The End-Permian insect mass extinction causes, severity, and recovery compared to the modern insect mass extinction

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Introduction

Insects hold great importance in the ecosystem. They first appeared in the Devonian period, 419 million years ago (Jouault et al. 2022). They make up most of terrestrial diversity (Basset et al. 2019) and constitute more than half of all known animal species (Montagna et al. 2019). They have the highest species-level diversity of any group of animals (Schachat et al. 2019). While many people have negative perceptions of insects due to their role in spreading disease, they are also highly important to humans. There are aesthetically pleasing insects such as butterflies which people are fond of. There are also pollinating insects which are important agriculturally and economically. Without pollination, major agricultural crops would cease to exist. Outside of human interest, insects play an important role in ecosystem services. Several species rely on insects. About half of insect species are herbivores that are therefore tied to the existence of their host plants. Insects spread seeds and spores from various plants which influence the existence of other insect populations and vertebrate populations. Insects also can defend plants from predators (Basset et al. 2019). The interconnectedness of species can trigger cascading extinctions and coextinctions (Kehoe et al. 2021). Insects are not only extremely diverse, but their role in the ecosystem is important to maintaining biodiversity.

There is some evidence that insects may be less prone to extinction than other taxa or at risk from different factors. However, this may be because few past insect extinctions have been documented (Dunn et al. 2005). In addition, insects have a greater number of generations per time which allows evolution to occur faster. Their small body size is also an advantage. These two traits are advantages in extinction events (Schachat et al. 2020). Like other taxa, extinction of narrow habitat specialists is common. In addition, there are coextinctions of affiliates with extinctions of their hosts. Insects also differ from other taxa in that they are of small size and therefore need less area. Despite being less prone to extinction than other taxa, most extinctions of the geologic past and those predicted are of insects (Dunn et al. 2005). The abundance and biomass decline of insects suggests that we are in the middle of an anthropogenic extinction crisis (Schachat et al. 2020). There are only two mass extinction events where insects were severely impacted: the end-Permian mass extinction event and the current Anthropocene mass extinction (Erwin 1996). This paper will compare the causes, severity, and effects of the End-Permian insect mass extinction to the current insect mass extinction.

There are issues with measuring insect extinctions because there are biases regarding the study of insects. Scientists do not tend to research insect extinctions and usually study vertebrate extinctions. When they do study insect extinctions, there is a bias towards medium-sized insects and towards the first and last occurrences of higher-level taxa (Schachat et al. 2020). The International Union for the Conservation of Nature (IUCN) Red List depends solely on the measures of population decline over the most recent ten years or three generations, whichever is longer. Since insect generation times are so fast, there is a bias by the start of the year (Fox et al. 2019). There is also a bias as to where insects are being studied. Most insects that are recorded are from islands since they are easier to search completely (Dunn et al. 2005). Tropical countries are losing the most insects, but they are not participating in most of the studies. There is also a lack of communication between various insect researchers. Most countries do not work together on studies (Valentine-Neto et al. 2021). The biases about studying insect extinctions and the flow of information make it difficult to quantify exact measurements.

There is a rich insect fossil record (Montagna et al. 2019). However, there are issues with relying on the fossil record to measure insect extinction. The insect fossil record contains larger temporal and taxonomic gaps than other fossil records (Schachat et al. 2020). Therefore, it is difficult to distinguish background extinctions from cascading extinctions (Kehoe et al. 2021). Insects do not usually live where fossils were typically formed. They don't have mineralized shells, nor do they live on the ocean floor. The formation of insect fossils usually occurs in resin deposits and near bodies of water. Because of this, higher altitudes generally lack insect fossils. The fossil record is biased against larger taxa, since their fossils are extremely rare. Smaller insects are more likely to be preserved in their entirety. Their size also influences which body parts of the insect were preserved. Most insect fossils are from fossil assemblages known as Lagerstättes, where vast numbers of insects were preserved. However, the distribution of Lagerstättes is inconsistent across space and time (Schachat et al. 2020). For example, most Permian Lagerstättes were in North America and Eurasia (Prevec et al. 2022), despite there likely being a high diversity of insects in tropical areas (Kehoe et al. 2021). Overall, Permian sites were also globally rare compared to other time periods (Prevec et al. 2022). While there is a rich insect fossil record, it is biased towards smaller insects of concentrated times and location, which presents challenges with relying on it fully to measure extinctions.

