Early evolution of beetles regulated by the end-Permian deforestation

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Abstract The end-Permian mass extinction (EPME) led to a severe terrestrial ecosystem collapse. However, the ecological response of insects—the most diverse group of organisms on Earth—to the EPME remains poorly understood. Here, we analyse beetle evolutionary history based on taxonomic diversity, morphological disparity, phylogeny, and ecological shifts from the Early Permian to Middle Triassic, using a comprehensive new dataset. Permian beetles were dominated by xylophagous stem groups with high diversity and disparity, which probably played an underappreciated role in the Permian carbon cycle. Our suite of analyses shows that Permian xylophagous beetles suffered a severe extinction during the EPME largely due to the collapse of forest ecosystems, resulting in an Early Triassic gap of xylophagous beetles. New xylophagous beetles appeared widely in the early Middle Triassic, which is consistent with the restoration of forest ecosystems. Our results highlight the ecological significance of insects in deep-time terrestrial ecosystems.

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Editor's evaluation

The study proposes a new evolutionary-ecological scenario for Late Paleozoic and early Mesozoic beetles, supported by the summary of all available knowledge about early beetle fossils, including analyses of their taxon and morphological diversity and phylogenetic relationships. The effects of xylophagous beetles during the Paleozoic may have played a fundamental role in global biochemical cycles. The results advance our understanding of the evolutionary success of beetles and the many ways in which large environmental changes may affect biodiversity in general.

Introduction

The end-Permian mass extinction (EPME; approximately 252 million years ago) was the most severe extinction event in the Phanerozoic (*Benton and Newell, 2014*). The EPME was primarily caused by the eruption of the Siberian flood basalts (*Burgess and Bowring, 2015*; *Fielding et al., 2019*), which generated excessive emissions of thermogenic methane, CO_2, and SO_2 that cascaded rapid global warming (*Wu et al., 2021*; *Black et al., 2018*), oceanic acidification and anoxia/euxinia (*Schobben et al., 2020*), aridification and other shifts in the hydrological cycle (*Sun et al., 2012*), acid rain (*Black et al., 2014*), wildfires (*Shen et al., 2011*), and ozone destruction (*Benca et al., 2018*). The response
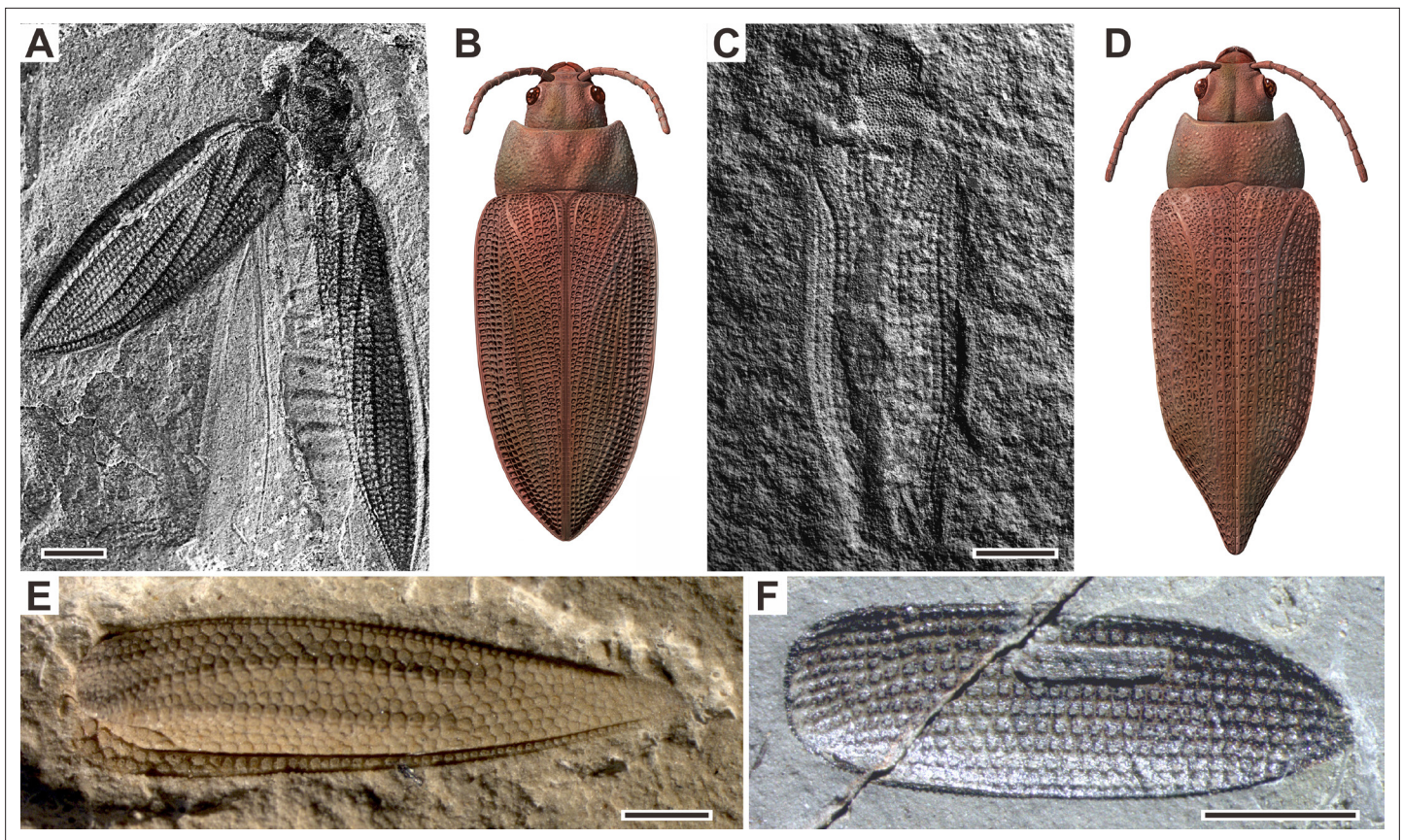
Figure 1. Examples of Permian beetles. (**A and B**) Tshekardocoleidae, *Moravocoleus permianus* Kukalová, 1969, photograph and reconstruction. (**C and D**) Permocupedinae, *Permocupes sojanensis* **Ponomarenko, 1969**, photograph and reconstruction. (**E**) Tshekardocoleidae, *Sylvacoleus richteri* Ponomarenko, 1963, elytra photograph. (**F**) Taldycupedinae, *Taldycupes reticulatus* **Ponomarenko, 1969**, elytra photograph. Scale bars represent 1 mm.

of terrestrial ecosystems to the EPME is quite heterogeneous, probably due to biotic, topographic, and latitudinal differences (*Fielding et al., 2019*; *Zhao et al., 2020*; *Dal Corso et al., 2020*). Moreover, how terrestrial ecosystems were affected during the EPME is still highly controversial (*Benton and Newell, 2014*; *Gastaldo, 2019*). Terrestrial tetrapods and plants are considered to have been severely affected by the EPME mostly based on diversity and taxonomic composition (*Benton and Newell, 2014*; *Viglietti et al., 2021*); however, such mass extinction was questioned by a more comprehensive dataset of plant macro- and microfossils (*Gastaldo, 2019*; *Nowak et al., 2019*). Similarly, Permian insects are thought to have suffered a significant extinction (*Labandeira and Sepkoski, 1993*; *Béthoux et al., 2005*; *Labandeira, 2005*; *Condamine et al., 2020*; *Condamine et al., 2016*), but this was not supported by other molecular phylogenetic and fossil record analyses (*Ponomarenko, 2016*; *Dmitriev et al., 2018*; *Montagna et al., 2019*; *Schachat et al., 2019*). In addition, the ecological response of insects to the EPME remains poorly understood (*Benton and Newell, 2014*; *Schachat et al., 2021*).

Beetles (Coleoptera) are the most speciose group of extant insects (*Stork, 2018*), with a stratigraphic range dating back to at least the lowest Permian (*Ponomarenko, 2016*; *Kirejtshuk et al., 2013*). They have a rich fossil record since the Permian and display a wide array of lifestyles (*Figure 1*; *Ponomarenko, 1969*; *Ponomarenko, 2003*). Their fossil record thus offers a unique and complementary perspective for studying the ecological response of insects to the EPME. The evolutionary history of Coleoptera has been widely investigated through molecular phylogenetic analyses (*Condamine et al., 2016*; *McKenna et al., 2019*; *Zhang et al., 2018*), morphological phylogenetic analyses (*Beutel et al., 2008*; *Beutel et al., 2019*), and fossil record analyses (*Ponomarenko, 2003*; *Ponomarenko, 2016*; *Smith and Marcot, 2015*). Although a long-term Palaeozoic-Mesozoic turnover of beetle assemblages is supported by almost all analyses, the detailed ecological response to the EPME and its explanatory mechanisms remain unclear. Most of the Permian and Triassic beetles

belong to stem groups (extinct suborders or families; *Figure 1*), and thus they show character combinations and evolutionary history that cannot be inferred or predicted from phylogenetic analysis of modern beetles. In particular, two problems were ignored by previous analyses. First, phylogenetic relationships of some key fossils remain poorly resolved, particularly in their evolutionary relationships to modern taxa. Second, there are two complementary taxonomic systems for Permian and Triassic beetles: one is artificial formal taxa (based on isolated elytra that cannot be definitely classified into any natural group), and the other is the natural taxonomy (commonly based on more complete fossils including bodies and elytra). The formal taxa, like trace fossil taxa, lack comprehensive phylogenetic data (*Ponomarenko, 2004*), and thus they cannot be used unreservedly for biodiversity and phylogenetic analyses, but can be helpful in the morphospace analysis. These issues cloud the temporal resolution of coleopteran biodiversity in deep time and complicate the evolutionary trajectory of beetles but can be overcome through a combination of multiple analytical methods. Therefore, taxonomic diversity, morphological disparity, and ecological shifts are best evaluated jointly to better understand how the EPME has shaped the evolutionary history of beetles.

