# CALAMARI THROUGH TIME: EXPLORING ANTAGONISTIC BIOTIC INTERACTIONS VICTIMIZING CEPHALOPODS THROUGHOUT GEOLOGIC HISTORY

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by
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The undersigned, appointed by the dean of the Graduate School, have examined the thesis entitled

CALAMARI THROUGH TIME: EXPLORING THE ROLE OF ANTAGONISTIC
BIOTIC INTERACTIONS VICTIMIZING CEPHALOPODS THROUGHOUT
GEOLOGIC TIME

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and hereby certify that, in their opinion, it is worthy of acceptance.

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# CALAMARI THROUGH TIME: EXPLORING ANTAGONISTIC BIOTIC INTERACTIONS VICTIMIZING CEPHALOPODS THROUGHOUT GEOLOGIC HISTORY

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## ABSTRACT

Cephalopods, a class of marine mollusks that include octopods, squids, and cuttlefish, have existed in Earth's oceans since the Cambrian period. During that time, they have played the roles of both predator and prey as they fill in key ecological roles within their communities. However, exploring those roles from fossil assemblages creates key challenges due to a combination of taphonomic challenges and sampling biases. In this study, we explore traces of biotic interactions – those that occur while all organisms involved in the interaction are living – victimizing cephalopods. Specifically, we conduct a statistical meta-analysis based upon peer-reviewed publications dating back over a century to identify the prevalence of traces of parasitism and predation upon cephalopods as well as influences on the number of fossil occurrences. We also review changes in the genus-level biodiversity of cephalopods throughout deep time. We ultimately find that environmental factors including temperature and carbon dioxide levels can substantially influence both the prevalence and preservation of these interactions. However, we also advise caution in interpretation of these results, hoping they inspire further collection and analysis of cephalopod fossils for traces of interactions.

# INTRODUCTION

Biotic interactions include any interactions that occur between two or more living organisms. A pack of wolves preying upon a solitary moose, a nematode laying eggs in a human's intestines, a bird laying eggs inside a hole in a tree, and a sea sponge encrusting the surface of coral are all fine examples of biotic interactions. An antagonistic biotic interaction is any interaction between live organisms that causes harm to one of the organisms involved. The predominant types of antagonistic interactions include predation and parasitism.

Our study seeks to explore the factors influencing both the presence of evidence of predation and parasitism as well as their prevalence throughout deep time in cephalopods, a group of mollusks with a fairly detailed fossil record. To do so, it is important to first explore these biotic interactions through ecological, climatic, and geological lenses. Then, a discussion of studies focusing on cephalopods and records of their biotic interactions will be introduced before elaborating on the relevance and importance of our contribution to this field.

## Predation

Simply put, predation can be defined by one animal consuming another for nutritional value (Hellmann, 2013). The term "predation" often colloquially refers to interactions between animals, such that an animal eating plants or fungi would not constitute predation. This type of interaction is ubiquitous in the animal kingdom, occurring in vastly different environments from mountainous regions to extraordinarily deep regions of the ocean. In fact, predators are still being discovered as the oceans are explored further. *Dulcibella camanchaca*, a predatory crustacean, was recently discovered at hadal depths (greater than 6,000 meters underwater) of the Atacama Trench (Weston et al., 2024).

Both predators and prey serve important roles in the ecosystems they occupy, indicating that predation is a systematically important interaction type. First and foremost, predators help control the populations of prey species (Erlinge et al., 1984; Bergerud and Snider, 1988). In fact, the existence of a predator within the same ecosystem as its prey is known to affect the prey's behavior (Lima, 1998; Nelson et al., 2004; Sheriff et al., 2020; Allen et al., 2022). Of course, it follows that the number of prey available to a predator would influence a predator's population. If there is not enough prey available to feed a predator population, the predators either starve, seek an additional food source, begin to scavenge, or adopt other behaviors conducive to filling the dietary gap (Parsons et al., 2022).

The United Nations Convention on Biological Diversity (1992) defines biodiversity to be a measure of variance within a community, ecosystem, or even within the genetics between individuals of a species. The role that predation plays in the biodiversity of the ecosystem in which it occurs is debated, though it is often seen as generally beneficial. In a classical exploration of a rocky intertidal area, Paine (1966) found that the presence of predators kept a small number of species from monopolizing the community. Similarly, Sergio et al. (2005) explored the biodiversity of sites occupied by five raptorial species in the Italian Alps, comparing these sites to controlled sites occupied by animals of lower trophic levels. The study found that apex predator-occupied sites frequently exhibited greater biodiversity than control sites, indicating that the presence of predators increases biodiversity in some ecosystems. However, when the predators are an invasive species, their effects on ecosystem biodiversity can be detrimental (Doherty et al., 2016; Pringle et al., 2019). Confounding the issue, Natsukawa and Sergio (2022) conducted a meta-analysis on the efficacy of using top predators as biodiversity indicators. Ultimately, they found that while top predators are often sufficient biodiversity indicators for species related to their dietary niche, this relationship is less clear for species that are less closely related. Thus, while the presence of predators generally increases ecosystem biodiversity, the relationship is often case dependent.

A less obvious role that predation plays in an ecosystem is its influence on ecological processes on a broad scale. Gable et al. (2020) conducted a study on the influence of wolf predation upon beaver populations, which are widely known as "ecosystem engineers" in their wetland environments. The analysis found that, when a wolf killed a beaver generating a new pond or recolonizing an older one, the newly engineered area remained unoccupied for the remainder of the year with disruptions potentially persisting for several more. Therefore, by influencing the beavers' behaviors after successful predation, the wolves altered wetland creation, recolonization, water storage, and nutrient flows in the ecosystem.

Marine ecosystems are no stranger to predation themselves. In fact, coastal regions experience a significant overlap in food webs due primarily to carrion and seabird colonies that carry parasites and prompt the appearance of scavenging insects (Polis and Hurd, 1995). Spiders on many of the small islands studied in this analysis were found to derive most of their energy from marine origins, feeding on these scavengers, parasites, and algae eating animals found on the beach. It is clear that terrestrial and marine ecosystems are not separate, insular entities.

Much like in terrestrial ecosystems, marine ecosystems can vary widely in predation patterns. Sanford et al. (2003) found that selection on behavior occurring at the local level can affect large scale latitudinal patterns in species interactions in marine communities. The dynamics of predatory interactions in marine communities can even elucidate relationships that are not necessarily specific to those communities, giving their continued research merit.

## Parasitism

Parasitism's definition is a bit more convoluted than that of predation. Bush et al. (2001, p. 6) says of the matter "We suspect that if you assemble 10 scientists and ask them to define parasitism, you would obtain 10 different answers." One key difference separating predation from parasitism lies with the eventual fate of the interaction's victim – a predator seeks to kill its prey for nutrition, while most parasites seek to keep their host alive for a continuous nutrient source. Parasitism, like predation, is ubiquitous in nature. It has been suggested that roughly 40% of all known species are parasitic (Dobson et al., 2008). Thus, like predation, parasitism plays a very important role in ecosystem structure and interactions.

The effects that parasites have on their host organisms have been studied in intimate detail, though there is still an abundance of parasitic relationships to explore. Parasites can alter the host's reproductive abilities and strategies (Reinhard, 1956; Baudoin, 1975; Minchella and Loverde, 1981; Polak and Starmer, 1998; Fogelman et al., 2009; Hartikainen and Okamura, 2012), behaviors (see Moore, 2002 and citations therein), and growth (Iwanowicz, 2011; Kelehear et al., 2011; Thumbi et al., 2013; Desprez-Loustau et al., 2014; Chiaverano et al., 2015). Likewise, the presence of parasites induces defense mechanisms in the host, often instigating immune responses that could potentially prevent other diseases from taking a foothold (Maizels and McSorley, 2016).

In addition to the direct effects a parasite has on an individual, parasitism can influence communities on a broader scale in multiple ways. Poulin (1999) investigated both the obvious and more understated effects that parasites can have within an animal community. Poulin found that the parasites within the community can have differential effects on multiple host species (thereby controlling their relative populations), can indirectly influence the importance a host species has within their community, and can even directly limit the importance the host species has in the community by affecting the host in ways described above (though at the time, no evidence had been unequivocally confirmed that this occurred in animal communities; see Chapter 9 of Ebert, 2005). In addition to noting the importance of predation in maintaining biodiversity in an ecosystem, Paine (1966) mentions that parasites play a similar role to predators in preventing resource monopolization by one species. Clearly, parasites play an integral part in their communities by influencing their host as well as their host's ecological role.

Many parasites have a rather complex life history, potentially infecting multiple intermediate hosts in addition to their definitive host. A familiar example is *Toxoplasma gondii*, the parasite responsible for toxoplasmosis. Infected cats, the definitive host of *T. gondii*, can pass oocysts in their feces capable of transmission to most birds and mammals through feed, water, or soil (Dubey, 1996). Dubey (1996) further elaborates that *T. gondii* can then be transmitted to carnivoran hosts – including humans and uninfected cats – via consuming infected tissues.

Naturally, parasites are not limited to the terrestrial realm. A recent study confirms the presence role of ascothoracidans as endoparasitic crustaceans that feed on their host corals (Zalota et al., 2025). Williams and Jones (1994) summarizes a wide variety of parasites infecting fishes, many with intermediate hosts. One particular disease observed in many fishes, black spot disease, is known to result from an infection of larval trematodes including *Cryptocotyle* spp. (Duflot et al., 2023). In their study of black spot disease, Duflot et al. (2023) examined 1586 fishes across seven species collected by bottom trawling in the English Channel and North Sea, finding encysted larvae in 325 of those fishes (a prevalence of 20.5%). Further, they found a wide variety of infection intensity, with up to 1104 parasites found in an individual fish. Therefore, it is fair to suggest that parasitism is omnipresent in marine communities as well as terrestrial ones.