There are issues with comparing fossils to current insect populations to measure extinction. First, temporal population trends are extremely difficult to find in fossils. They are also difficult to observe in living insects due to observation errors, environmental variability, and short life cycles (Fox et al. 2019). The current biotic crisis is measured in terms of loss of abundance and biomass rather than the loss of species, genera, or families. These are impossible to measure in the fossil record (Schachat et al. 2020). There are issues with identifying clades at systematic levels in fossils, and there are also unknown environmental factors such as volcanism and rainfall that could be at play (Jouault et al. 2022). Fossils are difficult to compare to current insect populations due to the difficulty of differentiating clades systematically in fossils and a lack of scientific study of modern insects.

Plant fossils are a better indicator of insect diversity and extinction than insect fossils. Plant fossils occur more evenly through time and space than insect fossils. Plant fossils can provide insight into insect herbivores even when insect fossils are lacking (Wilf 2008). Leaf herbivory can be used to estimate the causes, severity, and effects of insect mass extinction whether they are fossilized or in the present. There is a correlation between leaf chewing damage type, which is how the leaf is damaged by herbivory, and the damage maker riches, the type of insects. This is also directly observable in living forests. The fossil record shows that climate change and extinctions significantly affected the diversity of insect leaf-feeding damage. Climate conditions such as mean annual temperature and precipitation can be estimated using leaf margin characteristics and leaf size (Carvalho et al. 2014). Elevated temperatures increase insect growth rates and therefore increase herbivory. Overall, insect feeding diversity also tracks plant diversity (Wilf 2008). Plant fossils have a less biased fossil record that can be used to track insect diversity and extinction through herbivory, as well as show changes in climate conditions.

The Permian period began 298 million years ago and ended 251 million years ago. The end of the Permian is marked by the largest mass extinction event in geological history, with approximately 95% of all species going extinct (Benton et al. 2003). Of the five prior mass extinctions, only the Permian affected insects (Erwin 1996). The beginning of the sixth mass extinction is considered to have begun possibly as far back as 200,000 to 45,000 years ago, coinciding with the first expansion of modern humans out of Africa. Other scientists believe that it may have occurred 12,000 to 10,000 years ago during the development of agriculture, while others believe it began as recently as 180 years ago due to the industrial revolution. While extinctions have yet to reach 75% of all species needed to define it as a mass extinction (Cowie et al. 2022), this will occur within the next centuries. This modern mass extinction is also affecting insects. As the only mass extinction that impacted insects, the Permian can be used as a guideline to compare to the current mass extinction event occurring. Although climate change is the main cause of both the Permian mass insect extinction and the modern insect mass extinction, the latter is more severe, but recovery will likely be similar or even slower.

The Permian mass extinction causes compared to the current mass extinction

There have been five prior mass extinctions. These mass extinctions were all due to climate change that caused warming or cooling of at least 5°C. The climate changes were triggered by different causes such as glaciation, volcanic eruption, or asteroid impact. Both the Permian insect mass extinction and the modern insect mass extinction were caused by climate change, but what led to that change was different. The Permian mass extinction event occurred 251 million years ago and took place over the course of 60,000 years (Song et al. 2021). The mass extinction event was caused by climate change triggered by the eruption of the Siberian traps. The eruption led to massive amounts of carbon dioxide and sulfuric dioxide being released into the atmosphere. As a result of this there was ocean acidification and anoxia as well as acid rain. There was partial destruction of the ozone layer, and wildfires added additional carbon dioxide to the atmosphere (Zhao et al. 2021). Prior to the mass extinction event, there was gradual warming by approximately 12°C that led to initial environmental degradation (Gliwa et al. 2022). During the mass extinction, the climate warmed rapidly by about 10 °C (Song et al. 2021). Global warming caused entomofaunas as well as flora in the Northern Hemisphere to be displaced poleward. Cockroaches, which did not extend northwards beyond the semi-arid zone, reappeared from earlier epochs in more poleward zones. This shift is reflected in fossil deposits (Shcherbakov et al. 2007). The extinction of taxon from the Permian may be due to the turnover of flora or competition from new types of insects that diversified due to the diversification of plants (Zhang et al. 2022). During the late Permian, gymnosperm dominated forests collapsed and were replaced by other biomes (Zhao et al. 2021). These changes in floral assemblages were likely the strongest drivers of insect responses during the Permian extinction (Jouault et al. 2022). The Permian mass extinction was a global warming event which triggered the movement of floral assemblages, and therefore insects.