Here, we compile an updated database of beetles from the Early Permian to Middle Triassic based on the taxonomic revision of fossils (including formal taxa). We analyse the evolution of taxonomic diversity, morphological disparity, and palaeoecological shifts of beetles from the Early Permian to Middle Triassic through phylogenetic and palaeoecological reconstructions and morphospace analyses of fossil material. Our results suggest that xylophagous (feeding on or in wood) beetles probably played a key and underappreciated role in the Permian carbon cycle and that the EPME had a profound ecological influence on beetle evolution. These results provide new insights into the ecological role of insects in deep-time terrestrial ecosystems and the ecological response of insects to deforestation and global warming.

Results

Taxonomic diversity

We compiled an updated database of beetles (21 families, 125 genera, and 299 species) from the Early Permian to Middle Triassic based on the taxonomic revision of natural and formal taxa (*Figure 2—source data 1*). Our database contains 18 families, 109 genera, and 220 species of natural taxa. There is a steady increase of families from the Early Permian to Middle Triassic, which is consistent with the result of *Smith and Marcot, 2015*, whose analyses were only conducted at the family level. The diversity of natural taxa displays almost the same trajectory at both species and genus levels (*Figure 2C and E*). The diversity is roughly stable in the Early Permian (Cisuralian), mainly represented by Tshekardocoleidae (*Figure 1*), increases rapidly in the Middle Permian (Guadalupian) and Late Permian (Lopingian), with the rise of the major clades Permocupedidae (Permocupedinae and Taldycupedinae) and Rhombocoleidae. Subsequently, it plunges in the Early Triassic and recovered gradually from the Anisian (early Middle Triassic). In the Ladinian (late Middle Triassic), the diversity clearly exceeds that of the Late Permian (*Figure 2C and E*). From the Middle Triassic, the Permian coleopteran assemblage characterized by Tshekardocoleidae, Permocupedidae, and Rhombocoleidae is completely replaced by a Triassic assemblage dominated by Cupedidae, Phoroschizidae and Triaplidae.

Our database also contains 3 families, 17 genera, and 79 species of formal taxa. A considerable proportion of Permian beetles belong to such taxa (Permosynidae, Schizocoleidae, and Asiocoleidae). These formal taxa mostly belong to stem groups, but some should probably be attributed to the two extant suborders Adephaga and Polyphaga. Both species and genus-level diversities of formal taxa show a gradual increase from the Middle to Late Permian, but decrease distinctly from the Triassic (*Figure 2—figure supplement 1*). The mixed taxa diversity (combining natural and formal taxa) displays the same trajectory to that of natural taxa at both species and genus levels (*Figure 2D and F*).

Phylogeny

We carried out a phylogenetic analysis based on 93 adult and larval characters across 15 natural taxa representing all natural families of Coleoptera from the Early Permian to Middle Triassic (*Figure 3—source data 1*). Our parsimony analysis result is consistent with a previous analysis (*Beutel et al., 2008*), and confirms that Tshekardocoleidae, Permocupedidae (Permocupedinae and Taldycupedinae), and Rhombocolediae are the stem group of Coleoptera (*Figure 3A*, *Figure 3—figure supplement 1*).
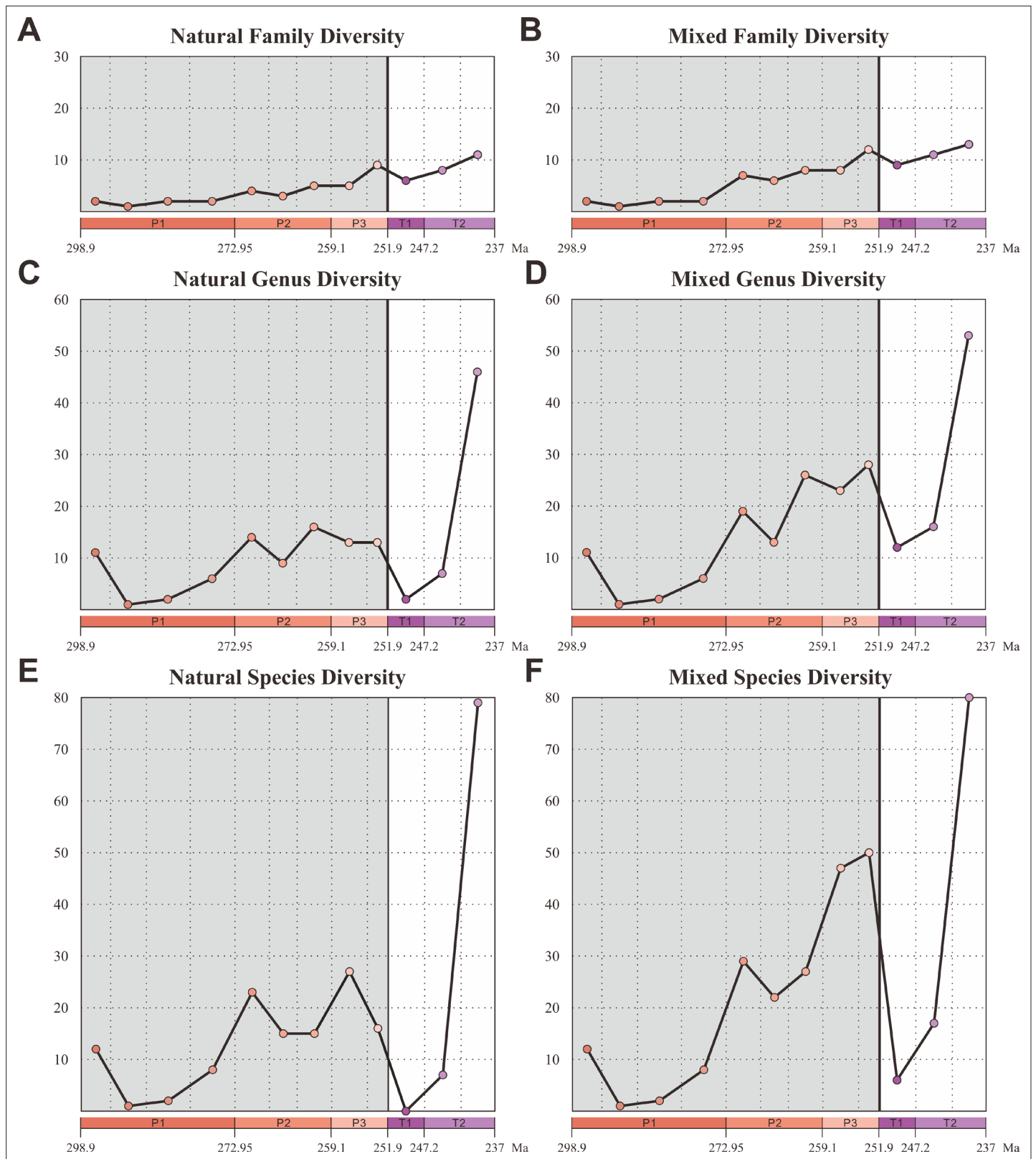
Figure 2. Diversity of Coleoptera from the Early Permian to Middle Triassic. Natural taxa and mixed taxa (natural taxa and formal taxa) are counted at family, genus, and species levels separately. (**A**) Family-level diversity of natural taxa. (**B**) Family-level diversity of mixed taxa. (**C**) Genus-level diversity of natural taxa. (**D**) Genus-level diversity of mixed taxa. (**E**) Species-level diversity of natural taxa. (**F**) Species-level diversity of mixed taxa. Abbreviations: P1, Early Permian; P2, Middle Permian; P3, Late Permian; T1, Early Triassic; T2, Middle Triassic.

Figure 2 continued on next page

Morphological disparity

We chose beetle elytra—hardened forewings primarily serving as protective covers for the hindwings and body underneath—to perform the morphological disparity analysis for three reasons: (1) elytra are the most commonly preserved fossils of Palaeozoic and Mesozoic beetles, and they are easily accessible in the literature and in online databases; (2) Permian and Triassic elytra display complex morphological structure (*Ponomarenko, 1969*); (3) elytra morphology has long been studied in relation to taxonomic diversity of living and extinct beetles (*Ponomarenko, 2004*; *Tong et al., 2021*).

