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## The rise of modern-type entomofauna in the Triassic

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### Abstract

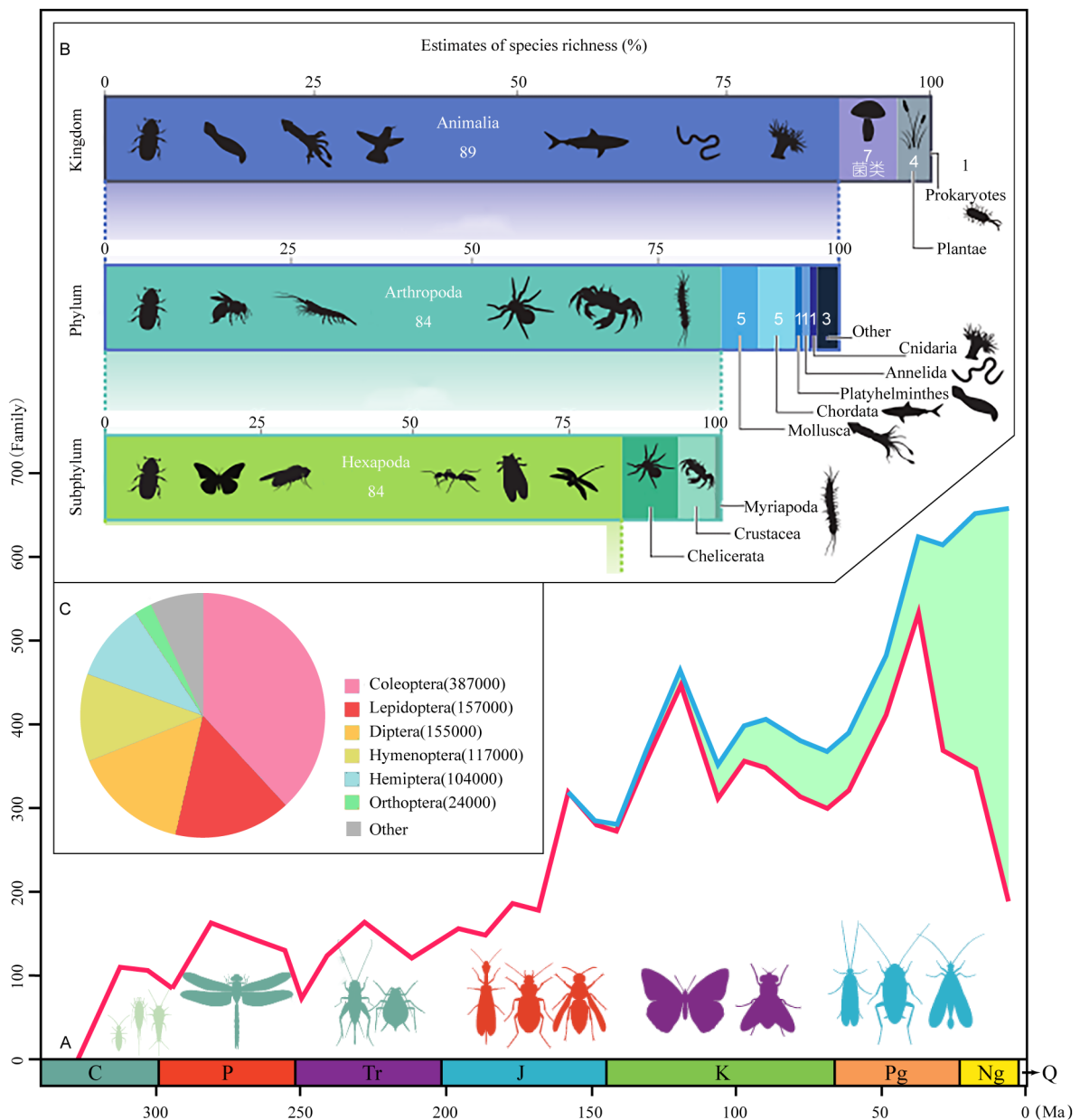
Insects are the major contributor of Earth's biodiversity, as the most diverse group in the modern biosphere. Considerable debates on the timing of entomofauna modernization remain, but most recent studies indicate it could have happened during the Triassic, following the “Great Dying” across the Permian–Triassic boundary. Using global insect diversity data and fossil records of select representative faunas, we performed computational analysis and comparative research to explore the compositional dynamics of entomofauna in the Permian and Triassic. Our analysis shows that: 1) following the Permian–Triassic mass extinction, insect diversity rapidly increased in the Anisian Stage of the Middle Triassic; 2) modern-dominating orders, such as Coleoptera, Diptera, Hymenoptera, Hemiptera, and Orthoptera exceeded half of the total diversity in the Ladinian; 3) In the Carnian of the Late Triassic, Coleoptera had emerged to be the dominating group of the entomofauna. These findings indicate that the rise of modern-typed entomofauna can be traced back to the Ladinian–Carnian (late Middle Triassic–early Late Triassic), much earlier than the Cretaceous Terrestrial Revolution.