## Geologic Record

In addition to the plethora of studies conducted exclusively on the ecology and interspecies dynamics of predation and parasitism, research on environmental influences (both modern and through deep time) on biotic interactions has been conducted. Perhaps unsurprisingly, there are many instances where the state of the environment plays a key role in mediating biotic interactions. While this is observable in extant taxa, deducing these relationships in the fossil record, as well as evidence for the biotic interactions themselves, is less simple.

The United States Geological Survey's Ecosystems Land Change Science Program (2022) describes a number of different paleoenvironmental proxies that can be used to estimate various environmental conditions from Earth's past, including physical, biological, and chemical proxies (see Table 1 for a summary of these proxies). Judd et al. (2024) used a combination of climate modeling and paleoenvironmental proxies to calculate global mean surface temperature gradients resolved to 2.5 degrees of paleolatitude as well as global carbon dioxide levels dating all the way back to the Early Ordovician. This publication is one of many recent studies demonstrating the power that climate proxies have in elucidating trends in environmental change throughout geologic time.

One primary goal pushing the exploration of the paleoenvironment is to relate climate and geography to ecosystem ecology at various times in Earth's history. In other words, paleoenvironmental studies often seek to parse out the environmental and geographical factors that play a role in creating ecosystems suitable for life to thrive. In a landmark meta-analysis of nearly 600 latitudinal diversity gradients, Hillebrand (2004) found one common theme: biodiversity is usually greater in tropical regions than in polar regions. This effect, which had predominantly only been studied for specific taxonomic groups prior, revealed that the latitudinal biodiversity gradient (LBG) is a consistently occurring phenomenon across both marine and terrestrial taxa.

| Proxy Category | | Proxy Type | Common uses |
|---|---|---|---|
| Physical | | Sediment Composition | Salinity, temperature, ice cover, oxygen levels, nutrient levels, geomorphology |
| | | Texture | Sediment transportation, energy of transportation type |
| | | Structure | Depositional environment, direction of fluid flow, local earthquake activity, potential for life |
| | | Color | Sediment composition, some environmental conditions |
| | | Density | Sediment composition, grain size, sediment porosity |
| | | Magnetism | Sediment origin, sediment age |
| Biological | Aquatic | Foraminifers | Water temperature and quality, Cretaceous to modern paleoclimate (planktic forams) |
| | | Ostracodes | Water temperature, salinity, oxygen levels, some other climatic tools |
| | | Diatoms | Water temperature, nutrients present, salinity, other physical aspects |
| | | Corals | Water temperature and chemistry |
| | | Dinoflagellate cysts | Water salinity and nutrients |
| | | Mollusks | Salinity, temperature, nutrients, water depth, substrate type |
| | Terrestrial | Pollen and spores | Vegetation patterns, some climate conditions |
| | | Plant macrofossils | Environmental needs of living plant taxa, past climate and environment |
| | | Charcoal | Frequency, magnitude, and distribution of ecosystem fires |
| Chemical | | Stable Isotopes | Temperature, humidity, atmosphere, animal diets, vegetation, many other climate aspects |
| | | Elemental analyses | Erosional activity, lake and ocean productivity, land use, precipitation |
| | | Biomarkers | Distribution and abundance of source organisms, some physical climate aspects |
| | | Biogenic silica | Biological productivity, temperature, salinity, circulation |

**Table 1.** Paleoenvironmental proxies and their common uses. Information from USGS Ecosystems Land Change Science Program (2022).

Attempts have been made to conduct similar analyses of ancient biodiversity from the fossil record with varying degrees of success. While one could theoretically count all taxa present in a modern community with enough resources and dedication, even the most rigorous approach to attain a species richness count in a fossil community would fall short. In a study of dozens of animal phyla, Nicol (1977) estimated that roughly only 8% of all past species would be likely to fossilize, indicating a need to account for sampling bias in biodiversity estimates. Common methodologies used to estimate fossil biodiversity that attempt to correct for sampling biases include statistical subsampling methods such as rarefaction (e.g., Miller and Foote, 1996) and shareholder-quorum subsampling (SQS; Alroy, 2010), both of which estimate diversity of a fossil community from an assumed representative sample of fossils from that community. While neither of these methods perfectly reflect the true number of species present, they provide innovative solutions to an unsolvable problem.

A similar issue arises when attempting to find and describe evidence of biotic interactions in the geological record. Whereas parasitism and predation are fairly easy to observe in nature in live animals, inferring these interactions from fossils is much more difficult and often ambiguous (Liow and Quental, 2008). In some cases, evidence for a syn-vivo interaction is obvious in the fossil record. An extraordinary fossil reported in Han (2023) shows a struggle between *Psittacosaurus lujiatunensis* and *Repenomanus robustus* preserved in a volcanic debris flow. Preserved interactions can also occur in the marine realm, with a prime example being the famous “Fish-within-a-fish” fossil exhibit at the Sternberg Museum of Natural History in Hays, Kansas (Walker, 2006). Fossils of two animals clearly interacting with each other whilst living are unfortunately rare, however. Pathological traces of interactions (such as bite marks, repair scars, and anomalous growths) are much more common, and far more difficult to confidently identify as an interaction trace.

De Baets and Huntley (eds., 2021a and 2021b) compiled evidence for parasitism in the fossil record across a wide range of taxa, including fossil evidence for parasitic viruses, bacteria, protozoa, worms, chelicerates, crustaceans, insects, and fungi. Additionally, the books feature chapters focusing on parasitism of vertebrates, bivalves, cephalopods, and other organisms. A non-exhaustive list of fossil finds indicative of parasitism can be found within the first chapter of De Baets and Huntley (2021b, pp. 5-19), including both direct and indirect lines of evidence (De Baets et al., 2021a). Direct lines of evidence for parasitism include, but are not limited to, parasite-host interactions trapped in amber, host erythrocytes, and parasite remains preserved in coprolite. Indirect evidence includes traces such as swellings, borings, and the presence of parasite eggs in coprolites.

Kowalewski (2002) discusses both direct and indirect traces of predation in the fossil record, summarizing five main types. The first type includes trace fossils left by predators on their prey such as drill holes, repair scars, tooth marks, gnaw marks, fractures, and other structural damage. The second type relates to the digestive system of the predator, where a predatory interaction can be identified by finding remains of the prey in coprolites or stomach contents. The third refers to “Exceptional Preservational Events,” as in the “Fish-within-a-fish” exhibit or the dueling dinosaur-mammal pair described above. Kowalewski (2002) names two categories of indirect predation traces that are a bit more circumstantial. Taphonomic patterns, such as the fragmentation of bone and shell material, the accumulation of mineralized materials in a localized area, and the association of predator and prey species preserved nearby can serve as potential indicators of predation occurring. The final line of evidence, also indirect, includes evolutionary morphological and phylogenetic changes that would be indicative of the presence of the threat of predation (such as shell thickening or behavioral traits shared with close relatives).

## Cephalopoda

Cephalopoda is a class of marine organisms within the phylum Mollusca, containing extant animals including octopods and squids as well as their extinct relatives. These animals have a long history in Earth’s oceans, with the first known appearance occurring in the Late Cambrian period (Dzik, 1981). Spatially, cephalopods are distributed across wide ranges latitudinally and in the water column. Guerra et al. (2006; figure 23) shows a global distribution of the giant squid *Architeuthis*, with specimens found from the northern coast of Norway to the waters south of New Zealand. Additionally, Jamieson and Vecchione (2020) notes that while cephalopods are largely restricted to shallower oceanic depths, an in-situ sighting of the octopod *Grimpoteuthis* sp. 6957 meters below the surface indicates that cephalopods have the potential to occupy up to 99% of the global seafloor.

Given their existence in a wide array of ecosystems and with rather diverse body forms, it would be a mistake to overlook how cephalopod evolution has affected their ecological role through time. The earliest known cephalopod fossil, *Plectronoceras cambria* from northern China’s Fengshan Formation (Walcott, 1905; Jaitly et al., 2022), is thought to have evolved from the monoplacophoran *Knightoconus* due to its extraordinarily similar body plan (Yochelson et al., 1973; Webers and Yochelson, 1989). Nishiguchi and Mapes (2007, figure 8.4, p. 175) show that cephalopods quickly radiated into a number of subclasses, superorders, and orders. They add that, though the number of cephalopod subdivisions reached nine subclasses, superorders, and orders by the Early Devonian, only two subclasses exist today: the nautiloids (Nautiloidea) and the coleoids (Coleoidea). In a review of cephalopod evolution, Kröger et al. (2011) summarizes the origins of the nautiloids and coleoids, the loss of external shells in most modern cephalopods, and how shell loss may relate to the Paleozoic diversification cephalopod with a focus on molecular evidence. They note that most extant cephalopods are coleoids with reduced, internalized shells, allowing for more varied and active modes of life, even though many of their ancestors had external shells (see also: Packard, 1972). Using a Bayesian relaxed molecular clock analysis including evidence from multiple other studies, Kröger et al. (2011) found that coleoid divergence from the extant and externally shelled *Nautilus* occurred at an age of 416 ± 60 Ma.