We assembled two discrete character matrices (at species and genus levels) based on 35 characters of 197 genera and 346 species (including undetermined species and unnamed specimens) for morphological disparity analyses (*Figure 4—source data 1*). The taxa were ordinated into a multivariate morphospace using both principal coordinates analysis (PcoA) and non-metric multidimensional scaling (NMDS) with two distance metrics, including the generalized Euclidean distance (GED) and maximum observable rescale distance (MORD). We chose both sum of variance (sov) and product of variance (pov) as the proxy for morphological disparity due to their robustness in sample size (*Simões et al., 2020*). The use of discrete characters produces results that have non-metric properties, but this approach can be used to elucidate broad patterns of similarities and clustering within multidimensional space (*Lloyd, 2016*; *Deline et al., 2018*).

The patterns of morphospace occupation of beetles in different time-bins are shown in three-dimensional plots delimited by combinations of the first three axes of the PcoA and NMDS results
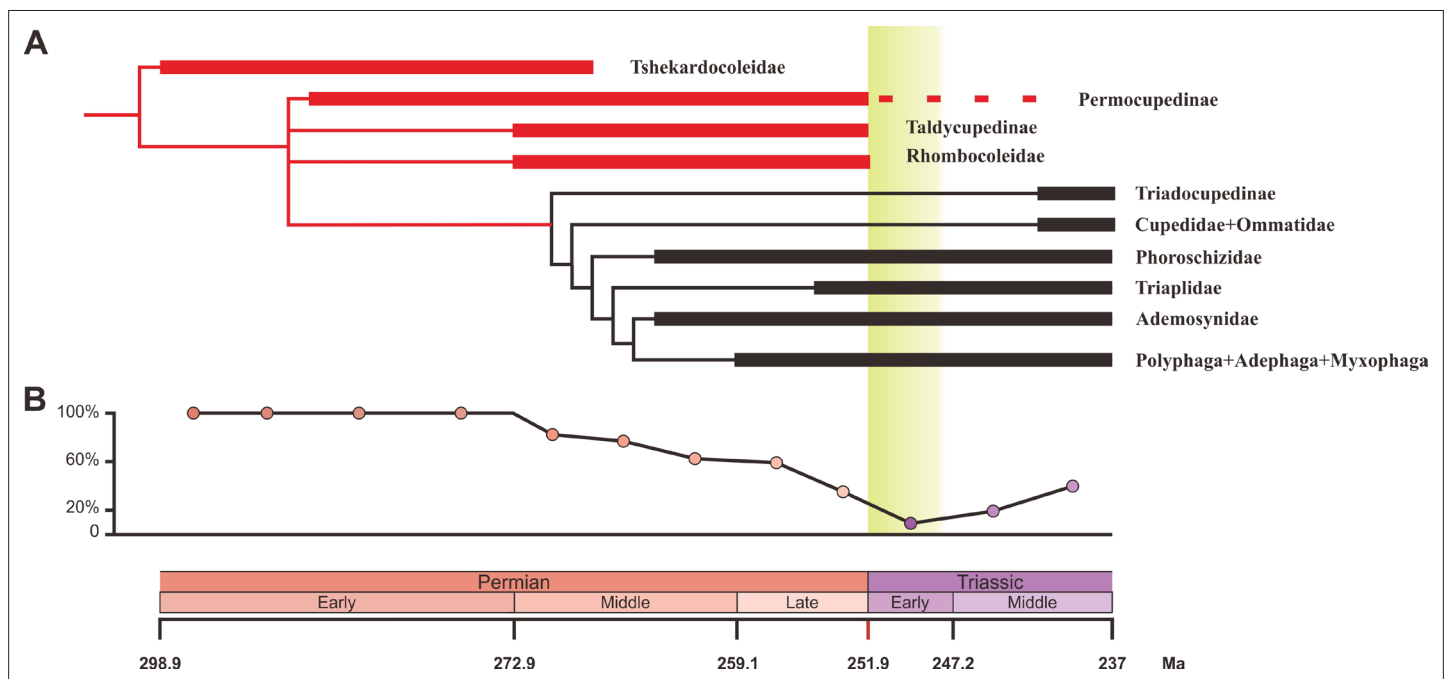

Figure 3. Ecological shifts of Coleoptera from the Early Permian to Middle Triassic. (**A**) Simplified phylogeny of Coleoptera from the Early Permian to Middle Triassic. Thick lines indicate the known extent of the fossil record. The branches representing stem groups are shown in red. The 'dead clade walking' pattern is symbolized by the dashed line. For details of the phylogenetic analysis, see *Figure 3—figure supplement 1*. (**B**) Genus percentage of xylophagous groups from the Early Permian to Middle Triassic. Yellow graded band represents the 'coal gap'.

The online version of this article includes the following figure supplement(s) for figure 3:

Source data 1. Character state matrix for the phylogenetic analysis.

Figure supplement 1. Strict consensus tree of three most parsimonious trees of Coleoptera.

based on MORD metrics (*Figure 4A*, *Figure 4—figure supplement 1*). The morphological disparity results of two ordination methods within the MORD and GED matrix shows the same trajectory at both genus and species levels. The evolutionary pattern of morphological disparity is robust in different disparity metrics. Disparity is low in the Early Permian, with a significant increase during the Middle Permian. It is roughly stable in the Middle and Late Permian, subsequently showing a distinct plunge in the Early Triassic, slightly recovering in the Middle Triassic but is still significantly lower than in the Middle and Late Permian (*Figure 4*, *Figure 4—figure supplements 1–8*).

Discussion

Our results demonstrate that beetles display a steady accumulation of taxonomic diversity throughout the Permian (*Figure 2*). The earliest definite beetles are Tshekardocoleidae (including the genus *Coleopsis*) from the Early Permian of Germany, Czech Republic, USA, and Russia (*Figure 1*), although the origin of Coleoptera is dated to the Carboniferous by molecular phylogenetic analysis (*McKenna et al., 2019*; *Zhang et al., 2018*; *Toussaint et al., 2016*). The coleopteran diversity radiation in the Middle Permian is consistent with an expansion of morphological disparity, corresponding to the appearance of multiveined, smooth, and striate elytra as well as some other patterns (*Figure 4*, *Figure 4—figure supplement 1*). Taxonomic diversity and morphological disparity were decoupled during the Late Permian when taxonomic diversity increased but morphological disparity was almost stable (*Figures 2 and 4*). The abrupt Middle Permian increase of coleopteran morphological disparity conforms to the early burst model of clade disparity commonly arising early in radiations (*Simões et al., 2020*; *Hughes et al., 2013*).

The Permian coleopteran assemblage was dominated by stem groups including Tshekardocoleidae, Permocupedidae (Permocupedinae and Taldycupedinae), and Rhombocoledidae in terms of richness and abundance. These ancient beetles were most likely xylophagous because they display a prognathous head, a characteristic elytral pattern with window punctures, a cuticular surface with tubercles (or scales), and a plesiomorphic pattern of ventral sclerites, very similar to the extant wood associated archostematans (*Figure 1*; *Kirejtshuk et al., 2013*; *Ponomarenko, 1969*). Moreover, Permian trace fossils showing wood boring provide convincing evidence for the xylophagous habit of these ancient beetles (*Naugolnykh and Ponomarenko, 2010*; *Feng et al., 2019*). Aquatic or semi-aquatic beetles including Phoroschizidae and Ademosynidae, belonging to the suborder Archostemata, first appeared in the Middle Permian and diversified in the Late Permian (*Ponomarenko, 2003*). The three other suborders of Coleoptera, comprising Polyphaga, Adephaga, and Myxophaga, most likely evolved by the Late Permian, but definite fossils are rare at this time.

Permian beetles probably played an important ecological role in forest ecosystems because most Permian beetles were most likely xylophagous insects that consumed living and dead woody stems (*Figure 3*). Some Permian xylophagous beetles fed on living wood tissues (*Feng et al., 2017*; *Feng et al., 2019*), which likely reduced tree productivity and could have caused extensive tree mortality. Insect-mediated tree mortality is known to result in large transfers of carbon from biomass to dead organic matter (*Seidl et al., 2018*; *Fei et al., 2019*). The other Permian xylophagous beetles were likely saproxylic (feeding on dead wood) (*Ponomarenko, 2003*), and they could also impact terrestrial carbon dynamics by accelerating wood decomposition (*Ulyshen, 2018*). Saproxylic animals first appeared in the Devonian and are mainly represented by small invertebrates such as oribatid mites, until the Permian (*Labandeira et al., 1997*; *Labandeira, 2007*). Whereas grazing by micro- and meso-invertebrates (nematodes, collembolans, enchytraeids and oribatid mites) did not significantly affect wood decomposition, consumption by macro-invertebrates (dominated by saproxylic beetles and termites in modern ecosystems) significantly sped up wood decomposition (*Tapanila and Roberts, 2012*). In addition to those that directly facilitated decomposition by consuming wood, Permian saproxylic beetles are likely to have had a variety of indirect effects on decomposition, including creating tunnels that facilitate the movement of fungi into wood (*Naugolnykh and Ponomarenko, 2010*; *Feng et al., 2017*), and vectoring fungi and other decay organisms on or within their bodies, like their extant counterparts (*Ulyshen, 2016*). In conclusion, Permian beetles that feed on living and dead wood probably could impact terrestrial carbon dynamics by reducing forests' carbon sequestration capacity, and by converting live materials to dead organic matter and subsequent decomposition.