**Key words:** Insect diversity; Faunal composition; Mass extinction; Terrestrial ecosystems; Coleoptera

### Introduction

Tracing the origins of modern ecosystems and their diversity is an important scientific issue for understanding the evolutionary history of Earth's habitability (Falkowski *et al.* 2004; Benton 2010; Zhu *et al.* 2021). Half a century ago, Vermeij (1977) proposed that a “marine revolution” occurred during the early and middle Mesozoic, establishing modern marine ecosystems. This conclusion came from the evidence that the shape and ornamentation of mollusk shells became much more complex from the end-Triassic to the Jurassic. Later statistical analyses of global fossil records revealed that the diversity and ecological structure of marine invertebrates experienced a distinct shift during the Permian–Triassic transition: the benthos dominated trophic-simple marine fauna of the Paleozoic was replaced by the Mesozoic marine fauna, which closely resembled the nekton-diversified and trophic-complex ecosystem of modern ocean (Sepkoski 1984; Bambach *et al.* 2002). The “Permo–Triassic transitional fauna”, which occurred in the immediate aftermath of the latest Permian extinction before the terminal disappearance in the earliest Triassic (Song *et al.* 2013), may have already exhibited the fundamental ecological structural characteristics of modern marine ecosystems (Song & Tong 2016). The Guiyang Biota found in the Early Triassic Induan of Guizhou (China), and the Paris Biota discovered in the Olenekian of Nevada (USA), consist mainly of non-benthic organisms, e.g., fishes and arthropods, showing significant ecological similarities with modern marine communities (Brayard *et al.* 2017; Dai *et al.* 2023). All of these studies hence indicate that the establishment of modern marine ecosystems began in the Early Triassic (Benton 2016).

However, scenarios on the timing of terrestrial ecosystems modernization vary (DiMichele *et al.* 2008; Sookias *et al.* 2012; Cleal & Cascales-Miñana 2014). The Cretaceous Terrestrial Revolution hypothesis, characterized by the rapid proliferation of angiosperms and insects, proposes that the modern-type terrestrial ecosystems took shape in the mid-Cretaceous (Nel 2015; Asar *et al.* 2022; Benton *et al.* 2022; Peris & Condamine 2024). Before the diversification of flowering plants, pollinating insects (such as bees, pollen wasps, various families of brachyceran flies and Lepidoptera) and herbivorous insects adapted to angiosperms also diversified rapidly (Grimaldi 1999; Peris & Condamine 2024), and social groups such as termites, ants, and bees occurred (Engel 2015). By contrast, according to the Mesozoic Lacustrine Revolution theory, the structure of some Triassic communities in lake facies is thought to have been very close to modern lacustrine biotic structures (Zheng *et al.* 2018; Benton & Wu 2022). The origin and radiation of dinosaurs during the Middle to Late Triassic are regarded as key indicators of the emergence of modern terrestrial ecosystems (Benton 2010). The expansion of herbivorous insects, rise of modern-type conifer families and an “amber burst” in the Carnian (early Late Triassic) also imply that vegetation was already very similar to that of the Cretaceous, with marked modern characteristics (Dal Corso *et al.* 2020).