In an in-depth analysis of evidence for the convergent evolution of cephalopods with fish on the basis of anatomy, physiology, behavior, and ecology, Packard (1972) finds that many qualities that coleoids boast today are derived from their interactions and competition with vertebrates. Looking back to the extinction of ammonites in the Cretaceous, Packard explores the evolutionary failures that did not allow them to persist into the Cenozoic. It is argued that, despite rapid speciation in ammonites during the Cretaceous, a combination of their thin shells and the ineffectiveness of their presumed pinhole-like eye in non-photic regions of the ocean prevented ammonites from avoiding predation and maintaining an ecological niche that fish could not outcompete them in.

Unlike these ammonites, *Nautilus* maintained its thick shell and was able to avoid the same selection pressures at the expense of the mobility that allow modern coleoids to successfully compete with vertebrates for similar resources (Packard, 1972). Clearly, predation upon cephalopods in conjunction with competition for resources have played significant roles in their evolutionary development.

Just as cephalopods have been preyed upon throughout deep time, they are also historically adept predators. Villanueva et al. (2017; see tables 1 and 2) summarizes biological and behavioral adaptations allowing modern cephalopods to hunt successfully. Anatomical and physiological adaptations utilized by cephalopods for predation include keen senses (notably well-developed eyes and tactile organs) used to search for prey, effective respiratory, circulatory, and nervous systems employed in the act of catching prey, physical features such as arms and suckers to assist in catching and handling prey, and advanced cognitive abilities used to learn and retain memories. Further, cephalopods have been found to employ a wide variety of hunting strategies, including ambushing, luring, pursuit, stalking, pouncing, scavenging, and even cooperation with others (Villanueva et al., 2017). Thus, it is fair to assess that many cephalopods lie in the intermediate levels of their trophic webs as they are often both predators and prey.

Neither extant nor extinct cephalopods are strangers to parasitism. In Chapter 7 of De Baets and Huntley (2021b, eds.), De Baets, Hoffmann, and Mironenko explore the fossil record of cephalopod pathologies associated with parasitism, once again summarizing a breadth of finds from numerous publications in table 7.1. The authors maintain that the most reliable ways to identify a parasitic interaction in fossil cephalopods include finding blister pearls or apertural shell growth anomalies, both of which are observed in modern analogs. However, even if parasitism is confidently determined as the cause of a pathological deformation, identifying the parasite that afflicted the fossil cephalopod is challenging due to the sheer diversity of parasitic taxa known to infect modern cephalopods (see Roumbedakis et al., 2018). De Baets et al. (2021b) notes that studies of fossil and modern cephalopods predominantly address different tissue types – fossil studies tend to examine mineralized tissues while modern studies focus on soft tissues. Further, Mesozoic ancestors of modern coleoids are mechanistically limited in fossil preservation even in deposits known for exceptional preservation (Clements et al., 2017), rendering a challenge in drawing comparisons between many extant cephalopods and their extinct relatives.

Despite the many challenges presented by the fossil record in preserving biotic interactions, research on the prevalence of predation and parasitism affecting marine invertebrates has persisted. Huntley and Kowalewski (2007) conducted a large-scale analysis of the Phanerozoic fossil record based upon a predation database of marine invertebrates (from which much of our dataset is derived), essentially demonstrating similar patterns in marine biodiversity and predation frequency. They found that rises in marine biodiversity were strongly correlated with rises in predation frequency upon invertebrates, with periods of relative stasis or decline in biodiversity displaying nearly identical trends in predation frequency.

Likewise, De Baets et al. (2021c) assembled a dataset of 2118 species-level occurrences of presumed parasitic interactions afflicting fossil marine invertebrates (from which most of our parasitism data was derived) to explore prevalence of parasitism throughout the Phanerozoic as it relates to biodiversity. The study first found that parasitism prevalence has generally increased throughout time since the Cambrian, while noting that limitations due to sampling bias may play a role in this pattern (see also: Smith, 2001; Smith and McGowan, 2007). Additionally, analogous to the results of Huntley and Kowalewski (2007), De Baets et al. (2021c) found that occurrences of parasitism are significantly correlated with mean sampled diversity – positively for mollusks and stalked echinoderms, and negative for arthropods and echinoids. The study also reviewed parasitism prevalence values across 373 single species occurrences (across multiple taxonomic groups) and found that, while parasitism prevalences in the Paleozoic (0.05, or 5%) and Mesozoic (0.04) were not statistically distinguishable, an analysis of taxa in the Cenozoic demonstrated a significantly larger prevalence (0.10).

## A study exclusively focusing on Cephalopoda

Previous literature has explored many aspects of parasitism and predation, including their effects on taxa involved and their surrounding communities at large. Many of these studies have focused on the marine realm, and some have included cephalopods as part of their study, though a study entirely dedicated to antagonistic interactions victimizing cephalopods has not yet been conducted. Our goal in this study is to expand on these analyses by exclusively focusing on the class Cephalopoda in order to elucidate how trends in cephalopod biodiversity, origination and extinction rates (the rates at which a new taxon first appears or goes extinct per unit time), age, and paleoenvironmental factors influence antagonistic interactions victimizing them.

Like other studies of its type, we will conduct a meta-analysis based on the databases of Huntley and Kowlewski (2007) and De Baets et al. (2021c), which have been expanded by a significant number of entries particularly pertaining to predation. Using similar statistical analyses like SQS to determine mean sampled diversity as well as generalized linear models (GLMs) and generalized additive models (GAMs), we aim to tell a more complete story of how cephalopods fit within their communities dating back hundreds of millions of years. Moreover, we seek to find what paleoenvironmental and paleogeographical factors contribute to how cephalopods interact with other organisms in their ecosystems, tackling their ecological setting from multiple angles.

# MATERIALS AND METHODS

Data collection for this study required combing through thousands of publications to identify potential traces of biotic interactions with cephalopods throughout deep time, building on top of existing databases featuring biotic interactions involving cephalopods (Huntley and Kowalewski, 2007; De Baets et al., 2021c). Primarily using Web of Science for newly added data, with Google Scholar playing a secondary role, search phrases such as “cephalopod predation fossil” and “fossil cephalopod predator” were entered. Then, resulting publications were reviewed for evidence of biotic interactions involving cephalopods, with references of and citations therein examined further. Additionally, paleogeographical and paleoenvironmental data was collected to supplement data sourced from the literature. Information collected from the literature included publication data (authors, title, journal, etc.), victim and assailant taxonomy, interaction frequency data, geographical location, stratigraphic unit and age, paleogeographical data, temperature and $CO_2$ data, and additional details where applicable. Each dataset entry includes occurrences featuring a single taxon of various ranks (some interactions have species-level specificity, others span more widely). A condensed version of the compiled dataset can be found in Appendix C.

Identifying traces of biotic interactions in the fossil record can be extraordinarily difficult (Liow and Quental, 2008), thus lending various degrees of certainty to data points. Primary lines of evidence include bite marks, repair scars, regurgitalites, coprolites, “frozen” interactions preserved in fossils, predator stomach contents, Housean pits, blister pearls, drillholes, and hard-shell deformities not easily explained by other processes (see Figs. 1 and 2 at the end of this section for examples of bite marks on cephalopods and parasitism, respectively). While some of these trace types, such as bite marks and drill holes, are readily indicative of biotic interactions, other traces are potentially attributable to alternative causes (e.g., blister pearls forming from non-parasitic causes, as in Stevens et al., 2020). Efforts were made to restrict dataset additions to traces where biotic interactions are suspected, though the nature of the fossil record makes these efforts inherently imperfect. Usually, this meant accepting the judgment made by the authors of the source publications and leaving the interaction out if some form of syn vivo interaction was not strongly suspected. In some publications, the interactions between the organisms clearly occurred during life, but the nature of the interactions were not explicitly stated (e.g., Ptychoceras spp. In Hoffmann et al, 2021). In these cases, we added the occurrence to the dataset without specifying an interaction type, thus not including the interaction in further analyses.

The dataset is composed of all biotic interactions affecting cephalopods, whether they were the assailant or the victim. Our study focuses specifically on those interactions victimizing cephalopods (i.e., where the cephalopods are parasitized or predated upon), though other studies can leverage other entries as needed. In an effort to control for outlier frequencies of parasitism or predation due to small sample size in our analyses of prevalence GAM, our quantitative analysis only incorporated taxa with at least ten analyzed specimens.

Geographical coordinates were collected using Google Earth locations based upon fossil localities described within the literature with varying degrees of precision. Of entries that contain geographical data, all coordinates are assumed to be within two degrees latitude and two degrees longitude of the collection site. When non-specific locality data was described in literature (e.g., fossils from the Pierre Shale of South Dakota without an included map), collection sites were approximated, often being cross-referenced with the ROCK'D mobile app's bedrock map based on the Macrostrat database (Peters et al., 2018).

Paleogeographical data was collected using GPlates version 2.5.0 (Müller et al., 2018). Using Scotese's PALEOMAP continental drift model and political boundaries as reference Plate IDs, as well as EarthByte's satellite model of Earth (see Wright et al., 2013), paleocoordinates were approximated for each entry where modern coordinates and age were available with GPlates' Kinematics tool (Scotese, 2016). The Kinematics tool allowed for a 10,000-year granularity, though the nature of the fossil record and difficulty in finding precise geographical coordinates in deep time limits the small-scale utility of this feature.

The best ages for the cephalopods, unless explicitly stated, were calculated using the mean of the oldest potential age and most recent potential age using the International Commission on Stratigraphy's chronostratigraphic chart v 2023/09 (Cohen et al., 2013, updated). For samples spanning greater than one stage, the ages at the beginning of the earliest possible stage and the end of the latest possible stage were used to find the mean. For example, the best age for a specimen described as being from the Jurassic period would be found by averaging the ages of the beginning of the Hettangian and the end of the Tithonian. Age ranges were not used in lieu of a singular numerical age due to constraints in R's processing of data.

