi.org/10.1126/sciadv.1500470

Black, B.A., Hauri, E.H., Elkins-Tanton, L.T. & Brown, S.M. (2014) Sulfur isotopic evidence for sources of volatiles in Siberian Traps magmas. *Earth and Planetary Science Letters*, 394, 58–69.
https://doi.org/10.1016/j.epsl.2014.02.057

Bond, D.P., Hilton, J., Wignall, P.B., Ali, J.R., Stevens, L.G., Sun, Y.D. & Lai, X.L. (2010) The Middle Permian (Capitanian) mass extinction on land and in the oceans. *Earth-Science Reviews*, 102 (1–2), 100–116.
https://doi.org/10.1016/j.earscirev.2010.07.004

Bottjer, D.J., Clapham, M.E., Fraiser, M.L. & Powers, C.M. (2008) Understanding mechanisms for the end-Permian mass extinction and the protracted Early Triassic aftermath and recovery. *GSA Today*, 18 (9), 4.
https://doi.org/10.1130/GSATG8A.1

Burgess, S.D. & Bowring, S.A. (2015) High-precision geochronology confirms voluminous magmatism before, during, and after Earth's most severe extinction. *Science Advances*, 1 (7), e1500470.
https://doi.org/10.1126/sciadv.1500470

Chao, A. & Jost, L. (2012) Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather

than size. *Ecology*, 93 (12), 2533–2547.
https://doi.org/10.1890/11-1952.1

Clapham, M.E., Karr, J.A., Nicholson, D.B., Ross, A.J. & Mayhew, P.J. (2016) Ancient origin of high taxonomic richness among insects. *Proceedings of the Royal Society B: Biological Sciences*, 283 (1824), 20152476.
https://doi.org/10.1098/rspb.2015.2476

Condamine, F.L., Clapham, M.E. & Kergoat, G.J. (2016) Global patterns of insect diversification: towards a reconciliation of fossil and molecular evidence? *Scientific Reports*, 6 (1), 19208.
https://doi.org/10.1038/srep19208

Dal Corso, J., Song, H.J., Callegaro, S., Chu, D.L., Sun, Y.D., Hilton, J., Grasby, S.E., Joachimski, M.M. & Wignall, P.B. (2022) Environmental crises at the Permian–Triassic mass extinction. *Nature Reviews Earth & Environment*, 3 (3), 197–214.
https://doi.org/10.1038/s43017-021-00259-4

Economo, E.P., Narula, N., Friedman, N.R., Weiser, M.D. & Guénard, B. (2018) Macroecology and macroevolution of the latitudinal diversity gradient in ants. *Nature Communications*, 9 (1), 1778.
https://doi.org/10.1038/s41467-018-04218-4

Eggleton, P. (2020) The state of the world's insects. *Annual Review of Environment and Resources*, 45, 61–82.
https://doi.org/10.1146/annurev-environ-012420-050035

Fattorini, S. (2022) Global patterns of earwig species richness. *Diversity*, 14 (10), 890.
https://doi.org/10.3390/d14100890

Feng, Z., Wei, H.B., Guo, Y., He, X.Y., Sui, Q., Zhou, Y., Liu, H.Y., Gou, X.D. & Lü, Y. (2020) From rainforest to herbland: New insights into land plant responses to the end-Permian mass extinction. *Earth-Science Reviews*, 204, 103153.
https://doi.org/10.1016/j.earscirev.2020.103153

Fielding, C.R., Frank, T.D., McLoughlin, S., Vajda, V., Mays, C., Tevyaw, A.P., Winguth, A., Winguth, C., Nicoll, R.S., Bocking, M. & Crowley, J.L. (2019) Age and pattern of the southern high-latitude continental end-Permian extinction constrained by multiproxy analysis. *Nature Communications*, 10 (1), 385.
https://doi.org/10.1038/s41467-018-07934-z

Gastaldo, R.A. (2019) Ancient plants escaped the end-Permian mass extinction. *Nature*, 567, 38–39.
https://doi.org/10.1038/d41586-019-00744-3

Grimaldi, D., Engel, M.S., Engel, M.S. & Engel, M.S. (2005) *Evolution of the insects*. Cambridge University Press, Cambridge, 755 pp.