The oxygen concentration of the atmosphere began to rise in the early Palaeozoic, probably with a peak in the Carboniferous and large decline from the beginning of the Permian (*Dahl et al.,*
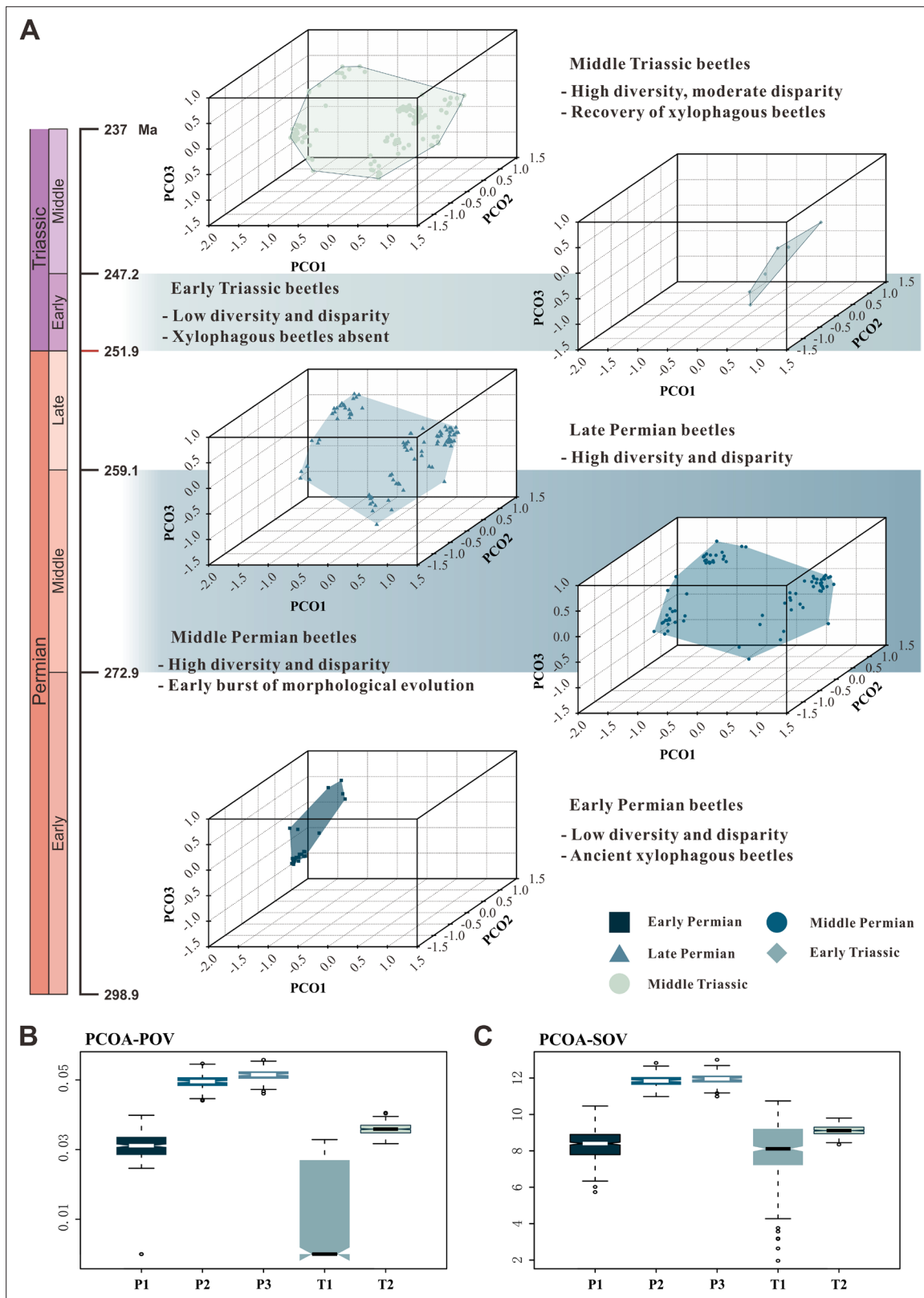
Figure 4. Morphospace comparisons of Coleoptera from the Early Permian to Middle Triassic. (**A**) Morphospace three-dimensional (3D) plot ordinated by principal coordinates analysis (PcoA), maximum observable rescale distance (MORD) matrices, based on species-level dataset. (**B and C**) Disparity comparisons ordinated by PcoA, MORD matrices, based on species-level dataset, proxy by pov and sov. Abbreviations: pov, product of variance; sov, sum of variance; P1, Early Permian; P2, Middle Permian; P3, Late Permian; T1, Early Triassic; T2, Middle Triassic.

Figure 4 continued on next page

Figure 4 continued

The online version of this article includes the following figure supplement(s) for figure 4:

Source data 1. Fossil character matrix for the morphospace analysis.

Source data 2. Result of permutation test for morphological disparity.

Figure supplement 1. Morphospace comparisons of Coleoptera from the Early Permian to Middle Triassic, maximum observable rescale distance (MORD) matrices, proxy by pov and sov.

Figure supplement 2. Morphospace comparisons of Coleoptera from the Early Permian to Middle Triassic, based on genus-level disparity analyses of generalized Euclidean distance (GED) matrices, proxy by pov and sov.

Figure supplement 3. Morphospace comparisons of Coleoptera from the Early Permian to Middle Triassic, based on species-level disparity analyses of generalized Euclidean distance (GED) matrices, proxy by pov and sov.

Figure supplement 4. Permutation tests with sample size corrected (maximum observable rescale distance [MORD]).

Figure supplement 5. Permutation tests with sample size corrected (generalized Euclidean distance [GED]).

Figure supplement 6. Disparity comparison and permutation tests with sample size corrected, under ordination method of principal coordinates analysis (PcoA), assuming that the age of the Grès à Voltzia specimens is Early Triassic.

Figure supplement 7. Disparity comparison and permutation tests with sample size corrected, under ordination method of non-metric multidimensional scaling (NMDS), assuming that the age of the Grès à Voltzia specimens is Early Triassic.

Figure supplement 8. Shepard 'goodness-of-fit' stress plot.

2010; *Berner, 2009*; *Krause et al., 2018*). The reason for this plunge was attributed to a tectonic- or climate-driven reduction in the extent of coal swamps (*Berner and Canfield, 1989*) or to the evolution of lignin-consuming fungi (*Floudas et al., 2012*). However, global recoverable coal is only equivalent to a few percent of the oxygen budget in the atmosphere, and thus cannot account for the large drop of atmospheric oxygen (*Nelsen et al., 2016*). Furthermore, lignin-consuming fungi may have been present before the Carboniferous (*Nelsen et al., 2016*). Recently, a new geochemical model proposed that the development of Permian terrestrial herbivores may have limited transport and long-term burial of terrestrial organic compounds in marine sediments, resulting in less organic carbon burial and attendant declines in atmospheric oxygen (*Laakso et al., 2020*). Herbivorous insects and amniotes are thought to be the major herbivorous animals during the Permian and thus are considered to be the most important drivers of the Permian change in biogeochemical cycles of carbon (*Laakso et al., 2020*). However, Permian herbivorous amniotes mainly fed on leaves, stems, roots, and rhizomes (*Sues and Reisz, 1998*; *Pearson et al., 2013*) and could normally digest cellulose by fermentation but could not consume lignin, as in extant herbivorous vertebrates (*Pearson et al., 2013*). The majority of terrestrial plant biomass is stored in forest woody tissue consisting of decay-resistant lignin (*Hibbett et al., 2016*; *Bar-On et al., 2018*). In modern forests, the total carbon stock in woody tissue (including living and dead wood) is approximately 340 Pg carbon, much more than 72 Pg carbon in roots (below ground), 43 Pg carbon in foliage, and 43 Pg carbon in litter (*Reich et al., 2014*; *Pan et al., 2011*). In extant forest ecosystems, insects may account for 29% of the total carbon flux from dead wood and thus they have a functional importance in the decomposition of dead wood and the carbon cycle (*Seibold et al., 2021*). During the Permian, beetles were probably the dominant consumers of woody tissue, while a few other insect groups may have sometimes fed on dead wood (such as stem dictyopterans and protelytropterans) (*Grimaldi and Engel, 2005*). Permian beetles had probably evolved close interactions with various microorganisms, especially lignin-consuming fungi (*Nelsen et al., 2016*), which also accelerated the decomposition of dead wood. The Early Permian onset of the decrease in oxygen concentrations is consistent with the origin and radiation of the xylophagous beetles in the fossil record. Therefore, we propose that Permian xylophagous beetles could have been responsible for at least part of the change in Permian biogeochemical cycles in Laakso's model (*Laakso et al., 2020*).