Using the paleobioDB package in R (developed by Varela et al., 2015), we downloaded cephalopod occurrence data taken at stage-level resolution from the

Paleobiology Database (PBDB). Then, with R's divDyn package (Kocsis et al., 2019), we conducted shareholder quorum subsampling (SQS) within each stage using a quorum value of 0.4 (see Alroy, 2010 for an in-depth explanation of SQS). In essence, for each stage, we sampled until the sum of the relative proportions of taxa (compared to the entire sampled community) reached 0.4, representing 40% coverage. From repeated iterations of SQS in each stage, we calculated mean sampled diversity, genus-level three-timer (3T) origination and extinction rates, and period midpoint ages (the average of the beginning and end ages of a period) were taken from the Paleobiology Database.

Stage-scale 3T origination and extinction rates were used to account for potential sampling biases, including the Pull of the Recent and Signor-Lipps Effect, by requiring species to be collected in focal stage as well as its adjacent time bins (Alroy, 2008). Based upon Alroy's (2008) formulation and the labels seen in Fig. 1 from Alroy (2010), 3T origination rate of time bin i can be calculated as:

$$\lambda = \ln \frac{t2_{i+1}}{t3 + p}$$

where $t2_{i+1}$ are the two-timers extending from time bin i to i+1, t3 are the three-timers around bin i, and p are the part-timers. Likewise, 3T extinction rate can be calculated as:

$$\mu = \ln \frac{t2_{i}}{t3 + p}$$

where $t2_i$ are two-timers extending from time bin i-1 to i. Essentially, 3T origination rates measure the amount of newly formed taxa (genera, in our case) in time bin i+1 relative to bin i, and 3T extinction rates measure the amount of taxa that disappear in time bin i relative to i-1.

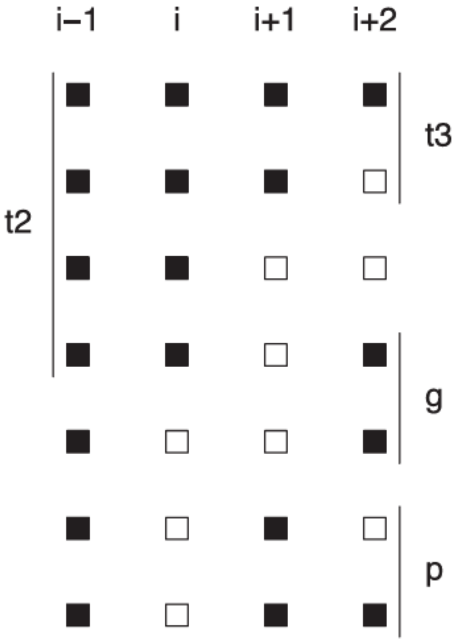

**Fig. 1.** Graphical representation of sampling patterns in a four-interval time window between times i-1 and i+2. Rows indicate taxa, with black squares representing their identification within the time interval. t2 = two-timer, t3 = three-timer, g = gap-filler, and p = part-timer. From Alroy (2014).

From the recent findings of Judd et al. (2024), we have incorporated stage-level temperature and $CO_2$ data into our analyses. For each occurrence with an age that has been resolved to a single stage and includes paleocoordinates, the temperatures at the equator, poles, and nearest latitude (at a 2.5-degree resolution) were recorded. Mean temperature gradients were found by taking the difference between equator and pole temperatures in each hemisphere and averaging the north pole-equator and south pole-equator gradients for each stage. This accounted for distinct temperature gradients affecting the two hemispheres differently. Thus, temperature gradients between the equator and poles, as well as “local” temperature, could be identified and included as metrics for modeling. Atmospheric $CO_2$ values (in parts per million) were also collected and recorded, though their values represent global carbon dioxide levels during a stage rather than localized or regional values.

Zaffos et al. (2017) finds that the degree to which continents are broken apart (the fragmentation index) is positively correlated with marine biodiversity. Their study leveraged paleocontinental geometries and positions sourced from a modified EarthByte tectonic plate reconstruction model (see Wright et al., 2013) as well as marine rock lithologic and distribution data sourced from Macrostrat (Peters et al., 2018). To account for some of the variance in assailed fossil cephalopod finds between different periods, we included the period-level fragmentation index values in modeling interaction prevalence.

Our analysis aims to answer five key questions. The first asks whether predation frequency upon cephalopods significantly differs between the Paleozoic and post-Paleozoic. Similarly, the second question asks about Paleozoic and post-Paleozoic parasitism prevalences. To answer these questions, we adopt a null hypothesis that Paleozoic and post-Paleozoic predation frequencies and parasitism prevalences are not statistically different.

The third question seeks to parse out which factors significantly influence prevalence of interactions victimizing cephalopods, and the fourth asks which factors influence the potential to preserve evidence for biotic interactions. Finally, we examined what variables significantly influence the stage-level mean sampled diversity of cephalopods at genus-level resolution. Regarding these questions, we assumed that none of the independent variables tested bore a statistically significant influence on interaction prevalence, occurrences, or mean sampled diversity unless our models proved otherwise.

To answer the first two questions, we employed Wilcoxon rank sum tests to compare frequencies of Paleozoic versus post-Paleozoic predation upon cephalopods, as well as Paleozoic versus post-Paleozoic parasitism of cephalopods. Wilcoxon rank sum tests were used because they are non-parametric, accounting for biases in sampling distribution between the two time bins (Mann and Whitney, 1947). Thus, despite having many more occurrences of cephalopods being predated upon in the post-Paleozoic, predation frequencies can still be compared with those of the Paleozoic.

To investigate factors significantly affecting the prevalence of biotic interactions, we included the following variables in a GAM: SQS mean sampled diversity, 3T origination and extinction rates, global $CO_2$ levels, latitudinally-constrained "local" temperature, the mean of the northern and southern hemisphere temperature gradients, and period midpoint age. The general form of a GAM is:

$$g(E(Y)) = \beta_0 + \sum_{i=1}^{N} s_i(x_i)$$

where E(Y) represents the expected value of the dependent variable (e.g., prevalence), g represents a link function used to transform outcome into a space specific to each distribution type (gamma, Poisson, Tweedie, etc.), $\beta_0$ is an intercept, and $s_i(x_i)$ represent smoothing functions for each independent variable (e.g., local temperature, period midpoint age) for N total independent variables. GLMs follow the same form, with each smoothing function being linear by definition. Data incorporated into our prevalence GAM was weighted by sample size to account for differences in number of specimens of each taxon analyzed, and the analysis was conducted on a reduced dataset comprised exclusively of single-taxon datasets containing at least ten examined fossil cephalopods. Because biotic interaction prevalence values are inherently between 0 and 1 and continuous in this range, we chose to use a beta regression link function to model prevalence (Ferrari and Cribari-Neto, 2004).

To explore the factors influencing the number of occurrences of biotic interactions discovered within each stage, we first refined our original dataset to only include occurrences temporally restricted to one stage. This aspect of the study is fundamentally different from our investigation of influences on interaction prevalence as we are instead seeking the factors most likely to affect the ability to preserve evidence of an antagonistic interaction, allowing us to include studies with sample sizes of less than ten cephalopods. Like in our prevalence model, a GAM was found to best model occurrences, with requisite components including carbon dioxide levels, equatorial temperature, mean sampled diversity, 3T origination and extinction rates, and continental fragmentation. However, because the number of single-taxon occurrences of evidence for antagonistic interaction in a stage represents a count instead of a proportion, a Poisson (logarithmic) link function was chosen four our data transformation.

Finally, in an exploration of influences on stage-level mean sampled diversity, we used the same dataset as in our GAM modeling occurrences. Variables tested in this analysis include the number of single-taxon occurrences in each stage, carbon dioxide levels, equatorial temperature, the mean of the northern hemispherical and southern hemispherical temperature gradients, and continental fragmentation. Experimentation with various families of models found that a Tweedie model with a power parameter of 2 yielded results with the least amount of variance (see Tweedie, 1984 for more on the Tweedie distribution).

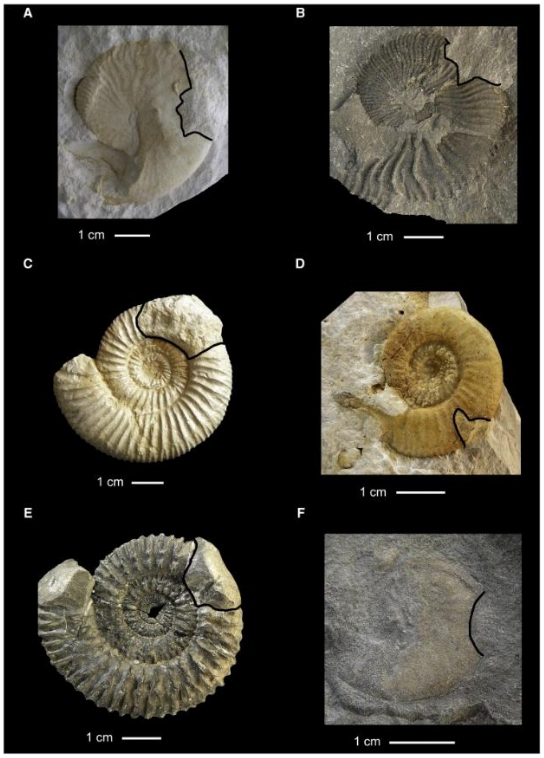

**Fig. 2.** Six Mesozoic ammonoids showing ventral damage from bite marks of a predator, outlined in black. Figure from Klompmaker et al. (2009).