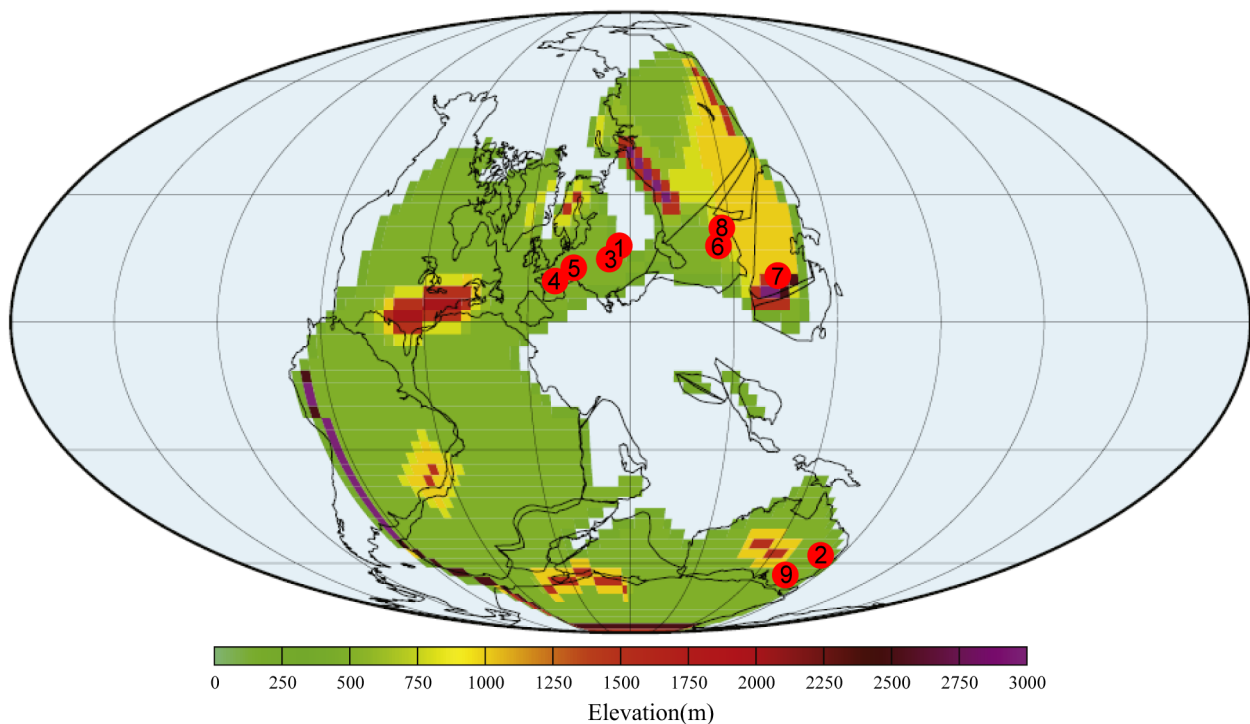


**Figure 1.** Evolution of insect diversity and the number (proportion) of modern insect diversity. **A**, Diversity curve at the insect family level (the blue curve includes living insects, the red curve includes only fossils, the figure is modified from Clapham *et al.* 2016); **B**, Estimates of global species richness, expressed as percentages of higher taxonomic groups (adapted from Eggleton 2020); **C**, Number and relative proportion of named species in the order Insects (data from Zhang 2011; figure adapted from Stork 2018). Insect silhouettes are from Misof *et al.* (2014).

In the extant biosphere, terrestrial habitats host greater biodiversity than oceans, accounting for 85% of the world's taxa (Vermeij & Grosberg 2010). The number of extant insect species is estimated to exceed 5.5 million, accounting for approximately 63% of all living species (Stork *et al.* 2015; Stork 2018; Eggleton 2020) (Fig. 1). However, the timing of the origin of modern insects remains highly controversial (Labandeira & Sepkoski 1993; Anderson *et al.* 1998; Clapham *et al.* 2016; Peris & Condamine 2024), limiting our understanding of the rise of modern-type terrestrial ecosystems and biodiversity. Here, we present a statistical study on diversity composition, with global insect occurrences and fossil records of selected local entomofauna, of Permian and Triassic, to constrain the timing of the rise of modern-type insects.

## Material and methods

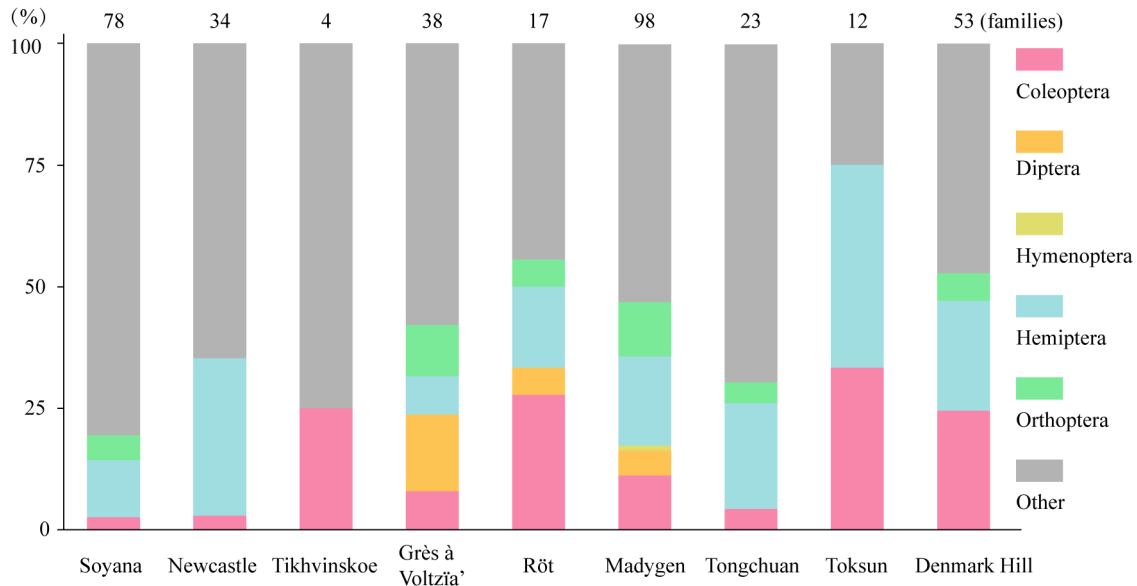
This study used the Paleobiology Database (PBDB, <https://paleobiodb.org/#/>) to collate the global Permian and Triassic insect fossil data. We preliminarily screened the data based on the following three criteria: (1) Indeterminate, unnamed taxa have been excluded; (2) multiple occurrences of the same taxa in a single collection are treated as a single occurrence; (3) collections with uncertain stratigraphic ranges are not include. Using these criteria, from over 5,000 records from more than 300 fossil sites worldwide (downloaded on May 31, 2024), we selected fossil records representing 1,749 genera and 3,648 species for subsequent computational analysis. The collected data were segmented and analyzed using Stages as time units. These Stages are: Asselian, Sakmarian, Artinskian, Kungurian, Roadian, Wordian, Capitanian, Wuchiapingian, and Changhsingian in the Permian; Induan, Olenekian, Anisian, Ladinian, Carnian, Norian, and Rhaetian in the Triassic.