Jarzembowski, E.A. & Ross, A.J. (1996) Insect origination and extinction in the Phanerozoic. *Geological Society, London, Special Publications*, 102 (1), 65–78.
https://doi.org/10.1144/GSL.SP.1996.001.01.05

Jouault, C., Nel, A., Perrichot, V., Legendre, F. & Condamine, F.L. (2022) Multiple drivers and lineage-specific insect extinctions during the Permo–Triassic. *Nature Communications*, 13 (1), 7512.
https://doi.org/10.1038/s41467-022-35284-4

Kristensen, N.P. (1999) Phylogeny of Endopterygota insects, the most successful lineage of living organisms. *European Journal of Entomology*, 96 (3), 237–254.

Kusnezov, N. (1957) Numbers of species of ants in faunae of different latitudes. *Evolution*, 11 (3), 298–299.
https://doi.org/10.1111/j.1558-5646.1957.tb02898.x

Labandeira, C.C. (1997) Insect mouthparts: ascertaining the paleobiology of insect feeding strategies. *Annual Review of Ecology and Systematics*, 28 (1), 153–193.
https://doi.org/10.1146/annurev.ecolsys.28.1.153

Labandeira, C.C. (2005) The fossil record of insect extinction: new approaches and future directions. *American Entomologist*, 51 (1), 14–29.
https://doi.org/10.1093/ae/51.1.14

Labandeira, C.C. (2006) Silurian to Triassic plant and insect clades and their associations: new data, a review, and interpretations. *Arthropod Systematics & Phylogeny*, 64, 53–94.

Labandeira, C.C. (2013) A paleobiologic perspective on plant–insect interactions. *Current Opinion in Plant Biology*, 16 (4), 414–421.
https://doi.org/10.1016/j.pbi.2013.06.003

Labandeira, C.C. & Sepkoski Jr, J.J. (1993) Insect diversity in the fossil record. *Science*, 261 (5119), 310–315.
https://doi.org/10.1126/science.11536548

Liu, H.Y., Wei, H.B., Chen, J., Guo, Y., Zhou, Y., Gou, X.D., Yang, S.L., Labandeira, C. & Feng, Z. (2020) A latitudinal gradient of plant–insect interactions during the late Permian in terrestrial ecosystems? New evidence from Southwest China. *Global and Planetary Change*, 192, 103248.
https://doi.org/10.1016/j.gloplacha.2020.103248

Mayhew, P.J. (2007) Why are there so many insect species? Perspectives from fossils and phylogenies. *Biological Reviews*, 82 (3), 425–454.
https://doi.org/10.1111/j.1469-185X.2007.00018.x

McKenna, D.D. & Farrell, B.D. (2006) Tropical forests are both evolutionary cradles and museums of leaf beetle diversity. *Proceedings of the National Academy of Sciences*, 103 (29), 10947–10951.
https://doi.org/10.1073/pnas.0602712103

Miller, A.I. & Foote, M. (1996) Calibrating the Ordovician radiation of marine life: implications for Phanerozoic diversity trends. *Paleobiology*, 22 (2), 304–309.
https://doi.org/10.1017/S0094837300016237

Montagna, M., Tong, K.J., Magoga, G., Strada, L., Tintori, A., Ho, S.Y. & Lo, N. (2019) Recalibration of the insect evolutionary time scale using Monte San Giorgio fossils suggests survival of key lineages through the End-Permian Extinction. *Proceedings of the Royal Society B*, 286 (1912), 20191854.
https://doi.org/10.1098/rspb.2019.1854

Nel, P., Bertrand, S. & Nel, A. (2018) Diversification of insects since the Devonian: a new approach based on morphological disparity of mouthparts. *Scientific Reports*, 8 (1), 3516.
https://doi.org/10.1038/s41598-018-21938-1