As the most taxonomically and functionally diverse group of living organisms on Earth (*Stork, 2018*), extant insects have significant effects on terrestrial carbon and nutrient cycling by modulating the quality and quantity of resources that enter the detrital food web (*Belovsky and Slade, 2000*; *Kurz et al., 2008*; *Yang and Gratton, 2014*; *Seibold et al., 2021*). However, the effects of insects on terrestrial ecosystems in deep time have been viewed as unimportant or overlooked (*Doughty, 2017*). Permian beetles were among the principal degraders of wood and played a fundamental role

in deep-time carbon and nutrient cycling and niche creation. Insects may have been one of the major regulating factors of forest ecosystems at least from the Permian.

Our results show that both the taxonomic diversity and morphological disparity dropped dramatically during the Early Triassic (*Figures 2 and 4*). Combined with the phylogenetic results (*Figure 3*), our suite of analyses yields a clear ecological signal from beetles across the Permian/Triassic boundary: all xylophagous stem-group beetles become extinct near the Permian-Triassic boundary or abruptly decreased in the Early Triassic (a pattern called 'dead clade walking'; *Barnes et al., 2021*), while aquatic phoroschizid and ademosynid lineages crossed the Permian/Triassic boundary and diversified in the Middle Triassic. Coleoptera recovered in taxonomic diversity during the Middle Triassic by the rise of new predatory and herbivorous groups, synchronized with the recovery of terrestrial ecosystems (*Zhao et al., 2020*). However, the morphological disparity is significantly lower than that of the Middle and Late Permian due to the lack of stem-group beetles that possess complex elytra structures (*Figure 4*, *Figure 4—figure supplement 1*). Polyphagan groups increased in taxonomic diversity during the Middle Triassic, which is a transitory epoch from a Palaeozoic stem-group beetle assemblage to a Mesozoic polyphagan-dominated assemblage.

Xylophagous groups are absent or rare in Early Triassic coleopteran assemblages, becoming widespread again from the Middle Triassic, mainly represented by more derived archostematans (such as Cupedidae) and polyphagans (*Ponomarenko, 2003*). This gap in xylophagous beetles coincided chronologically with the gap in coal deposition ('coal gap'), a time during which peat-forming forests were rare or absent (*Figure 3B*), extending across at least the entire Early Triassic (*Benton and Newell, 2014*; *Retallack et al., 1996*; *Nowak et al., 2020*; *Zhao et al., 2020*). During the latest Permian and earliest Triassic, gymnosperm-dominated forests abruptly collapsed (*Vajda et al., 2020*) and were replaced by other biomes (such as isoetalean-dominated herbaceous heathlands; *Feng et al., 2020*) in most areas due to extreme conditions including aridity (*Sun et al., 2012*), wildfires (*Shen et al., 2011*), and ozone destruction (*Benca et al., 2018*). In some regions, the plant extinction was less severe, or the recovery was rapid (*Hochuli et al., 2010*), or there may have been multiple crises during the Early Triassic (*Schneebeli-Hermann et al., 2017*), but even short-term ecosystem disruption could have led to extinctions among xylophagous beetles. Previous studies have not provided a clear picture of insect evolution in response to possible environmental stresses, nor of their response to the EPME (*Benton and Newell, 2014*). Our results show for the first time that the demise of most forests (deforestation event; *Vajda et al., 2020*) most likely resulted in the extinction of most Palaeozoic xylophagous beetles, analogous to the extinction of tree-dwelling birds and mammals resulting from end-Cretaceous deforestation (*Field et al., 2018*; *Hughes et al., 2021*).

Our results reveal an Early Triassic gap in xylophagous beetles, suggesting that early archaic beetles experienced the severe ecological consequences of end-Permian deforestation. Extant insects are suffering from dramatic declines in abundance and diversity largely due to the anthropogenic deforestation and global warming (*van Klink et al., 2020*; *Wagner et al., 2021*). However, xylophagous insects have been largely neglected in studies of the current extinction crisis (*van Klink et al., 2020*). In particular, the diversity and abundance of xylophagous beetles are extremely sensitive to climate change and can also entail forest collapse and carbon cycle disturbance (*Kurz et al., 2008*; *Fei et al., 2019*; *Šamonil et al., 2020*). Our findings may help to better understand future changes in insect diversity and abundance and its consequences faced with global environmental change.

Materials and methods
Diversity analysis
We compiled an updated database of all coleopteran species from the Early Permian to Middle Triassic from published literature in the early 1800s through to early 2020. In addition, we incorporated data from other open access database projects, including the Fossil Insect Database (EDNA) and Paleobiology Database (PBDB). We re-examined all published occurrences and taxonomy of Coleoptera from the Early Permian to Middle Triassic (*Figure 2—source data 1*). We standardized and corrected for nomenclatural consistency of all taxa using a classification of extinct beetle taxa above the genus rank (*Bouchard et al., 2011*). The data were filtered and cleaned by removing or reassigning illegitimate, questionable, and synonymous taxa and converting local to global chronostratigraphic units (*Supplementary file 1*).

We allocated fossil species into 12 stage-level time-bins covering the Early Permian-Middle Triassic interval (from the Asselian to Ladinian, 298–237 Ma). Considering the short duration of the Induan and Olenekian stages, we combined both stages into one time-bin. The formal taxa were erected based only on isolated elytra that cannot be classified definitely into any natural group. Thus, we separately counted the diversity of natural, formal, and mixed groups (*Figure 2*, *Figure 2—figure supplement 1*). The species *Coleopsis archaica* was attributed to Tschekardocoleidae by *Kirejtshuk et al., 2013*, but was later elevated to a new family Coleopseidae by *Kirejtshuk, 2020*. We followed the former opinion because it is premature to erect a family without a detailed cladistic analysis. We determined the stratigraphical ranges of families, genera, and species as the maximum and minimum ages in stage-level time-bins. All diversity was calculated using the range-through method.

Phylogenetic analysis

In light of the new taxa and characters available for further testing the phylogenetic status of ancient stem-group beetles, we reconstructed the phylogenetic relationships among the stem groups by incorporating the presently described new taxa and revised characters coding into the previous dataset (*Beutel et al., 2008*). The morphological characters used for phylogenetic analysis comprise 93 adult and larval characters (*Figure 3—source data 1*). Unknown characters were coded as '?'. The taxon sampling contains two megalopterans as outgroups (*Sialis* and *Chauliodes*) and 13 coleopteran ingroup taxa (five extant and eight extinct) representing all four coleopteran extant suborders and their stem groups (*Supplementary file 2*). Compared to previous character matrices, we added the subfamily Taldycupedinae and three new characters (*Supplementary file 3*). The matrix was analysed in TNT version 1.1, through parsimony analysis and using traditional search (*Goloboff et al., 2008*). All characters were equally weighed and unordered (1000 replicates and 1000 trees saved per replication). Bootstrap values, consistency index, and retention index were provided (*Figure 3—figure supplement 1*).

Morphospace analysis

We performed morphospace analyses with our newly assembled discrete character matrices (*Figure 4—source data 1*; *Supplementary file 4*). The analyses were performed using the free software R. 4.0.4. Both the MORD matrix and GED matrix were calculated based on two discrete character matrices (*Lloyd, 2016*; *Wills, 1998*). Recent research has revealed that the GED matrix creates a systematic bias in cases with a high percentage of missing data, and the MORD matrix can provide greater fidelity under these circumstances (*Lloyd, 2016*; *Lehmann et al., 2019*). We then ordinated all taxa into a multivariate morphospace with both PcoA and NMDS.

For PcoA, we used the function 'ordinate cladistic matrix' in package 'Claddis' with a cailliez method to correct the negative eigenvalues (*Lloyd, 2016*). Two disparity matrices were used to evaluate the volume of the morphospace, including the sum and product of the variances (*Wills et al., 2016*). The product metrics was normalized by taking the nth root (n equals the number of axes used for calculating disparity metrics). We used the scores on all axes that together comprise 90 % of total variance to calculate those disparity metrics. We chose a permutation test (two-tailed) to test the null hypothesis of no difference between insect disparity of different time-bins. Each test run used 5000 replications. The test statistic was obtained by using the disparity metric of an older time-bin to minus that of a younger time-bin. If the proportion in the null distribution greater than the observed value of the test statistic is smaller than 0.025, the insect disparity of an older time-bin was considered significantly larger than that of a younger time-bin, and if the proportion was greater than 0.975, the insect disparity of a younger time-bin was considered significantly larger than that of an older time-bin (*Figure 4—source data 2*).

We also performed permutation tests with sample size corrected. For two design groups with different sample sizes, we first performed subsampling of the group with more samples to obtain equal sample sizes. Based on the newly obtained two groups with equal sample sizes, we calculated the observed value of the test statistic. Then we randomly permutated those species into different groups once and calculated a test statistic. We repeated this procedure (subsampling and permutation) 10,000 times and obtained a null distribution plus a group of observed values. We then calculated a set of proportions greater than the observed values in the null distribution. By analogy, if the median of the proportions is equal to or smaller than 0.025, the insect disparity of an older time-bin is

significantly larger than that of a younger time-bin. If the median proportion is considered significantly greater than 0.975, the insect disparity of a younger time-bin is larger than that of an older time-bin (*Figure 4—figure supplements 4–7*).