The sixth mass extinction is considered to have begun possibly as far back as 200,000 to 45,000 years ago or as recently as the nineteenth century during the industrial revolution (Cowie et al. 2022). Based on the predicted rates of extinction, the criteria for mass extinction will be reached by amphibian, bird, and mammalian standards in around 240 to 540 years (Barnosky et al. 2011). If insect extinctions were included this date would likely be sooner. The mass extinction event was also caused by climate change. This climate change was caused primarily by human activities. Due to burning fossil fuels, and at a faster pace since the Industrial Revolution, more carbon dioxide has been released into the atmosphere. Agricultural activity has led to deforestation and habitat fragmentation which led to less carbon sequestering. Animal husbandry led to the increased release of methane. As a result of global warming, there will be higher rates of extinction amongst insects. 40% of insect species in temperate countries may face extinction over the next few decades (Basset et al. 2019). The temperature has already risen 1°C since 1880 (Zhang et al. 2022). It is predicted that by 2050 the temperature will have risen by over 1.5°C (Tong et al. 2019). It is expected that the temperature might even increase up to 5.8ºC by 2100 (Menéndez 2007). At this pace, the estimate that mass extinction will occur in around 240 years is not unlikely. Similarly to the Permian extinction, there was gradual global warming prior to the main extinction pulse warming. However, unlike the Permian extinction, some of this warming is occurring within a more condensed margin of time.

There is already evidence global warming currently affects insects. Insects are passing through their larval stages faster, and there are changes in species distributions expanding into new climatic areas and disappearing from others. These movements are towards cool, upper altitudinal and latitudinal limits. An example of this is that Lepidoptera have shifted northwards and to higher elevations along with beetles, dragonflies, and grasshoppers (Menéndez 2007). The main question is whether insect distribution can keep up with the rapid temperature change. Plants are also shifting phenologically and geographically towards cooler, upper altitudinal and latitudinal limits (Harvey et al. 2015). This lends credence to the idea that changes in floral assemblages are major drivers of insect responses during extinction.

In addition to climate change caused primarily by humans, people also are taking actions that will lead to increased insect extinction. People are willing to cause the extinction of insects when they cause economic or disease related issues (Dunn et al. 2005). The intentional introductions of biocontrol agents can lead to local or global extinction of a variety of insects (Dunn et al. 2005). Insecticides also trigger secondary extinctions by killing species directly. They also lead to bioaccumulation, which occurs through population dynamics and food webs (Kehoe et al. 2021). Humans also introduce invasive species, which can lead to coextinctions of plants and insects. When trying to save other species threatened by extinction, captive-bred animals and endangered plants are deloused or doused without regard to parasites (Dunn et al. 2005). Anthropogenic causes and direct human actions are contributing to the increased rate of extinction of insects.

The Permian mass extinction event and the period leading up to it had global warming of approximately 22°C. 12°C of this warming took place gradually over millions of years (Gliwa et al. 2022), while 10°C of this warming took place within a relatively short geological time of 60,000 years (Song et al. 2021). The current mass extinction is also due to global warming. While there has been gradual background warming, the planet has already warmed by 1.5°C on an extremely rapid geological time scale (Tong et al. 2019). Within the next century, it is predicted that the temperature will have risen by 5.8°C (Menéndez 2007). Compared to the Permian extinction, this is extremely rapid global warming. This climate change has been spurred on by human activities. Due to climate change from the Permian mass extinction, insects shifted towards cool, upper altitudinal and latitudinal limits. During the current mass extinction, insects are following the same pattern shifts as they did during the Permian mass extinction.

The Permian mass extinction severity compared to the current mass extinction

The severity of the Permian insect mass extinction and the current mass extinction are debated. The Permian extinction's severity is disputed since it led to a severe terrestrial ecosystem collapse, but the insect response is poorly understood (Zhao et al. 2021). While fossil-based studies show a drop in diversity during the Permian mass extinction, phylogenetic studies do not support a mass extinction event (Condamine et al. 2020). The current mass extinction is also disputed. Some people argue that human-caused extinctions are a natural phenomenon and result in new speciation. But extinctions are occurring faster than speciation. Another critique is that estimated extinction rates have been exaggerated and that the current rate is not much greater than the background rate. However, the estimated rate is 100 to 1,000 times greater than the background rate (Cowie et al. 2022). Both the Permian extinction and the current insect extinctions are disputed.