Novotny, V., Drozd, P., Miller, S.E., Kulfan, M., Janda, M., Basset, Y. & Weiblen, G.D. (2006) Why are there so many species of herbivorous insects in tropical rainforests? *Science*, 313 (5790), 1115–1118.
https://doi.org/10.1126/science.1129237

Nowak, H., Schneebeli-Hermann, E. & Kustatscher, E. (2019) No mass extinction for land plants at the Permian–Triassic transition. *Nature Communications*, 10 (1), 384.
https://doi.org/10.1038/s41467-018-07945-w

Pinheiro, E.R., Iannuzzi, R. & Duarte, L.D. (2016) Insect herbivory fluctuations through geological time. *Ecology*, 97 (9), 2501–2510.
https://doi.org/10.1002/ecy.1476

Ponomarenko, A.G. (2006) Changes in terrestrial biota before the Permian-Triassic ecological crisis. *Paleontological Journal*, 40 (4), S468–S474.
https://doi.org/10.1134/S0031030106100066

Ponomarenko, A.G. (2016) Insects during the time around the Permian–Triassic crisis. *Paleontological Journal*, 50 (2), 174–186.
https://doi.org/10.1134/S0031030116020052

Retallack, G.J. (2013) Permian and Triassic greenhouse crises. *Gondwana Research*, 24 (1), 90–103.
https://doi.org/10.1016/j.gr.2012.03.003

Retallack, G.J., Sheldon, N.D., Carr, P.F., Fanning, M., Thompson, C.A., Williams, M.L., Jones, B.G. & Hutton, A. (2011) Multiple Early Triassic greenhouse crises impeded recovery from Late Permian mass extinction. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 308 (1–2), 233–251.
https://doi.org/10.1016/j.palaeo.2010.09.022

Retallack, G.J., Veevers, J.J. & Morante, R. (1996) Global coal gap between Permian–Triassic extinction and Middle Triassic recovery of peat-forming plants. *Geological Society of America Bulletin*, 108 (2), 195–207.
https://doi.org/10.1130/0016-7606(1996)108<0195:GCGBPT>2.3.CO;2

Romano, M., Bernardi, M., Petti, F.M., Rubidge, B., Hancox, J. & Benton, M.J. (2020) Early Triassic terrestrial tetrapod fauna: a review. *Earth-Science Reviews*, 210, 103331.
https://doi.org/10.1016/j.earscirev.2020.103331

Schachat, S.R. & Labandeira, C.C. (2015) Evolution of a complex behavior: the origin and initial diversification of foliar galling by Permian insects. *The Science of Nature*, 102, 1–8.
https://doi.org/10.1007/s00114-015-1266-7

Schachat, S.R. & Labandeira, C.C. (2021) Are insects heading toward their first mass extinction? Distinguishing turnover from crises in their fossil record. *Annals of the Entomological Society of America*, 114 (2), 99–118.
https://doi.org/10.1093/aesa/saaa042

Scotese, C.R., Song, H., Mills, B.J. & van der Meer, D.G. (2021) Phanerozoic paleotemperatures: The earth's changing climate during the last 540 million years. *Earth-Science Reviews*, 215, 103503.
https://doi.org/10.1016/j.earscirev.2021.103503

Sepkoski, J.J. (1984) A kinetic model of Phanerozoic taxonomic

diversity. III. Post-Paleozoic families and mass extinctions. *Paleobiology*, 10 (2), 246–267. https://doi.org/10.1017/S0094837300008186

Shu, W.C., Tong, J.N., Yu, J.X., Hilton, J., Benton, M.J., Shi, X., Diez, J.B., Wignall, P.B., Chu, D.L., Tian, L., Yi, Z.X. & Mao, Y.D. (2023) Permian-Middle Triassic flora succession in North China and implications for the great transition of continental ecosystems. *GSA Bulletin*, 135, 1747–1767. https://doi.org/10.1130/B36316.1

Signor, P.W. & Lipps, J.H. (1982) Sampling bias, gradual extinction patterns, and catastrophes in the fossil record. *In*: Silver, L.T. & Schultz, P.H. (Eds), *Geological implications of impacts of large asteroid and comets on the Earth*. Geological Society of America Press, Boulder, pp. 291–296. https://doi.org/10.1130/SPE190-p291

Shcherbakov, D.E. (2008) Insect recovery after the Permian/Triassic crisis. *Alavesia*, 2, 125–131.