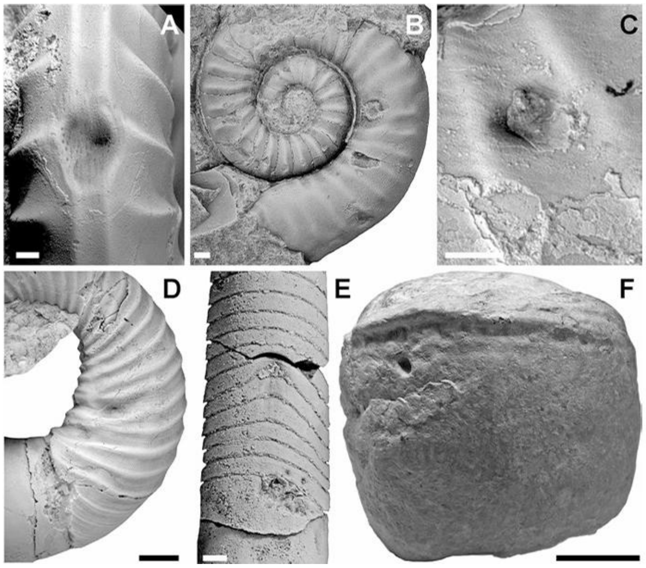

**Fig. 3.** Six nautiloids displaying blister pearls from parasites. Scale bar = 1 mm. Figure from De Baets et al. (2021b).

# RESULTS

Our core dataset contained 420 single-taxon entries, including instances where cephalopods were victims and others where cephalopods were assailants. We proceeded to filter the results to only include occurrences victimizing cephalopods (n = 294). A density distribution plot of interaction occurrences (where cephalopods were preyed upon or hosted parasites) used in our study can be found in Fig. 4. To create our prevalence GAM, we reduced this dataset further to only include single-taxon occurrences where at least ten specimens were examined for traces of biotic interactions (n = 136), thus omitting many publications reporting traces found in a single individual or select few. By limiting the amount of data analyzed and weighing it by sample size, we were able to elucidate large-scale trends demonstrating how parasitism and predation prevalence have varied over time (see Fig. 5).

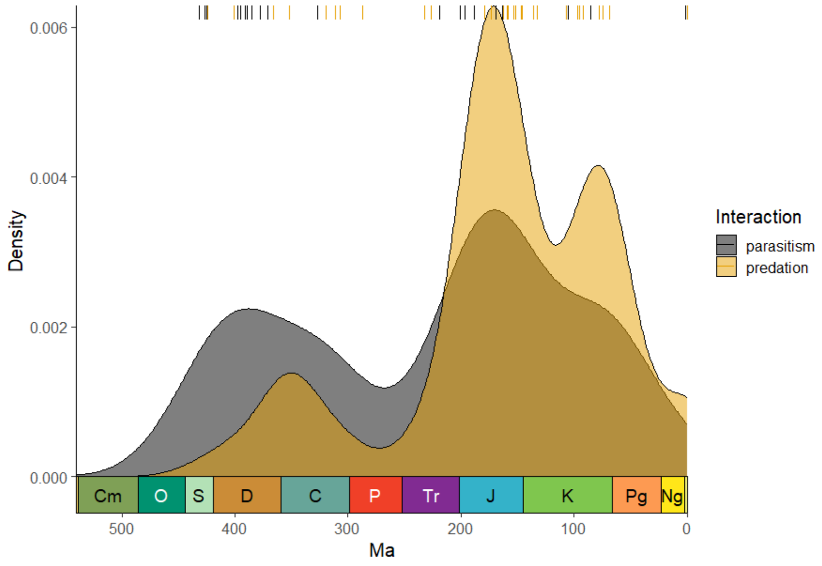

**Fig. 4.** Interaction occurrence density distributions, separated by interaction type. The rug plot at the top denotes single-taxon occurrences used in this analysis.

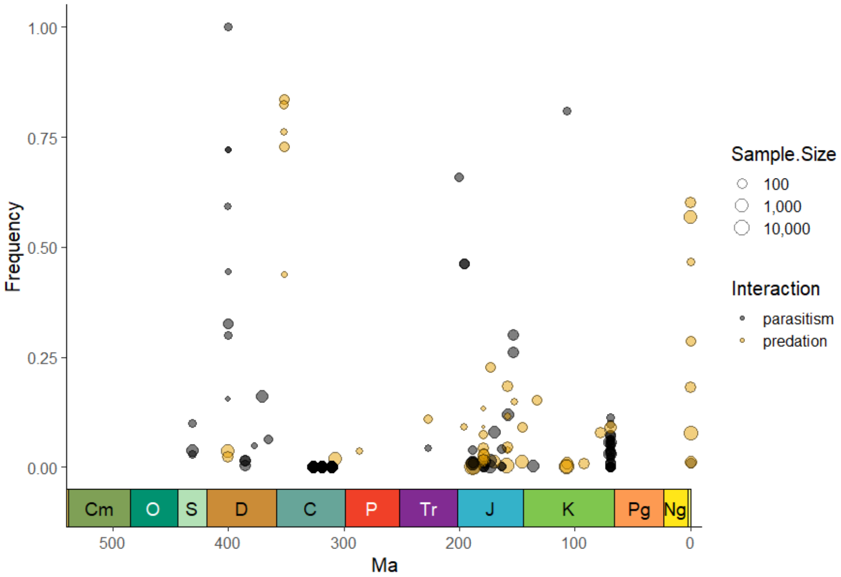

**Fig. 5.** Distribution of interaction prevalence data, with dot size weighted by sample size.

Wilcoxon rank sum tests were used to compare single-taxon predation frequencies between the Paleozoic and post-Paleozoic as well as single-taxon Paleozoic and post-Paleozoic parasitism prevalences (see Fig. 6). The median frequency of Paleozoic predation across our single-taxon occurrences was 0.4375 (43.75%) based on 9 included occurrences, whereas the median frequency of post-Paleozoic predation was 0.0776 based on 35 occurrences. The Wilcoxon rank sum test for single-taxon predation frequency showed that differences in Paleozoic and post-Paleozoic frequencies were not statistically significant (p = 0.0712) at the 95% confidence level within each taxa, though a chi-squared test reveals that overall frequencies between the Paleozoic (318/3,116; 0.1021) and post-Paleozoic (1,723/122,685; 0.0140) were statistically significant (p < 2.2e-16).

There were 41 Paleozoic occurrences and 51 post-Paleozoic occurrences of parasitism that met our criteria above. Based on raw counts, we found an overall Paleozoic prevalence of 669 victims out of 17,283 individuals examined (0.0387) and a post-Paleozoic prevalence of 256 victims out of 13,956 individuals examined (0.0183). The differences between Paleozoic and post-Paleozoic single-taxon parasitism prevalences were also statistically insignificant (p = 0.43) at the 95% confidence level, though a chi-squared test would show overall prevalences were significantly different (p < 2.2e-16).

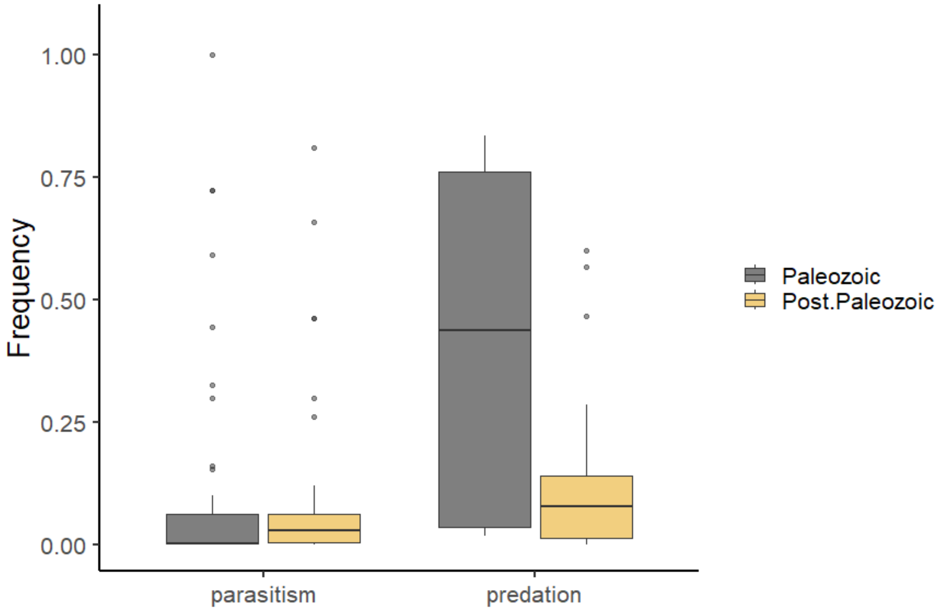

**Fig. 6.** Median Paleozoic vs. post-Paleozoic frequencies of parasitism and predation single-taxon occurrences.

Plots for our calculations of stage-level SQS-derived mean sampled diversity, genus-level 3T origination rates, and genus-level 3T origination rates can be found in Fig. 7. Note that we have mean sampled diversity data spanning from the Cambrian to modern, but our 3T origination and extinction rates date back to the Ordovician.