The Permian insect mass extinction was less severe than the estimated impacts for the current insect mass extinction. Some argue that the crisis during the Permian can't be compared to the current one because the Permian extinction was part of a diversification event (Schachat et al. 2020). Many insect orders around today originated or diversified during the Permian period (Jouault et al. 2022). It is argued that it was more of a floral turnover than a mass extinction for insects (Schachat et al. 2020). It is shown that plant diversification is linked to insect diversification. With new plants, insect life is originally sparce before they develop analogous adaptations (Farrell et al. 1992). Therefore, floral turnover and mass extinctions are intrinsically connected. The diversification of insects takes place due to floral turnover, though this takes time. Thus, there is mass extinction, but diversification occurs afterwards. During the Permian, plant composition shifted and consequentially, so did the composition of insects. Due to the Permian mass extinction, 82.6% of insect genera went extinct (Jouault et al. 2022). Of the 26 insect orders known from the Permian, six became extinct (Ponomarenko 2016). Overall, 50% of animal families died out (Shcherbakov et al. 2007). There were heterogenous effects of extinction events across major insect clades. No extinction occurred at the family level for all the major clades of insects (Jouault et al. 2022). The Permian extinction was part of a diversification event of insects due to floral turnover that started with extinctions.

Currently, there are no new types of plants that are taking over the landscape. Instead, certain plants are gaining in abundance and range, and the overall diversity of plants is dropping. This will affect the composition of insects. It is likely that 5 to 10% of insect species have gone extinct since the industrial era (Cardoso et al. 2020). It is predicted that 40% of insect species will go extinct in the next few decades (Basset et al. 2019). So far, geographic specialists are at the highest risk of extinction. This is foreshadowed by local extinctions such as the specialist carabid species and specialist butterfly species that are declining in Europe more than the generalist species (Samways 2006). Unlike the Permian mass extinction, a floral turnover is not occurring and therefore there is not a dip and increase of insect diversity.

The Permian mass extinction recovery and implications for current mass extinction

After the Permian mass extinction, major insect groups that went extinct were replaced by new orders and families. Several major insect groups went extinct including Palaeodictyoptera (medium to large six-winged insects) and Megasecoptera (two pairs of wings and fine processes projecting from the body) (Montagna et al. 2019). The Palaeozoic insect fauna mostly went extinct. K-selected species persisted the longest in degraded habitats but were unlikely to persist (Kehoe et al. 2021). Ecological collapse made niches available for wide range expansion by stress and threat tolerant species (Bassett. 2019). While geographically limited rare specialists were the most likely to go extinct, they were also the most likely to survive (Samways 2006). Recovery was delayed and slow due to extreme environmental conditions and the nature of the dominance of r-selected taxa during the initial recovery (Tong et al. 2007). During recovery, Mesozoic insects began to take over including Diptera (flies), Hymenoptera (bees, wasps, and fire ants), Hemipterodea (lice, cicadas, aphids), and Coleoptera (beetles) (Jouault et al. 2022). Prehistoric losses of insect diversity at levels of order and family appear to have been driven by competition with biotic replacement, insuring minimal losses in taxonomic diversity (Schachat et al. 2020). Recovery after the Permian mass extinction restored insect diversity to its prior levels since it was driven by competition with biotic replacement.

The Permian mass extinction event was the largest extinction event, and recovery took the longest compared to other mass extinction events (Tong et al. 2007). It took almost the entirety of the Early Triassic period, which lasted around 6 million years, to recover. In some cases, recovery was quicker and took place in 1 to 2 million years due to favorable environmental conditions (Tong et al. 2007). During the aftermath of the Permian mass extinction, fossils show that there was a size decrease, displaying the Lilliput effect (Twitchett 2007). Since the current mass extinction is expected to be more severe, it is likely that recovery will take more time and that there will also be presence of the Lilliput effect.