For NMDS, we used the function 'metaMDS' in package 'vegan' with the number of dimension settings to 3 (*Dixon, 2003*). Both non-metric fit and linear fit were very high (larger than 0.90; *Figure 4—figure supplements 4–7*) and the stresses were smaller than 0.2, which implies that the ordinations are relatively good. Then we repeated all the previous analyses with this NMDS morphospace and acquired a similar result. The two disparity metrics of each time-bin were calculated based on two different distance matrices and two different ordination methods (*Figure 4*, *Figure 4—figure supplements 1–5*). The distribution was simulated under 500 bootstraps. Thirty-one undetermined specimens from the Grès à Voltzia Formation (Lower/Middle Triassic boundary, France) were included in our database and their age was attributed to the early Middle Triassic in our analysis (*Figure 4*, *Figure 4—figure supplements 1–5*). Considering that the age of these specimens is controversial, we repeated all our analyses assuming that the age of these specimens is Early Triassic; the result is consistent with the previous one (*Figure 4—figure supplements 6 and 7*).

Additional information

Author contributions

Xianye Zhao, Data curation, Formal analysis, Investigation, Methodology, Software, Validation, Visualization, Writing - original draft, Writing - review and editing; Yilun Yu, Formal analysis, Investigation, Methodology, Software, Validation, Visualization, Writing - original draft, Writing - review and editing; Matthew E Clapham, Investigation, Validation, Writing - review and editing; Evgeny Yan, Investigation, Visualization, Writing - review and editing; Jun Chen, Formal analysis, Investigation, Methodology, Writing - review and editing; Edmund A Jarzembowski, Xiangdong Zhao, Investigation, Writing - review and editing; Bo Wang, Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing - original draft, Writing - review and editing

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Additional files

Supplementary files
- Supplementary file 1. Taxonomic revisions.
- Supplementary file 2. List of taxa used for the phylogenetic analysis.
- Supplementary file 3. Characters used for the phylogenetic analysis.
- Supplementary file 4. Characters used for the morphospace analysis.
- Transparent reporting form

Data availability
All source data are available at https://doi.org/10.5061/dryad.7m0cfxpvd. In addition, the source data files (Supplementary Data 1-4) have been provided for figures 2-4 and appendix figures 1-10.

The following dataset was generated:

Author(s)	Year	Dataset title	Dataset URL	Database and Identifier
Zhao X, Yu Y, Clapham M, Yan E, Chen J, Jarzembowski E, Zhao X, Wang B	2021	Dataset of Early evolution of beetles regulated by the end-Permian deforestation	https://doi.org/10.5061/dryad.7m0cfxpvd	Dryad Digital Repository, 10.5061/dryad.7m0cfxpvd

References

Bar-On YM, Phillips R, Milo R. 2018. The biomass distribution on Earth. *PNAS* **115**: 6506–6511. DOI: https://doi.org/10.1073/pnas.1711842115, PMID: 29784790

Barnes BD, Sclafani JA, Zaffos A. 2021. Dead clades walking are a pervasive macroevolutionary pattern. *PNAS* **118**: e2019208118. DOI: https://doi.org/10.1073/pnas.2019208118, PMID: 33827921

Belovsky GE, Slade JB. 2000. Insect herbivory accelerates nutrient cycling and increases plant production. *PNAS* **97**: 14412–14417. DOI: https://doi.org/10.1073/pnas.250483797, PMID: 11106378

Benca JP, Duijnstee IAP, Looy CV. 2018. UV-B-induced forest sterility: Implications of ozone shield failure in Earth's largest extinction. *Science Advances* **4**: e1700618. DOI: https://doi.org/10.1126/sciadv.1700618, PMID: 29441357

Benton MJ, Newell AJ. 2014. Impacts of global warming on Permo-Triassic terrestrial ecosystems. *Gondwana Research* **25**: 1308–1337. DOI: https://doi.org/10.1016/j.gr.2012.12.010

Berner RA, Canfield DE. 1989. A new model for atmospheric oxygen over Phanerozoic time. *American Journal of Science* **289**: 333–361. DOI: https://doi.org/10.2475/ajs.289.4.333, PMID: 11539776

Berner RA. 2009. Phanerozoic atmospheric oxygen: new results using the GEOCARBSULF model. *American Journal of Science* **309**: 603–606. DOI: https://doi.org/10.2475/07.2009.03

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

Beutel RG, Ge S, Hörnschemeyer T. 2008. On the head morphology of Tetraphalerus, the phylogeny of Archostemata and the basal branching events in Coleoptera. *Cladistics* **24**: 270–298. DOI: https://doi.org/10.1111/j.1096-0031.2007.00186.x

Beutel R.G, Pohl H, Yan EV, Anton E, Liu SP, Ślipiński A, McKenna DD, Friedrich F. 2019. The phylogeny of Coleopterida (Hexapoda) - morphological characters and molecular phylogenies. *Systematic Entomology* **44**: 75–102. DOI: https://doi.org/10.1111/syen.12316

Black B.A, Hauri EH, Elkins-Tanton LT, Brown SM. 2014. Sulfur isotopic evidence for sources of volatiles in Siberian Traps magmas. *Earth and Planetary Science Letters* **394**: 58–69. DOI: https://doi.org/10.1016/j.epsl.2014.02.057

Black BA, Neely RR, Lamarque J-F, Elkins-Tanton LT, Kiehl JT, Shields CA, Mills MJ, Bardeen C. 2018. Systemic swings in end-Permian climate from Siberian Traps carbon and sulfur outgassing. *Nature Geoscience* **11**: 949–954. DOI: https://doi.org/10.1038/s41561-018-0261-y

Bouchard P, Bousquet Y, Davies A, Alonso-Zarazaga M, Lawrence J, Lyal C, Newton A, Reid C, Schmitt M, Slipinski A, Smith A. 2011. Family-Group Names In Coleoptera (Insecta). *ZooKeys* **88**: 1–972. DOI: https://doi.org/10.3897/zookeys.88.807

Burgess SD, Bowring SA. 2015. High-precision geochronology confirms voluminous magmatism before, during, and after Earth's most severe extinction. *Science Advances* **1**: e1500470. DOI: https://doi.org/10.1126/sciadv.1500470, PMID: 26601239

Condamine FL, Clapham ME, Kergoat GJ. 2016. Global patterns of insect diversification: towards a reconciliation of fossil and molecular evidence? *Scientific Reports* **6**: 1–13. DOI: https://doi.org/10.1038/srep19208

Condamine FL, Nel A, Grandcolas P, Legendre F. 2020. Fossil and phylogenetic analyses reveal recurrent periods of diversification and extinction in dictyopteran insects. *Cladistics* **36**: 394–412. DOI: https://doi.org/10.1111/cla.12412, PMID: 34619806

Dahl TW, Hammarlund EU, Anbar AD, Bond DPG, Gill BC, Gordon GW, Knoll AH, Nielsen AT, Schovsbo NH, Canfield DE. 2010. Devonian rise in atmospheric oxygen correlated to the radiations of terrestrial plants and large predatory fish. *PNAS* **107**: 17911–17915. DOI: https://doi.org/10.1073/pnas.1011287107, PMID: 20884852

Dal Corso J, Mills BJW, Chu D, Newton RJ, Mather TA, Shu W, Wu Y, Tong J, Wignall PB. 2020. Permo-Triassic boundary carbon and mercury cycling linked to terrestrial ecosystem collapse. *Nature Communications* **11**: 2962. DOI: https://doi.org/10.1038/s41467-020-16725-4, PMID: 32528009

Deline B, Greenwood JM, Clark JW, Puttick MN, Peterson KJ, Donoghue PCJ. 2018. Evolution of metazoan morphological disparity. *PNAS* **115**: E8909–E8918. DOI: https://doi.org/10.1073/pnas.1810575115, PMID: 30181261

Dixon P. 2003. VEGAN, a package of R functions for community ecology. *Journal of Vegetation Science* **14**: 927–930. DOI: https://doi.org/10.1111/j.1654-1103.2003.tb02228.x

Dmitriev VYu, Aristov DS, Bashkuev AS, Vasilenko DV, Vřanský P, Gorochov AV, Lukashevitch ED, Mostovski MB, Ponomarenko AG, Popov YuA, Rasnitsyn AP, Sinitshenkova ND, Sukatsheva ID, Tarasenkova MM, Khramov AV, Shmakov AS. 2018. Insect diversity from the Carboniferous to Recent. *Paleontological Journal* **52**: 610–619. DOI: https://doi.org/10.1134/S0031030118060047

Doughty CE. 2017. Herbivores increase the global availability of nutrients over millions of years. *Nature Ecology & Evolution* **1**: 1820–1827. DOI: https://doi.org/10.1038/s41559-017-0341-1