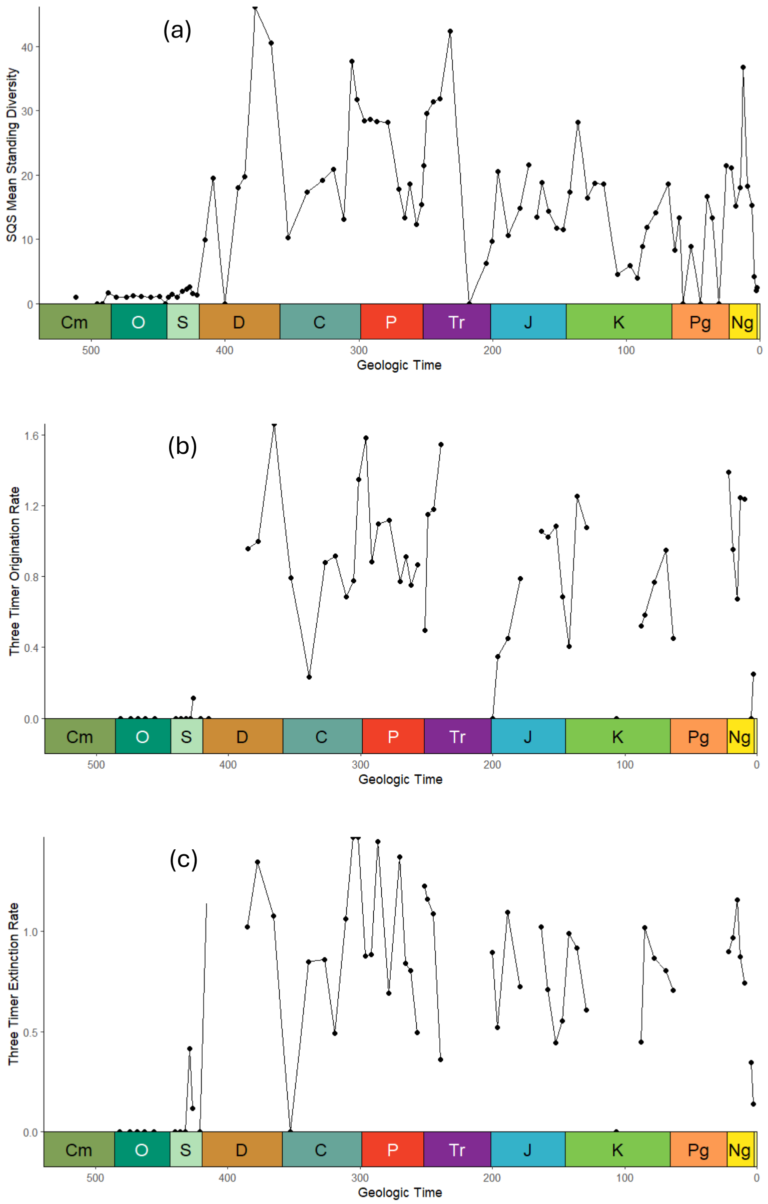

**Fig. 7.** SQS-derived (a) stage-level mean standing diversity, (b) stage-level 3T origination rates, and (c) genus-level 3T extinction rates of cephalopods throughout the Phanerozoic.

We adjusted our data in producing the prevalence GAM to only include fossil occurrences of interactions victimizing cephalopods with a sample size of at least ten specimens examined. To do so, we filtered out the eight modern occurrences that met all non-temporally based criteria, leaving 128 single-taxon occurrences to be analyzed (see Fig. 8).

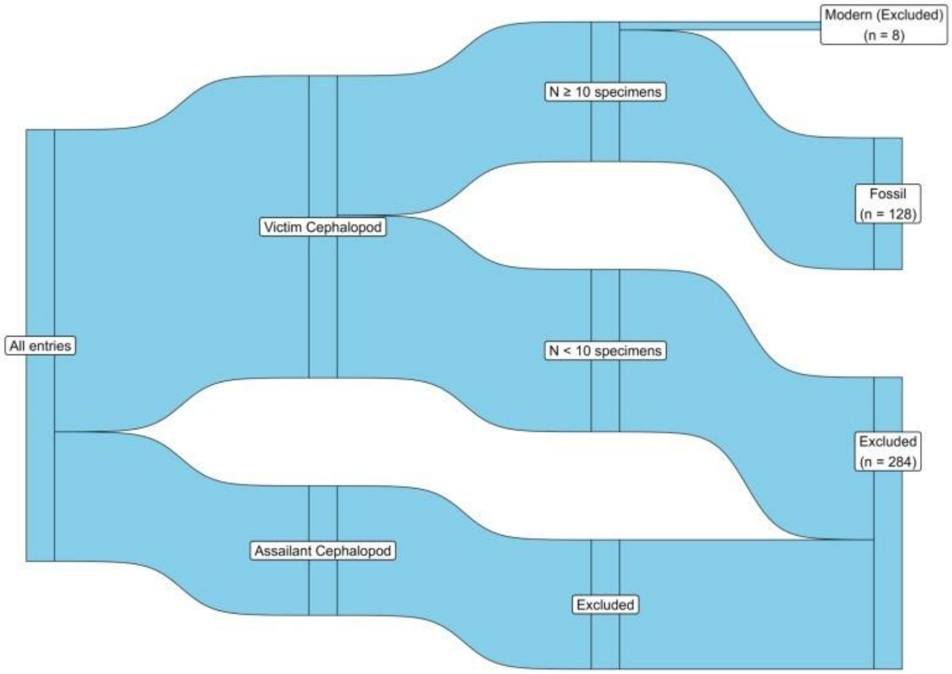

**Fig. 8.** Sankey diagram demonstrating filters applied to reach 128 fossil specimens. Made using ggsankey R package (Sjoberg, 2025).

Of the 128 single-taxon occurrences with fossil cephalopod victims and a sample size of at least ten specimens, 57 were ultimately utilized in constructing the GAM due to missing data values essential to the model. At the 95% confidence level, local temperature (p = 1.61e-05), carbon dioxide levels (p = 0.0004), and mean latitudinal temperature gradient (p = 0.0246) exhibited statistically significant relationships with interaction prevalence. By contrast, SQS-derived mean sampled diversity (p = 0.2526), 3T origination rate (p = 0.2815), 3T extinction rate (p = 0.0627), and age (p = 0.1485) did not exhibit significant relationships with prevalence at the 95% confidence level. As can be seen in Fig. 9, all partial effects of variables measured exhibited linear relationships with prevalence aside from mean sampled diversity and 3T extinction rate. Overall, 72.9% of the deviance was explained by our prevalence GAM.

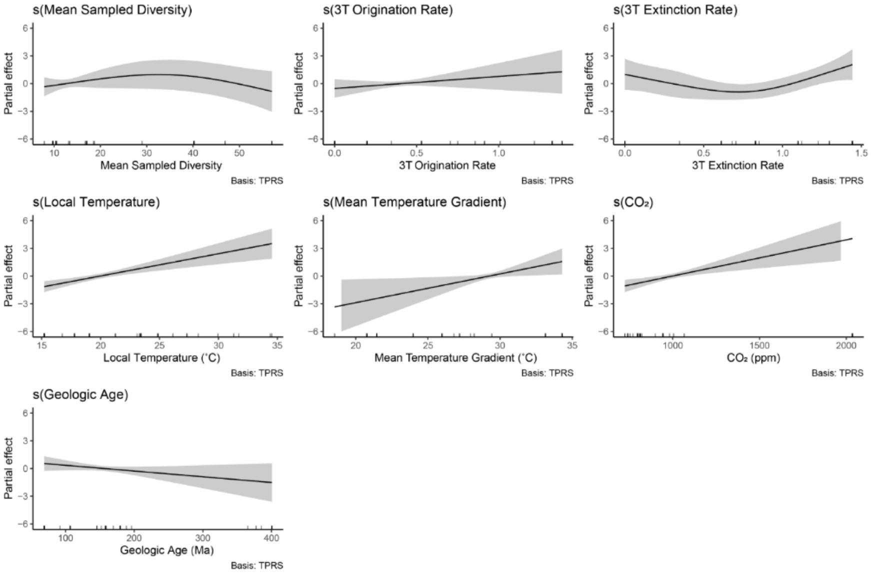

**Fig. 9.** Partial effects of the seven variables tested against prevalence, with the grey shaded area representing the 95% confidence interval. Rug plots at the bottom mark data points used in the analysis.

In our analysis of factors influencing the number of single-taxon occurrences in each stage, hereafter referred to as our occurrence GAM, we reorganized our original dataset to display the number of single-taxon occurrences temporally restricted to a single stage. Our reorganized and refined dataset contained at least one occurrence meeting this criterion in 21 different stages ranging from the Gorstian (Silurian) to the Maastrichtian (Cretaceous). At the 95% confidence level, equatorial temperature ($p < 2e-16$), carbon dioxide levels ($p < 2e-16$), SQS-derived mean sampled diversity ($p < 2e-16$), 3T extinction rate ($p = 1.02e-6$), and continental fragmentation ($p = 0.0002$) exhibited significant relationships with occurrences. 3T origination rates ($p = 0.1369$) is the only variable of the six that did not exhibit a statistically significant relationship with occurrences. Of these variables, only carbon dioxide levels and equatorial temperatures exhibited a linear relationship with occurrences, with equatorial temperature demonstrating a negative relationship (see Fig. 10).