**Figure 2.** Distribution map of representative insect fossil communities from the Permian–Triassic period. **1**, Soyana in Arkhangelsk Oblast, Russia (Roadian); **2**, Newcastle in the Sydney Basin, Australia (Wuchiapingian–Changhsingian); **3**, Tikhvinskoe in the Yaroslavl Region, Russia (Olenekian); **4**, Grès à Voltzia in northern Vosges, France (Anisian); **5**, Röt in Lower Franconia and Thuringia, Germany (Anisian); **6**, Madygen in Kyrgyzstan (Ladinian–Carnian); **7**, Tongchuan in Shaanxi, China (Ladinian–Carnian); **8**, Toksun in Xinjiang, China (Carnian); **9**, Denmark Hill in Queensland, Australia (Norian). The paleogeographic map and elevation data are sourced from Roscher *et al.* (2011).

We also compiled diversity data from published literature for nine Permian–Triassic insect fossil sites that were well-studied and regionally representative (Fig. 2, 3). Specifically, these include the Soyana insect fossil assemblage (Middle Permian, Roadian) from Arkhangelsk, Russia (Rasnitsyn *et al.* 2015); the Newcastle insect fossil assemblage (Late Permian, Wuchiapingian–Changhsingian) from the Sydney Basin, Australia (Jell 2004); the Tikhvinskoe insect

fossil assemblage (Early Triassic, Olenekian) from the Yaroslavl region, Russia (Aristov *et al.* 2013); the Grès à Voltzia insect fossil assemblage (Early Anisian, Middle Triassic) from northern Vosges, France (Gall & Grauvogel-Stamm 2005); the Röt insect assemblage (Early Anisian, Middle Triassic) from Lower Franconia and Thuringia, Germany (Bashkuev *et al.* 2012); the Madygen insect fossil assemblage (Middle–Late Triassic, Ladinian–Carnian) from Kyrgyzstan (Shcherbakov 2008b); the Tongchuan insect assemblage (Middle–Late Triassic, Ladinian–Carnian) from Shaanxi, China (Zhang *et al.* 2022); the Toksun insect fossil assemblage (Late Triassic, Carnian) from Xinjiang, China (Zhang *et al.* 2022); and the Denmark Hill insect fossil assemblage (Late Triassic, Norian) from Queensland, Australia (Rix 2021). We organized and analyzed the taxonomic records at the family, genus and species levels from relevant published literature and clarified several fossil records with uncertain family-level classifications.



**Figure 3.** The proportion of insect orders in different insect fossil communities in the Permian-Triassic. Soyana, Arkhangelsk Oblast, Russia, Roadian (data from Rasnitsyn *et al.* 2015); Newcastle, Sydney Basin, Australia, Wuchiapingian–Changhsingian (data from Jell 2004); Tikhvinskoe, Yaroslavl Region, Russia, Olenekian (data from Aristov *et al.* 2013); Grès à Voltzia, northern Vosges, France, Anisian (data from Gall & Grauvogel-Stamm 2005); Röt, Lower Franconia and Thuringia, Germany, Anisian (data from Bashkuev *et al.* 2012); Madygen, Kyrgyzstan, Ladinian–Carnian (data from Shcherbakov 2008b); Tongchuan, Shaanxi, China, Ladinian–Carnian (data from Zhang *et al.* 2022); Toksun, Xinjiang, China, Carnian (data from Zhang *et al.* 2022); Denmark Hill, Queensland, Australia, Norian (data from Rix 2021).