Fei SL, Morin RS, Oswalt CM, Liebhold AM. 2019. Biomass losses resulting from insect and disease invasions in US forests. *PNAS* **116**: 17371–17376. DOI: https://doi.org/10.1073/pnas.1820601116, PMID: 31405977

Feng Z, Wang J, Rößler R, Ślipiński A, Labandeira C. 2017. Late Permian wood-borings reveal an intricate network of ecological relationships. *Nature Communications* **8**: 556. DOI: https://doi.org/10.1038/s41467-017-00696-0, PMID: 28916787

Feng Z, Bertling M, Noll R, Ślipiński A, Rößler R. 2019. Beetle borings in wood with host response in early Permian conifers from Germany. *PalZ* **93**: 409–421. DOI: https://doi.org/10.1007/s12542-019-00476-9

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

Field DJ, Bercovici A, Berv JS, Dunn R, Fastovsky DE, Lyson TR, Vajda V, Gauthier JA. 2018. Early evolution of modern birds structured by global forest collapse at the end-Cretaceous mass extinction. *Current Biology* **28**: 1825-1831.. DOI: https://doi.org/10.1016/j.cub.2018.04.062, PMID: 29804807

Fielding CR, Frank TD, McLoughlin S, Vajda V, Mays C, Tevyaw AP, Winguth A, Winguth C, Nicoll RS, Bocking M, Crowley JL. 2019. Age and pattern of the southern high-latitude continental end-Permian extinction constrained by multiproxy analysis. *Nature Communications* **10**: 385. DOI: https://doi.org/10.1038/s41467-018-07934-z, PMID: 30674880

Floudas D, Binder M, Riley R, Barry K, Blanchette RA, Henrissat B, Martínez AT, Otillar R, Spatafora JW, Yadav JS, Aerts A, Benoit I, Boyd A, Carlson A, Copeland A, Coutinho PM, de Vries RP, Ferreira P, Findley K, Foster B, et al. 2012. The Paleozoic origin of enzymatic lignin decomposition reconstructed from 31 fungal genomes. *Science* **336**: 1715–1719. DOI: https://doi.org/10.1126/science.1221748, PMID: 22745431

Gastaldo RA. 2019. Ancient plants escaped the end-Permian mass extinction. *Nature* **567**: 38–39. DOI: https://doi.org/10.1038/d41586-019-00744-3, PMID: 30824877

Goloboff PA, Farris JS, Nixon KC. 2008. TNT, a free program for phylogenetic analysis. *Cladistics* **24**: 774–786. DOI: https://doi.org/10.1111/j.1096-0031.2008.00217.x

Grimaldi D, Engel MS. 2005. Evolution of the Insects. Cambridge University Press.

Hibbett D, Blanchette R, Kenrick P, Mills B. 2016. Climate, decay, and the death of the coal forests. *Current Biology* **26**: R563–R567. DOI: https://doi.org/10.1016/j.cub.2016.01.014, PMID: 27404250

Hochuli PA, Hermann E, Vigran JO, Bucher H, Weissert H. 2010. Rapid demise and recovery of plant ecosystems across the end-Permian extinction event. *Global and Planetary Change* **74**: 144–155. DOI: https://doi.org/10.1016/j.gloplacha.2010.10.004

Hughes M, Gerber S, Wills MA. 2013. Clades reach highest morphological disparity early in their evolution. *PNAS* **110**: 13875–13879. DOI: https://doi.org/10.1073/pnas.1302642110, PMID: 23884651

Hughes JJ, Berv JS, Chester SGB, Sargis EJ, Field DJ. 2021. Ecological selectivity and the evolution of mammalian substrate preference across the K–Pg boundary. *Ecology and Evolution* **10**: 8114. DOI: https://doi.org/10.1002/ece3.8114

Kirejtshuk AG, Poschmann M, Prokop J, Garrouste R, Nel A. 2013. Evolution of the elytral venation and structural adaptations in the oldest Palaeozoic beetles (Insecta: Coleoptera: Tshekardocoleidae). *Journal of Systematic Palaeontology* **12**: 575–600. DOI: https://doi.org/10.1080/14772019.2013.821530

Kirejtshuk AG. 2020. Taxonomic review of fossil coleopterous families (Insecta, Coleoptera). Suborder Archostemata: superfamilies Coleopseoidea and Cupedoidea. *Geosciences* **10**: 73. DOI: https://doi.org/10.3390/geosciences10020073

Krause AJ, Mills BJW, Zhang S, Planavsky NJ, Lenton TM, Poulton SW. 2018. Stepwise oxygenation of the Paleozoic atmosphere. *Nature Communications* **9**: 4081. DOI: https://doi.org/10.1038/s41467-018-06383-y, PMID: 30287825

Kurz WA, Dymond CC, Stinson G, Rampley GJ, Neilson ET, Carroll AL, Ebata T, Safranyik L. 2008. Mountain pine beetle and forest carbon feedback to climate change. *Nature* **452**: 987–990. DOI: https://doi.org/10.1038/nature06777, PMID: 18432244

Laakso TA, Strauss JV, Peterson KJ. 2020. Herbivory and its effect on Phanerozoic oxygen concentrations. *Geology* **48**: 410–414. DOI: https://doi.org/10.1130/G47085.1

Labandeira CC, Sepkoski JJ. 1993. Insect diversity in the fossil record. *Science* **261**: 310–315. DOI: https://doi.org/10.1126/science.11536548, PMID: 11536548

Labandeira CC, Phillips TL, Norton RA. 1997. Oribatid mites and the decomposition of plant tissues in Paleozoic coal-swamp forests. *Palaios* **12**: 319. DOI: https://doi.org/10.2307/3515334

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

Labandeira CC. 2007. The origin of herbivory on land: initial patterns of plant tissue consumption by arthropods. *Sect Science* **14**: 259–275. DOI: https://doi.org/10.1111/j.1744-7917.2007.00152.x

Lehmann OER, Ezcurra MD, Butler RJ, Lloyd GT, Angielczyk K. 2019. Biases with the Generalized Euclidean Distance measure in disparity analyses with high levels of missing data. *Palaeontology* **62**: 837–849. DOI: https://doi.org/10.1111/pala.12430

Lloyd GT. 2016. Estimating morphological diversity and tempo with discrete character-taxon matrices: implementation, challenges, progress, and future directions. *Biological Journal of the Linnean Society* **118**: 131–151. DOI: https://doi.org/10.1111/bij.12746

McKenna DD, Shin S, Ahrens D, Balke M, Beza-Beza C, Clarke DJ, Donath A, Escalona HE, Friedrich F, Letsch H, Liu SL, Maddison D, Mayer C, Misof B, Murin PJ, Niehuis O, Peters RS, Podsiadlowski L, Pohl H, Scully ED, et al. 2019. The evolution and genomic basis of beetle diversity. *PNAS* **116**: 24729–24737. DOI: https://doi.org/10.1073/pnas.1909655116, PMID: 31740605

Montagna M, Tong KJ, Magoga G, Strada L, Tintori A, Ho SYW, 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. Biological Sciences* **286**: 20191854. DOI: https://doi.org/10.1098/rspb.2019.1854, PMID: 31594499

Naugolnykh SV, Ponomarenko AG. 2010. Possible traces of feeding by beetles in coniferophyte wood from the Kazanian of the Kama River Basin. *Paleontological Journal* **44**: 468–474. DOI: https://doi.org/10.1134/S0031030110040131

Nelsen MP, DiMichele WA, Peters SE, Boyce CK. 2016. Delayed fungal evolution did not cause the Paleozoic peak in coal production. *PNAS* **113**: 2442–2447. DOI: https://doi.org/10.1073/pnas.1517943113, PMID: 26787881

Nowak H, Schneebeli-Hermann E, Kustatscher E. 2019. No mass extinction for land plants at the Permian-Triassic transition. *Nature Communications* **10**: 384. DOI: https://doi.org/10.1038/s41467-018-07945-w, PMID: 30674875

Nowak H, Vérard C, Kustatscher E. 2020. Palaeophytogeographical Patterns Across the Permian–Triassic Boundary. *Frontiers in Earth Science* **8**: 613350. DOI: https://doi.org/10.3389/feart.2020.613350

Pan Y, Birdsey RA, Fang J, Houghton R, Kauppi PE, Kurz WA, Phillips OL, Shvidenko A, Lewis SL, Canadell JG, Ciais P, Jackson RB, Pacala SW, McGuire AD, Piao S, Rautiainen A, Sitch S, Hayes D. 2011. A large and persistent carbon sink in the world's forests. *Science* **333**: 988–993. DOI: https://doi.org/10.1126/science.1201609, PMID: 21764754

Pearson MR, Benson RBJ, Upchurch P, Fröbisch J, Kammerer CF. 2013. Reconstructing the diversity of early terrestrial herbivorous tetrapods. *Palaeogeography, Palaeoclimatology, Palaeoecology* **372**: 42–49. DOI: https://doi.org/10.1016/j.palaeo.2012.11.008

Ponomarenko AG. 1969. Historical development of archostematan beetles. *Trudy Paleontologicheskogo Instituta AN SSSR* **125**: 1–240.