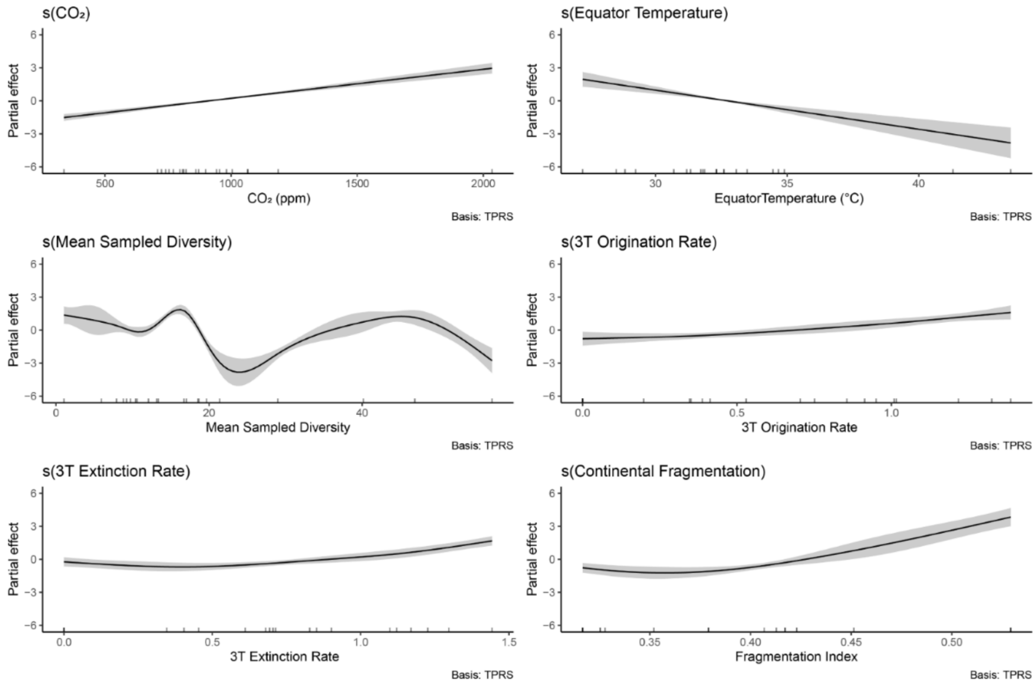

**Fig. 10.** Partial effects of the six variables tested against occurrences, with the grey shaded areas representing the 95% confidence interval. Rug plots at the bottom mark data points used in the analysis.

In determining the factors that are strong predictors of stage-level cephalopod mean sampled diversity, we found that a generalized linear model using Tweedie distribution with an index parameter of 2 explains a significant amount of model deviance. In fact, our five tested variables accounted for over 92.3% of the model's deviance. Predictors of mean sampled diversity at the 95% confidence level include the number of occurrences observed in that stage ($p = 0.0003$), the mean latitudinal temperature gradient ($p = 5.07e\text{-}07$), continental fragmentation ($p = 1.47e\text{-}07$), and the model-determined intercept ($p = 0.0292$). Carbon dioxide ($p = 0.7892$) and equatorial temperature ($p = 0.6028$) were not strong predictors of stage-level mean sampled diversity. Negative relationships were observed between mean sampled diversity and both the number of stage-level interaction occurrences as well as the mean latitudinal temperature gradient (see Fig. 11).

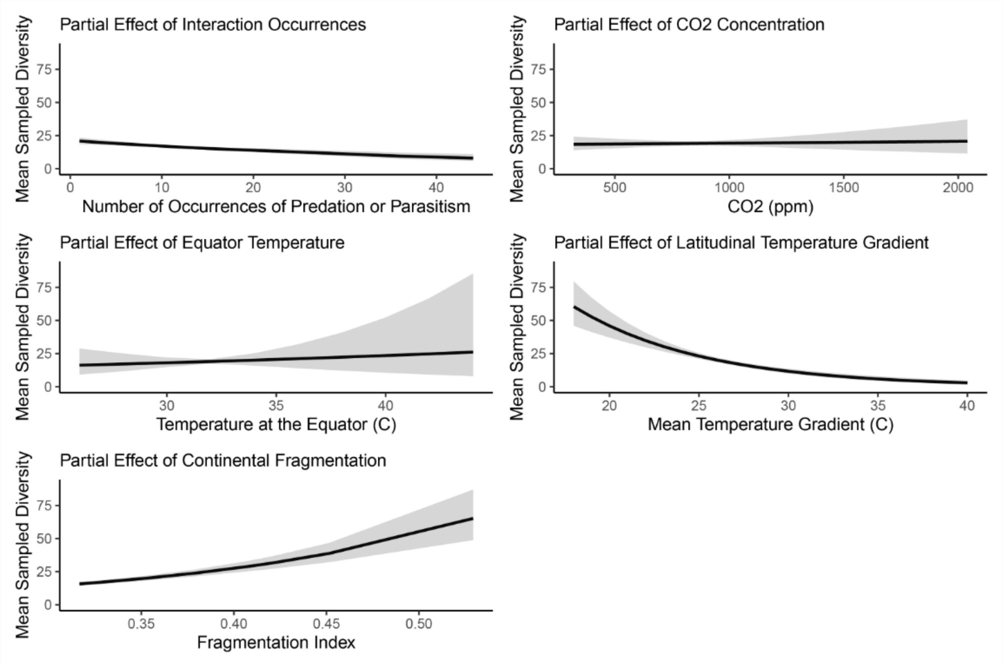

**Fig. 11.** Partial effects of the five variables tested against mean sampled diversity, with the grey areas representing 95% confidence intervals.

# DISCUSSION

Detecting evidence for biotic interactions between two organisms requires exceptional circumstances. First, in most cases, one organism would have to leave a distinct mark (or, in the case of many parasites, influence their host to repair itself in a noticeable way) on the mineralized parts of another. Then, post-mortem processes must preserve evidence of the interaction as the organism undergoes diagenesis. During and after diagenesis, an array of geological processes (e.g., tectonic activity, metamorphism, etc.) can wipe away the fossilization progress made by the organism. Finally, the fossilized organism would have to be found and shown to a researcher who can evaluate the fossil for evidence of parasitism or predation. It is then easy to understand the limitations of paleoecology and why relatively few studies tackle predation and parasitism in fossil communities in tandem.

In our analysis, we sought to answer key questions regarding the prevalence of each interaction type through time, which variables contribute significantly to prevalence, which variables contribute significantly to counts of single-taxon occurrences in any given stage, and which variables are strong predictors of mean sampled diversity. Herein, we will address each question individually.

## 1. Does predation frequency differ between the Paleozoic and post-Paleozoic?

Referring back to Fig. 6, the untrained eye might declare a substantial decrease in predation frequency moving from the Paleozoic into the post-Paleozoic. However, sample size plays a significant role in creating this illusion. Whereas our filtered dataset included 35 post-Paleozoic occurrences, only 9 Paleozoic occurrences were useable in this analysis. Thus, it is not particularly surprising that the relationship between these large temporal bins and frequency of predation within each taxon are not statistically significant. In a case study of ammonoids and nautiloids from the Upper Carboniferous of Texas, Mapes and Chaffin (2003) found extremely high frequencies of potentially fatal predation traces, with 88% of recovered ammonoids (n = 206), 33% of *Liroceras* nautiloids (n = 297), and between 33%-83% of other nautiloids (combined n = 395) displaying such traces, though they explicitly note that frequencies of sublethal repairs may not be accurate indicators of predation frequency.

Huntley and Kowalewski (2007) observe an opposite trend in frequency of predation traces, albeit in a study of all marine invertebrates. They show a roughly bimodal distribution in predation trace frequency, demonstrating predation trace frequencies of roughly 0.08 in the mid-Paleozoic followed by a subsequent drop in frequency that does not reach the mid-Paleozoic level until approximately 100 Ma (see Fig. 12). It is worth noting that our predation frequency value for cephalopods overall approaches the value found in their analysis. Our overall post-Paleozoic predation prevalence of 0.0140 is significantly less than Huntley and Kowalewski's findings for the combination of all marine invertebrates, suggesting that an increase in studies of predation on Paleozoic cephalopods in particular may provide data that lowers the Paleozoic frequency to a similar value. Taken at face value, our overall Paleozoic predation frequency is over seven times greater than that of the post-Paleozoic. We believe that this could be due to biases in sampling or sample analysis, where a trace-rich community may be more likely to be explored, or vague markings on Paleozoic specimens may be misinterpreted as resulting from a predatory attack. It is also possible that, as coleoids began to thrive in the post-Paleozoic, predators of cephalopods may have consumed these soft-bodied cephalopods in the place of shelled ones (thereby decreasing preserved interactions). Based on the statistical significance of the chi-squared test and insignificance of the Wilcoxon rank sum test between the Paleozoic and post-Paleozoic, we can conclude that while in-taxon predation frequency (i.e., the frequencies of predation upon any given taxa) remained fairly consistent between taxa across time, overall predation frequency may not have.