## Results

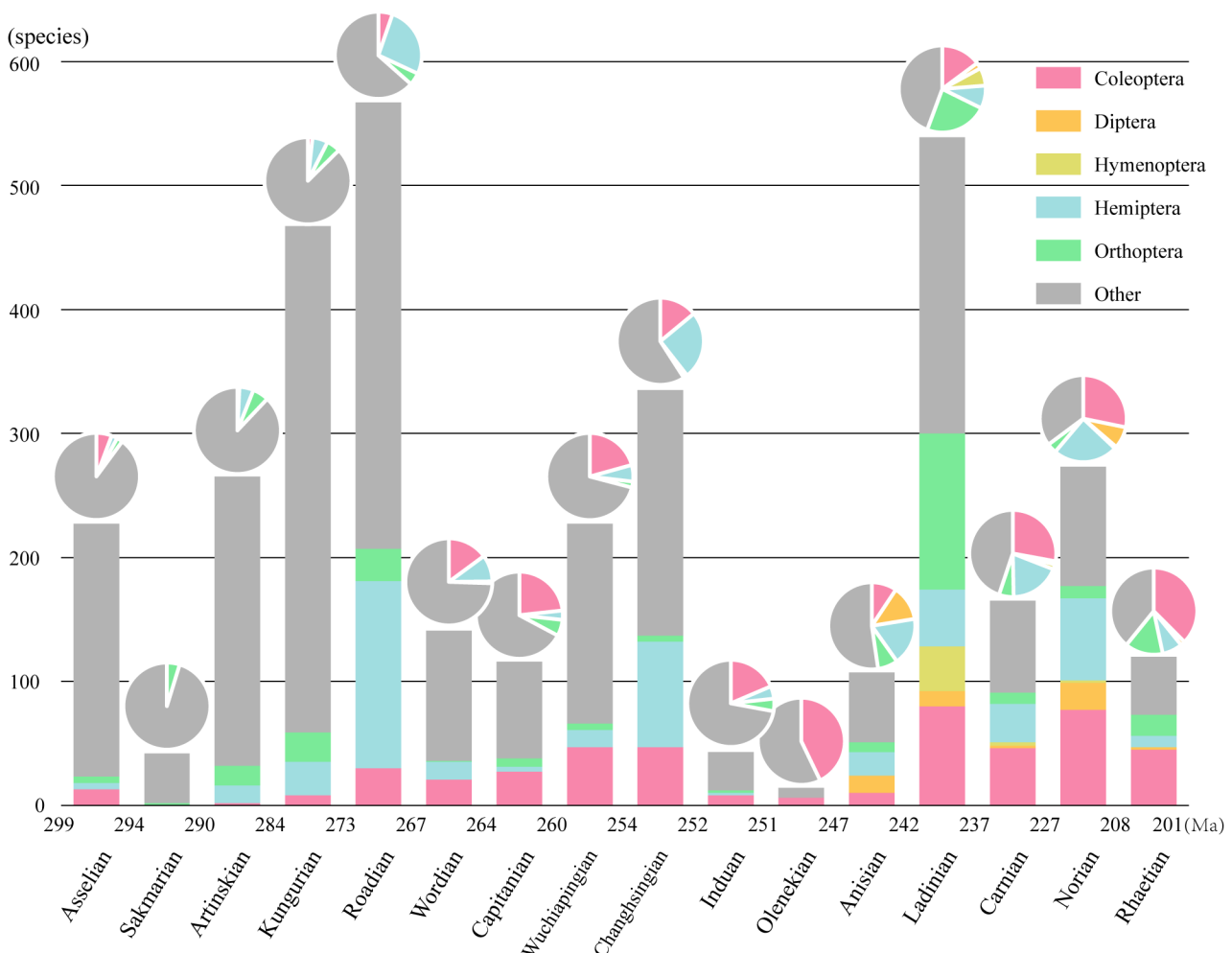
### *Diversity compositions of selected regional entomofauna*