Shcherbakov, D.Y. (1984) Systematics and phylogeny of Permian Cicadomorpha (Cimicada and Cicadina). *Paleontological Journal*, 18 (2), 87–97.

Song, H.J., Wignall, P.B., Chu, D.L., Tong, J.N., Sun, Y.D., Song, H.Y., He, W.H. & Tian, L. (2014) Anoxia/high temperature double whammy during the Permian-Triassic marine crisis and its aftermath. *Scientific Reports*, 4 (1), 4132. https://doi.org/10.1038/srep04132

Stork, N.E. (2018) How many species of insects and other terrestrial arthropods are there on Earth? *Annual Review of Entomology*, 63, 31–45. https://doi.org/10.1146/annurev-ento-020117-043348

Stork, N.E., McBroom, J., Gely, C. & Hamilton, A.J. (2015) New approaches narrow global species estimates for beetles, insects, and terrestrial arthropods. *Proceedings of the National Academy of Sciences*, 112 (24), 7519–7523. https://doi.org/10.1073/pnas.1502408112

Sun, Y.D., Joachimski, M.M., Wignall, P.B., Yan, C.B., Chen, Y.L., Jiang, H.S., Wang, L.N. & Lai, X.L. (2012) Lethally hot temperatures during the Early Triassic greenhouse. *Science*, 338 (6105), 366–370. https://doi.org/10.1126/science.1224126

Uhl, D., Jasper, A., Hamad, A.M.A. & Montenari, M. (2008) Permian and Triassic wildfires and atmospheric oxygen levels. *Ecosystems*, 9, 179–187.

Viglietti, P.A., Benson, R.B., Smith, R.M., Botha, J., Kammerer, C.F., Skosan, Z., Butler, E., Crean, A., Eloff, B., Kaal, S., Mohoi, J., Molehe, W., Mtalana, N., Mtungata, S., Ntheri, N., Ntsala, T., Nyaphuli, J., October, P., Skinner, G., Strong, M., Stummer, H., Wolvaardt, F.P. & Angielczyk, K.D. (2021) Evidence from South Africa for a protracted end-Permian extinction on land. *Proceedings of the National Academy of Sciences*, 118 (17), e2017045118. https://doi.org/10.1073/pnas.2017045118

Vajda, V., McLoughlin, S., Mays, C., Frank, T.D., Fielding, C.R., Tevywa, A., Lehsten, V., Bocking, M. & Nicoll, R.S. (2020) End-Permian (252 Mya) deforestation, wildfires and flooding-An ancient biotic crisis with lessons for the present. *Earth and Planetary Science Letter*, 529, 115875. https://doi.org/10.1016/j.epsl.2019.115875

Wappler, T., Kustatscher, E. & Dellantonio, E. (2015) Plant–insect interactions from Middle Triassic (late Ladinian) of Monte Agnello (Dolomites, N-Italy)—Initial pattern and response to abiotic environmental perturbations. *PeerJ*, 3, e921. https://doi.org/10.7717/peerj.921

Wappler, T., Labandeira, C.C., Rust, J., Frankenhäuser, H. & Wilde, V. (2012) Testing for the effects and consequences of mid Paleogene climate change on insect herbivory. *PLoS ONE*, 7 (7), e40744. https://doi.org/10.1371/journal.pone.0040744

Xiong, C.H. & Wang, Q. (2011) Permian–Triassic land-plant diversity in South China: Was there a mass extinction at the Permian/Triassic boundary? *Paleobiology*, 37 (1), 157–167. https://doi.org/10.1666/09029.1

All Supplementary materials are available at:
https://doi.org/10.11646/palaeoentomology.6.5.6

Supplementary materials:
Table S1 Dataset of the collected Permo-Triassic insect fossils
Table S2 Raw and subsampled taxa richness