Permian mass extinction recovery shows that recovery from a major crisis is possible. The phenomenon of quickly returning to pre-crisis diversity levels has also been recorded in ammonoids and is called flash recovery (Jouault et al. 2022). There were similar findings in plants for this quick recovery, showing that plants and insects may not have been as dramatically affected by the Permian mass extinction as initially thought. This has implications in the resilience of extreme extinction events (Montagna et al. 2019). Broad insect life is linked to broad plant life (Prevec et al. 2022). The mass extinction event had a profound ecological influence on beetle evolution. During the Permian period they were dominated by xylophagous stem groups. New xylophagous beetles appeared in the early Middle Triassic, consistent with the restoration of the forest ecosystem. Presumably, this was also the same case with other insect species (Zhao et al. 2021). Insects quickly returned to pre-crisis diversity levels after the Permian mass extinction due to the link to flora.

Currently, insects have diversified into around 5.5 million species (Montagna et al. 2019). Recovery from the Permian extinction suggests that it will also occur after the sixth mass extinction. However, the recovery process from the End-Permian extinction took 6 million years, which while it is rapid in geological time, is an extremely long time for humans. Hominids have existed for about 2 million years, while Homo sapiens sapiens have existed for around 200,000 years (Cowie et al. 2022). In terms of geological time, this is a relatively short time period, especially when compared to the length of the Permian period: approximately 47 million years. The fact that humans have caused an acceleration towards the next mass extinction event, or have already started it, shows just how rapidly we change our environment.

The Permian mass extinction coextinctions compared to the current mass extinction

Coextinction is when the loss of a host species results in the loss of an affiliate species. This leads to cascading effects across trophic levels (Dunn et al. 2009). As a side effect of coextinction, there is floral and insect turnover. Climate change can have an impact on coextinctions. Temporal mismatches occur when one species is not in the proper life stage or present at the correct time to interact with the affiliated species. Climate change can affect the life stages of a species. Spatial mismatches occur when the host and affiliate species are not in the same location. Due to global warming, hosts and affiliates are moving, but they might not be doing so at the same rates. (Kehoe et al. 2021). Climate change caused coextinctions due to the movement of hosts and affiliates, causing the extinction of insects during the Permian and current mass extinction.

Scientists believe that mass extinction events could have been aggravated by co-extinction events (Butler 2015). Unfortunately, it is not possible to compare the impact of coextinctions on the Permian insect mass extinction to modern times. It can only be inferred that coextinctions did occur during the Permian extinction, but fossil evidence does not support any conclusions. Few historical and even contemporary coextinction events have been recorded (Dunn et al. 2009). Unlike the Permian mass extinction event, the current coextinctions have additional drivers besides climate change. They are also influenced by habitat loss, overkill, and invasion (Dunn et al. 2009). Current coextinctions are often insects that are specialized to a specific plant or animal. When that animal or plant goes extinct or moves out of geographic range or time of the insect, the insect becomes extinct. Higher altitude insects are at a greater risk of extinction (Moir et al. 2014). The more specialized host species are, the more likely the affiliates are to go extinct. This suggests that parasites and mutualists are at the most risk (Dunn et al. 2009). Climate change will reduce the population size of many plant species. 57% of plant species will lose more than half their current range by 2080. This decline in plant populations will affect plant-dwelling insects (Moir et al. 2014). While Permian insect coextinctions can't be compared to current mass extinctions, there are subtle implications that the current coextinctions will be more severe due to the lack of an increase in plant diversity.

Conclusion

The Permian insect mass extinction and modern insect mass extinction were caused by climate change and took place over a relatively short geological time frame. However, the global warming during the Permian mass extinction was caused by volcanic eruptions while the warming during the current mass extinction is due to the anthropogenic effects. During the current mass extinction, insects are following the same movement poleward and towards higher altitudes that were documented from the Permian mass extinction. The Permian insect mass extinction is estimated to be less severe than the modern mass insect extinction will be. This is because the Permian extinction was due to floral turnover towards new plants, which led to increased insect diversity after the dip. However, currently, floral turnover is becoming less diverse and therefore there will not be as much of a chance for insects to diversify during recovery. Despite these extinction events, recovery after the Permian insect mass extinction suggests that there will be recovery after the modern insect mass extinction event. Since the Permian mass extinction recovery took about 6 million years and the current extinction is estimated to be more severe, recovery will likely take longer. The recovery time would take place during a longer period than hominids have existed. It is not possible to compare the coextinction events of the Permian mass extinction to the coextinction events of the modern mass extinction. Since both the End-Permian mass insect extinction and the current mass insect extinction were both caused by global warming and created similar effects on insects thus far, it can be inferenced that the current extinction is more severe, and while recovery will occur, it will likely take longer.

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