The middle Permian insect community from Soyana was dominated by typical Paleozoic taxa, such as Grylloblattida, Odonata, etc. (62 families, accounting for 62% of the total family number), while Hemiptera, Orthoptera, and Coleoptera made up a much smaller proportion (about 20%). In the late Permian at Newcastle, Reculida and a few other Paleozoic groups (such as Mecoptera) held a relatively dominant position, accounting for 65% of the total family, while Coleoptera remained in low proportion (about 3%) and Hemiptera increased significantly to around 32% of the total family number. The Tikhvinskoe community in Russia, dating to the Olenekian of the Early Triassic, has low diversity: only a few Blattodea, Coleoptera, and Grylloblattida have been reported (four families). In Grès à Voltzia in France and Röt in Germany (both Anisian in age), Coleoptera are the dominant group at the species level, replacing earlier dominant groups like Grylloblattida, Blattodea, and Hemiptera. However, most of the Coleoptera from the Grès à Voltzia are poorly preserved and difficult to classify at higher taxonomic levels (family level), resulting in a small proportion of Coleoptera in family-level statistics (three families, 7.9% of the total family number). Hemiptera is the most dominant group in the Madygen (Kyrgyzstan) faunas from the Middle–Late Triassic (Ladinian–Carnian), followed by Coleoptera. Hemiptera and Orthoptera are the dominant groups of the Tongchuan fauna, with Coleoptera being much less documented (1 family). At Denmark Hill (Norian of the Late Triassic in Australia), Coleoptera surpassed Hemiptera in both family and species levels, becoming the largest insect group (13 families, 24.5% of the total family number; 61 species, 42.0% of the known species number).

*Global insect diversity composition from Permian to Triassic*

The global insect fossil records show that the faunal composition changed dramatically during the Permian and Triassic (Fig. 4). In the Asselian, the overall proportion of Coleoptera, Hemiptera, and Orthoptera was as low as 10.1%. During the Sakmarian, alongside the overall decline in diversity, no fossil records of Coleoptera and Hemiptera have been reported. From Artinskian to Roadian, total insect diversity increased rapidly, and the overall proportion of Coleoptera, Hemiptera, and Orthoptera rose significantly from 12.1% to 36.5%. Hemiptera diversified rapidly, comprising 26.6% of the total diversity in the Roadian. Although total diversity declined during the Wordian and Capitanian, the proportion of Coleoptera increased from 5.3% in the Roadian to 23.3% in the Capitanian. By the Changhsingian of the Late Permian, the combined proportions of Coleoptera, Hemiptera, and Orthoptera further increased to 40.9%. During this time, Hemiptera became the dominant group, comprising 42.9%, while the proportion of Coleoptera declined to 14.0%. In the Early Triassic, insect diversity was extremely low, but the proportion of Coleoptera reached 42.9% in the Olenekian. In the Anisian of the Middle Triassic, the proportion of modern dominant insect groups (Coleoptera, Diptera, Hemiptera, and Orthoptera) reached 47.7%. By the Ladinian, these groups accounted for more than half (55.7%) of the total insect population for the first time, and continued to dominate through the end of the Late Triassic. The proportion of Coleoptera was relatively low in the Anisian (9.3%), but it continued to increase in the subsequent stages. In the Carnian of the Late Triassic, the proportion of Coleoptera rose to 27.9%, surpassing Hemiptera at 18.8% and becoming the largest insect group. By the Rhaetian, at the end of the Late Triassic, the proportion of Coleoptera further rose to 37.5%, solidifying its position as the dominant group.

Overall, the proportions of the orders Coleoptera, Diptera, Hymenoptera, Hemiptera, and Orthoptera continuously increased from the Permian through the Triassic (Fig. 4). Starting in the Ladinian, the diversity of these five orders surpassed that of all other insect types, establishing them as the dominant assemblage at 56%. Hemiptera and Orthoptera have shown a high proportion of species since the middle Permian. Diptera and Hymenoptera first appeared in the Middle Triassic but remained relatively scarce until the Late Triassic. Coleoptera emerged as the most dominant group starting from the Carnian.



**Figure 4.** Diversity bar chart and relative proportion chart of Permian-Triassic insect fossil orders.

## Discussion

### *Features of Modern Insect Communities*

Some studies on early insect fossil diversity suggest that modern insect communities began to emerge during the Late Triassic (Labandeira & Sepkoski 1993; Anderson *et al.* 1998). Clapham *et al.* (2016) found that most of the living insect families began to appear in the Jurassic and increased rapidly after the Cenozoic. Peris & Condamine (2024) argued that the modern insect ecosystem began to take shape only after the Cretaceous–Paleogene mass extinction. These different views are not only due to differences in research materials and methods, but also due to inconsistent standards/indicators for the entomofauna modernization. Clapham *et al.* (2016) identified the emergence of most living families as the main indicator; Peris & Condamine (2024) considered the diversification of pollinators a key feature of modern insect communities; Vera *et al.* (2023) suggested that abundant Diptera (Chironomidae), Lepidoptera, Coleoptera, and Ephemeroptera characterize modern insect assemblages.