Ponomarenko AG. 2003. Ecological evolution of beetles (Insecta: Coleoptera). *Acta Zoologica Cracoviensia* **46**: 319–328.

Ponomarenko AG. 2004. Beetles (Insecta, Coleoptera) of the late Permian and early Triassic. *Paleontological Journal* **38**: S185–S196.

Ponomarenko AG. 2016. Insects during the time around the Permian—Triassic crisis. *Paleontological Journal* **50**: 174–186. DOI: https://doi.org/10.1134/S0031030116020052

Reich PB, Luo YJ, Bradford JB, Poorter H, Perry CH, Oleksyn J. 2014. Temperature drives global patterns in forest biomass distribution in leaves, stems, and roots. *PNAS* **111**: 13721–13726. DOI: https://doi.org/10.1073/pnas.1216053111, PMID: 25225412

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

Šamonil P, Phillips JD, Pawlik Ł. 2020. Indirect biogeomorphic and soil evolutionary effects of spruce bark beetle. *Global and Planetary Change* **195**: 103317. DOI: https://doi.org/10.1016/j.gloplacha.2020.103317

Schachat SR, Labandeira CC, Clapham ME, Payne JL. 2019. A Cretaceous peak in family-level insect diversity estimated with mark-recapture methodology. *Proceedings. Biological Sciences* **286**: 2054. DOI: https://doi.org/10.1098/rspb.2019.2054, PMID: 31847775

Schachat SR, Labandeira CC, Dyer L. 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**: 99–118. DOI: https://doi.org/10.1093/aesa/saaa042

Schneebeli-Hermann E, Hochuli PA, Bucher H. 2017. Palynofloral associations before and after the Permian–Triassic mass extinction, Kap Stosch, East Greenland. *Global and Planetary Change* **155**: 178–195. DOI: https://doi.org/10.1016/j.gloplacha.2017.06.009

Schobben M, Foster WJ, Sleveland ARN, Zuchuat V, Svensen HH, Planke S, Bond DPG, Marcelis F, Newton RJ, Wignall PB, Poulton SW. 2020. A nutrient control on marine anoxia during the end-Permian mass extinction. *Nature Geoscience* **13**: 640–646. DOI: https://doi.org/10.1038/s41561-020-0622-1

Seibold S, Rammer W, Hothorn T, Seidl R, Ulyshen MD, Lorz J, Cadotte MW, Lindenmayer DB, Adhikari YP, Aragón R, Bae S, Baldrian P, Barimani Varandi H, Barlow J, Bässler C, Beauchêne J, Berenguer E, Bergamin RS, Birkemoe T, Boros G, et al. 2021. The contribution of insects to global forest deadwood decomposition. *Nature* **597**: 77–81. DOI: https://doi.org/10.1038/s41586-021-03740-8, PMID: 34471275

Seidl R, Klonner G, Rammer W, Essl F, Moreno A, Neumann M, Dullinger S. 2018. Invasive alien pests threaten the carbon stored in Europe's forests. *Nature Communications* **9**: 1626. DOI: https://doi.org/10.1038/s41467-018-04096-w, PMID: 29691396

Shen S, Crowley JL, Wang Y, Bowring SA, Erwin DH, Sadler PM, Cao C, Rothman DH, Henderson CM, Ramezani J, Zhang H, Shen Y, Wang X, Wang W, Mu L, Li W, Tang Y, Liu X, Liu L, Zeng Y, et al. 2011. Calibrating the end-Permian mass extinction. *Science* **334**: 1367–1372. DOI: https://doi.org/10.1126/science.1213454, PMID: 22096103

Simões TR, Vernygora O, Caldwell MW, Pierce SE. 2020. Megaevolutionary dynamics and the timing of evolutionary innovation in reptiles. *Nature Communications* **11**: 3322. DOI: https://doi.org/10.1038/s41467-020-17190-9, PMID: 32620878

Smith DM, Marcot JD. 2015. The fossil record and macroevolutionary history of the beetles. *Proceedings. Biological Sciences* **282**: 20150060. DOI: https://doi.org/10.1098/rspb.2015.0060, PMID: 25788597

Stork NE. 2018. How Many Species of Insects and Other Terrestrial Arthropods Are There on Earth? *Annual Review of Entomology* **63**: 31–45. DOI: https://doi.org/10.1146/annurev-ento-020117-043348, PMID: 28938083

Sues HD, Reisz RR. 1998. Origins and early evolution of herbivory in tetrapods. *Trends in Ecology & Evolution* **13**: 141–145. DOI: https://doi.org/10.1016/S0169-5347(97)01257-3

Sun YD, Joachimski MM, Wignall PB, Yan CB, Chen YL, Jiang HS, Wang LN, Lai XL. 2012. Lethally hot temperatures during the Early Triassic greenhouse. *Science* **338**: 366–370. DOI: https://doi.org/10.1126/science.1224126, PMID: 23087244

Tapanila L, Roberts EM. 2012. The earliest evidence of holometabolan insect pupation in conifer wood. *PLOS ONE* **7**: e31668. DOI: https://doi.org/10.1371/journal.pone.0031668, PMID: 22355387

Tong Y-J, Yang H-D, Jenkins Shaw J, Yang X-K, Bai M. 2021. The relationship between genus/species richness and morphological diversity among subfamilies of jewel beetles. *Sects* **12**: 24. DOI: https://doi.org/10.3390/insects12010024, PMID: 33401400

Toussaint EFA, Seidel M, Arriaga-varela E, Hájek J, Král D, Sekerka L, Short AEZ, Fikáček M. 2016. The peril of dating beetles. *Systematic Entomology* **42**: 1–10. DOI: https://doi.org/10.1111/syen.12198

Ulyshen MD. 2016. Wood decomposition as influenced by invertebrates. *Biological Reviews of the Cambridge Philosophical Society* **91**: 70–85. DOI: https://doi.org/10.1111/brv.12158, PMID: 25424353

Ulyshen MD. 2018. Saproxylic Insects: Diversity, Ecology and Conservation. Springer. DOI: https://doi.org/10.1007/978-3-319-75937-1

Vajda V, McLoughlin S, Mays C, Frank TD, Fielding CR, Tevyaw A, Lehsten V, Bocking M, Nicoll RS. 2020. End-Permian (252 Mya) deforestation, wildfires and flooding—an ancient biotic crisis with lessons for the present. *Earth and Planetary Science Letters* **529**: 115875. DOI: https://doi.org/10.1016/j.epsl.2019.115875

van Klink R, Bowler DE, Gongalsky KB, Swengel AB, Gentile A, Chase JM. 2020. Meta-analysis reveals declines in terrestrial but increases in freshwater insect abundances. *Science* **368**: 417–420. DOI: https://doi.org/10.1126/science.aax9931, PMID: 32327596

Viglietti PA, Benson RBJ, Smith RMH, Botha J, Kammerer CF, 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, et al. 2021. Evidence from South Africa for a protracted end-Permian extinction on land. *PNAS* **118**: e2017045118. DOI: https://doi.org/10.1073/pnas.2017045118

Wagner DL, Grames EM, Forister ML, Berenbaum MR, Stopak D. 2021. Insect decline in the Anthropocene: death by a thousand cuts. *PNAS* **118**: e2023989118. DOI: https://doi.org/10.1073/pnas.2023989118, PMID: 33431573

Wills MA. 1998. Crustacean disparity through the Phanerozoic: comparing morphological and stratigraphic data. *Biological Journal of the Linnean Society* **65**: 455–500. DOI: https://doi.org/10.1111/j.1095-8312.1998.tb01149.x

Wills MA, Briggs DEG, Fortey RA. 2016. Disparity as an evolutionary index: a comparison of Cambrian and Recent arthropods. *Paleobiology* **20**: 93–130. DOI: https://doi.org/10.1017/S009483730001263X

Wu Y, Chu D, Tong J, Song H, Dal Corso J, Wignall PB, Song H, Du Y, Cui Y. 2021. Six-fold increase of atmospheric pCO2 during the Permian–Triassic mass extinction. *Nature Communications* **12**: 2137. DOI: https://doi.org/10.1038/s41467-021-22298-7

Yang LH, Gratton C. 2014. Insects as drivers of ecosystem processes. *Current Opinion in Insect Science* **2**: 26–32. DOI: https://doi.org/10.1016/j.cois.2014.06.004, PMID: 32846721

Zhang SQ, Che LH, Li Y, Pang H, Ślipiński A, Zhang P. 2018. Evolutionary history of Coleoptera revealed by extensive sampling of genes and species. *Nature Communications* **9**: 205. DOI: https://doi.org/10.1038/s41467-017-02644-4, PMID: 29335414

Zhao XD, Zheng DR, Xie GW, Jenkyns HC, Guan CG, Fang YN, He J, Yuan XL, Xue NH, Wang H, Li S, Jarzembowski EA, Zhang HC, Wang B. 2020. Recovery of lacustrine ecosystems after the end-Permian mass extinction. *Geology* **48**: 609–613. DOI: https://doi.org/10.1130/G47502.1