Based on existing diversity data of modern insects (Fig. 1), three obvious features can be identified: 1) The total diversity is extremely high with more than 5.5 million species (Eggleton 2020); 2) Coleoptera, Lepidoptera, Diptera, Hymenoptera, Hemiptera, and Orthoptera are the dominant groups, as species from these six orders comprising more than 90% of all insect diversity (Zhang 2011); 3) Coleoptera is the most diverse (Fig. 1C) group, accounting for about 40% of all insect diversity (Zhang 2011). Therefore, this study uses these three characteristics as primary indicators of modern insect communities to trace the time points of insect community modernization.

### *The Evolution of Insect Community Composition*

The statistical results of global fossil occurrences indicate that insects experienced a significant extinction event at the Permian–Triassic boundary (Fig. 4). Some authors proposed that the lower insect fossil diversity after this mass extinction could be an artefact deriving from a general lack of terrestrial deposits worldwide in the Early Triassic (Shcherbakov 2008; Schachat & Labandeira 2021), but more recent analysis at both family and genus levels has produced further evidence supporting the Permian–Triassic insect extinction (Jonault *et al.* 2022). Our species-level analysis shows that insect diversity was extremely low in the Early Triassic, with a clear rebound in the Middle–Late Triassic, exceeding the number of taxa from the Permian. In previous studies, researchers have primarily focused on insect diversity at the family and/or genus levels when assessing overall insect diversity (Labandeira & Sepkoski 1993; Labandeira 2005). Gui *et al.* (2023) conducted statistical analyses at the family, genus, and species levels showing that whilst species-level and some genus-level data present clear signs of insufficient sampling, genus- and family-level data for most periods are relatively well-sampled. Our species-level diversity curve (Fig. 4), however, shows similar trends to those observed in published family or genus curves from previous research (Labandeira & Sepkoski 1993; Labandeira 2005; Shcherbakov 2008a; Clapham *et al.* 2016; Jouault *et al.* 2022; Gui *et al.* 2023).

Labandeira (2005) identified insect fossils into two major evolutionary groups: the Paleozoic groups, with apterygotes, paleopterous insects, and early basal lineages of Orthoptera and Hemiptera, and the modern insect groups, which are primarily characterized by holometabolous insects and more derived branches of Orthoptera and Hemiptera. Several other studies indicate that: 1) the insect community in the Permian was primarily composed of Blattodea and Grylloblattida, as well as some paleopterans (Rasnitsyn *et al.* 2005; Aristov *et al.* 2013); 2) During the Permian–Triassic boundary mass extinction, Paleodictyopterans and several stem-group orders disappeared completely (Engel 2015); 3) Holometabolous insects, which make up about 95% of modern insect species, underwent significant diversification during the Early and Middle Triassic (Wang *et al.* 2022).

The earliest known records of major insect groups were discovered in the Triassic as the oldest Diptera discovered in the Middle Triassic (Lukashevich 2021) and Lepidoptera discovered in the Lower Triassic and Middle Triassic (van Eldijk *et al.* 2018). The global insect fossil data collected in this study show that the dominant insect groups of modern entomofauna, including Coleoptera, Diptera, Hymenoptera, Hemiptera and Orthoptera, have been dominant since the Ladinian (Middle Triassic; Fig. 4). The insect communities of the Late Triassic exhibit distinct modern features as the above five groups dominated diversity composition, with only a few Paleozoic lineages surviving into the Carnian and later stages. This finding is consistent with the results of earlier studies (Labandeira & Sepkoski 1993; Anderson *et al.* 1998; Labandeira 2001), which indicate the modernization of entomofauna during the Middle–Late Triassic.

### *Early Diversification of Coleoptera and Lepidoptera*

Coleoptera originated in the early Permian (Cai *et al.* 2022) but maintained low diversity until the late Permian (Shcherbakov 2008a; Schachat & Labandeira 2021). In the Early Triassic, Coleoptera dominated in a few localities: the

majority of the insect fossils in the Maltsevo Group in the Kemerovo region (Kuznetsk Basin; Russia) are Coleoptera (Żyła *et al.* 2013), but Coleoptera did not exhibit dominance in terms of species diversity in the Nedubrovo of Russia (Shcherbakov 2008a).

Consistent with the previous studies, our data also show that Coleoptera diversified rapidly from the Anisian of the Middle Triassic and became the dominant group by the Carnian of the Late Triassic (Papier *et al.* 2005; Rix 2021; Zhao *et al.* 2021). In the Röt (Germany) insect fossil community of the Anisian (Middle Triassic), Coleoptera were the most dominant insect group at both family and species levels (Fig. 3). In the contemporaneous fossil assemblage of the Grès à Voltzia of France, Coleoptera had the highest number of species (Fig. 3), although fewer Coleoptera were recorded at the family level (Gall & Grauvogel-Stamm 2005; Bashkuev *et al.* 2012). In the family-level analysis of both the Ladinian and Carnian insect fossils from Madygen in Kyrgyzstan and Tongchuan in China, Coleoptera did not show dominance, even though the number of Coleoptera specimens found was the largest (Shcherbakov 2008b; Zheng *et al.* 2018; Zhang *et al.* 2022). The most likely reason for the statistical differences in the number of families, species, and specimens of Coleoptera in the Early and Middle Triassic is that most Coleoptera fossils are preserved only as individual elytra, making their identification and classification challenging (Papier *et al.* 2005). Some studies suggest that the two major superfamilies of Coleoptera, Curculionoidea and Staphylinoidea, are estimated to have appeared much later than the Triassic (McKenna *et al.* 2009; Lü *et al.* 2020). Due to the scarcity of fossil records, there is an issue with insufficient sampling at species and genera levels (Gui *et al.* 2023). Therefore, statistical studies within superfamily/family require much more fossil materials to be discovered in the future.

Lepidoptera, as the second-largest modern insect group, rarely appears in Triassic fossil records (Grimaldi & Engel 2005). The main reason for this might be the preservation bias caused by their morphology, which leads to heavy incomplete fossil records (Sohn *et al.* 2015). Lacking of a hard body, leave them more difficult to preserve compared to Coleoptera. Lepidoptera has typical scales on their wings with a light and small body. These scaled wings enable Lepidoptera to float on the water surface (Schachat & Labandeira 2021), preventing them from sinking into the sediments at the bottom of water bodies.

#### *Ecological and climatic dynamics for the rise of modern entomofauna in Triassic*

Several ecological factors may have triggered the rise of modern-type insects, with climate, especially temperature, being a primary factor. In the Early Triassic, intense heat caused most insect species to go extinct; however, in the subsequent Middle and Late Triassic periods, as global temperatures decreased, insect populations began to recover (Scotese *et al.* 2021). Additionally, the drastic environmental changes at the Permian–Triassic transition—such as the rapid temperature increase and significant drop in oxygen levels—leading to the most severe extinction event in biological history, created ample ecological space for the rise of modern insects (Gui *et al.* 2023).

Additionally, variables related to plant diversity were consistently identified as important potential drivers of insect evolution (Labandeira 2006, 2013; Wappler *et al.* 2012, 2015; Pinheiro *et al.* 2016; Nel *et al.* 2018; Liu *et al.* 2020; Asar *et al.* 2022). Jouault *et al.* (2022) found, through a birth-death model study, that gymnosperms, Polypodiales ferns, and non-Polypodiales ferns were significantly positively correlated with insect diversity during the Permian–Triassic, suggesting that these plant groups may have been key drivers of insect diversity dynamics. Insect origin was found to be negatively correlated with the relative diversity of Polypodiales ferns and positively correlated with that of non-Polypodiales ferns. Increases in the relative diversity of Polypodiales ferns slowed insect diversification, while fluctuations in the diversity of non-Polypodiales ferns accelerated it. A rise in gymnosperm diversity tended to slow insect extinction rates, whereas increased diversity of non-Polypodiales ferns accelerated these rates. Based on insect damage to plants, herbivorous insects primarily fed on gymnosperms and non-Polypodiales ferns during the Permian and Triassic periods, and on Polypodiales ferns in the Triassic (Labandeira 1997; Labandeira *et al.* 2016). Polypodiales ferns first appeared at the end of the Permian or in the early Triassic and underwent large-scale diversification in the Late Mesozoic, whereas non-Polypodiales ferns, an ancient group, declined sharply during the Permian and Triassic periods (Lehtonen *et al.* 2017). Additionally, the origin of most modern conifers traces back to the Late Triassic (Benton & Wu 2022). These transformations and the diversification of plant life also promoted new insect predation methods, contributing to greater insect diversity (Dal Corso *et al.* 2020).

## **Conclusion**

Statistical analysis of the faunal composition dynamics of Permo–Triassic insects using fossil records from selected regional representative fauna and global Permian–Triassic occurrences data, shows that: 1) after the mass extinction at

the Permian–Triassic transition, insect diversity recovered rapidly in the Middle Triassic, and surpassed Permian levels in the Ladinian and Late Triassic; 2) Coleoptera, Diptera, Hymenoptera, Hemiptera and Orthoptera, which dominate modern entomofauna, began to comprise over half of the total diversity from the Ladinian of Middle Triassic; 3) The most diverse order of modern insects, Coleoptera, began to diversify rapidly in the Middle Triassic and became the dominant group during the Carnian of the Late Triassic. All the above findings indicate that the modern-type insects emerged during the Middle–Late Triassic.

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