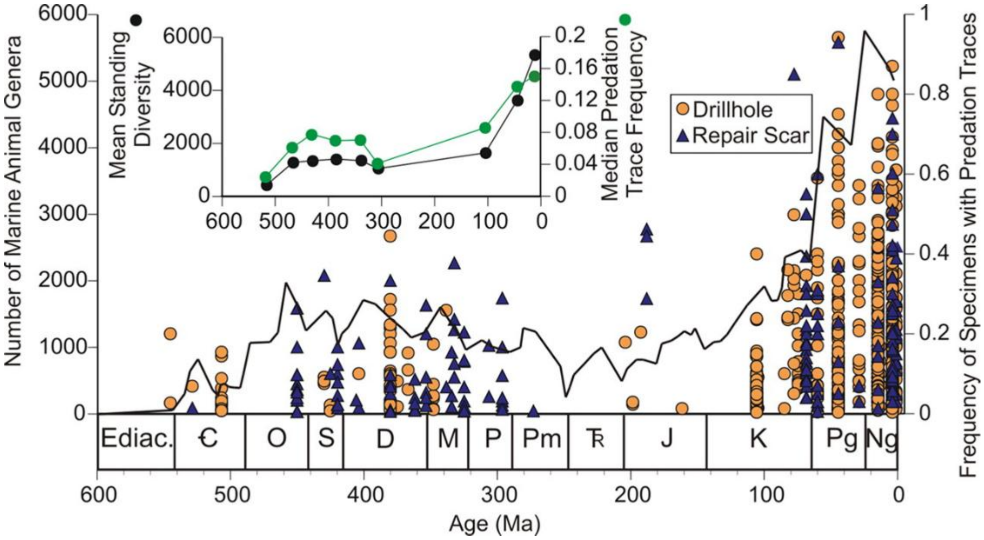

**Fig. 12.** A comparison of marine invertebrate mean sampled diversity (black line) and predation frequency throughout geologic time. The inset figure compares trends in mean standing diversity (black) and median predation trace frequency (green). From Huntley and Kowalewski (2007).

## 2. Does parasitism prevalence differ between the Paleozoic and post-Paleozoic?

Once again referring to Fig. 6, there is a slight increase in prevalence of parasitism between the Paleozoic and post-Paleozoic. The median values demonstrate a far lower prevalence than in predation, though we suspect that the difficulty in recognizing parasitic traces in the fossil record in tandem with the difficulty in preserving such traces in the first place may play a significant role. Both our Paleozoic and post-

Paleozoic values display opposite effects of the cephalopods examined in De Baets et al. (2021c; see their supplementary data). Their study found a parasitism prevalence of 42 out of 1992 individuals (0.0211) in the Paleozoic (albeit only from the Silurian and Devonian) and 100 out of 17068 individuals (.0059) in the post-Paleozoic. A simple Chi-squared test reveals that these values are statistically significant at the 95% confidence level ($p = 2.131e-13$), indicating that the difference in prevalences between the two broad timespans are reflective of actual trends. In a similar fashion to predation, these results allow us to argue that in-taxon prevalences of parasitism remain fairly consistent across taxa of both time intervals, though parasitism frequency increases by around two-fold overall.

### 3. What factors influence the prevalence of interactions victimizing cephalopods?

Environmental factors including local temperature, carbon dioxide levels, and the mean temperature gradients were found to be statistically significant, but their degree of influence on interaction prevalence can certainly vary. In partial effect plots like those in Fig. 5 and Fig. 6, overall shape matters most in interpretation. At any given value of an independent variable (local temperature, carbon dioxide levels, etc.) in an individual partial effects plot, the partial effect value relative to zero represents the degree of influence that point has on the outcome variable (e.g., prevalence) with all other independent variables held equal.

Focusing on our three statistically significant variables, we find that increases in local temperature, carbon dioxide levels, and mean temperature gradient all lead to an increase in prevalence, all else the same. In particular, greater local temperatures seem to have a particularly strong influence on prevalence. Though carbon dioxide levels show a similar trend with a high partial effect value at substantial values, the rug plot at the bottom shows that there is only one stage (Emsian) included in the analysis with levels greater than 1500 ppm (2034.949 ppm). Thus, this partial effect plot's influence on prevalence should be interpreted cautiously. Lastly, though mean temperature gradient exhibits a significant relationship with interaction prevalence, it does not seem to influence values of prevalence as significantly as either local temperature or carbon dioxide.

A positive relationship between environmental temperature and predation intensity is a known phenomenon in both terrestrial predators (Rall et al., 2010) and marine predators (Ashton et al., 2022). In their analysis of fish and other large, mobile marine predators, Ashton et al. (2022) finds that water temperature is more strongly related to predation intensity than latitude, confirming that local temperature plays a significant role in predation frequency even if latitudinal trends do not reflect the relationship as closely. Both Rall et al. (2010) and Vucic-Pestic et al. (2010) argue that increased temperatures lead to increased metabolic rates, requiring the predator to consume more prey to match energy output. It is reasonable to assume that this relationship holds for marine predators as well. Likewise, Godwin et al. (2020) found that during years of increased temperature, wild juvenile salmon were exposed to substantially greater populations of parasitic sea louse than years of less extreme temperature. Thus, intensity of parasitic interactions in marine environments are also intimately linked to temperature.

Allan et al. (2017) studied the effects of elevated temperature and carbon dioxide levels on coral reef fish, finding that predators demonstrated greater capture rates at higher temperatures alone, higher carbon dioxide levels alone, or both when compared to controls. This finding suggests that in our study, elevated carbon dioxide levels may positively encourage enough interactions (specifically predatory interactions) to counteract shell dissolution instigated by elevated carbon dioxide levels (see Nienhuis et al., 2010), though this interpretation would need significantly more study for confirmation as we suspect creating predation traces may accelerate shell dissolution. Another interpretation could be that, since elevated temperatures and carbon dioxide levels are often interrelated, an increase in one may cause an increase in the other. Under that interpretation, it is possible that prevalence rises significantly with the increase of one of those factors while the other influences prevalence merely by association with a rise in the first. The most likely cause for the significant relationship between carbon dioxide and prevalence is that a handful of well-preserved cephalopod samples from the Emsian persisted despite extremely high carbon dioxide levels, heavily skewing the partial effects plot and expected count as a result.

### 4. What factors influence the potential to preserve evidence of biotic interactions?

Paleoenvironmental factors, paleogeographical factors, cephalopod diversity, and 3T extinction rates all present a significant relationship with our single-taxon occurrence data according to our occurrence GAM. Our occurrence GAM accounted for 100% of the deviance in occurrence data, though this is likely due to overfitting of the GAM around relatively few data points (21 stages) as can be observed on the partial effect plot of mean sampled diversity. Of the variables displaying a significant relationship with interaction occurrences, carbon dioxide levels, equatorial temperature, and continental fragmentation seemed to bear the most influence. Carbon dioxide levels may influence the occurrence GAM via the same mechanism that they influenced prevalence – by increasing successful rates of predator capture, thus leaving more cephalopod shells to preserve. However, it is once again more likely due to skewing by Emsian data entries.

Equatorial temperatures tell a very different story in occurrences than they did in our prevalence GAM. Only lower equatorial temperatures seem to have a moderately significant influence on preservation of interaction occurrences, and that effect is negative. In other words, increased equatorial temperature seems to contribute to less preserved occurrences (to an extent). It is possible to interpret equatorial temperature's effect on occurrences in tandem with their effect on prevalence. In the same way that increased temperature leads to increased predation frequency and success (Allan et al., 2017; Ashton et al., 2022) as well as parasitic activity (Godwin et al., 2021), it is fair to assume that the biosphere as a whole is more active. Perhaps, increased temperatures could influence predators to consume cephalopods wholly, without leaving a trace.

Davidson et al. (2013) found that the burrowing habits of the crustacean *Sphaeroma quoianum* increased levels of bioerosion with increased temperature. They also determine that increased seawater temperatures will increase bioerosion rates of other species, affecting marine habitats and structures. Then, it is feasible to predict that increased biological processes, including bioerosion, may play a role in hiding interaction occurrences.

Lastly, continental fragmentation exhibits a strong positive influence on the number of occurrences recovered, especially when continents are fragmented to a great degree. This relationship may exist due to taphonomic effects. As Shaw et al. (2021) found, shallow, near-shore environments tend to have a much greater fossilization potential than open ocean environments. As continents fragmented further, more near-shore environments were inherently generated, thus allowing for more environments with greater fossil preservation potential to exist and preserve the cephalopods occupying those regions.

### 5. What factors influence the mean sampled diversity of cephalopods?

Predictors of cephalopod mean sampled diversity include the number of single-taxon occurrences in a stage (negative relationship), the mean latitudinal temperature gradient (negative), and the degree of continental fragmentation (positive). It is important to note that while our partial effects plot of occurrences versus mean sampled diversity show a negative relationship (i.e., an increase in number of single-taxon occurrences with preservation of an interaction predicts a decrease in mean sampled diversity), the relationship is weak as denoted by the shallow slope (see Fig. 11). Mean latitudinal temperature gradient and continental fragmentation seem to have much more predictive power.

When reviewing the effects of mean latitudinal temperature gradients on diversity, careful interpretation is required. Low temperature gradient values do not imply a lower global temperature overall. In fact, they might tell the opposite story. Times when mean latitudinal temperature gradients are minimized may be associated with greater global temperatures overall, an idea corroborated by Gaskell et al. (2022). Chaudhary and Costello (2023) show that marine species turnover is greatest at the equator (where Earth is generally warmest), with species richness showing a dip at the equator but bimodal peaks in equator-adjacent latitudes. Further, they show a clearly positive relationship between species richness and species turnover in general. Succinctly, lower latitudinal temperature gradients may imply periods of warmth, which show greater species turnover rates with potential links to taxonomic richness. However, more data is needed to confirm this phenomenon in cephalopods alone.

Continental fragmentation's role in mean sampled diversity seems relatively straightforward. As continents are fragmented further, more near-shore environments are created, allowing for more niches to be formed. This phenomenon effectively reflects the principles underlying species-discovery curves applied to a marine realm: as more coastline environments are created, which tend to be more biodiverse than pelagic areas (see Belgrano et al., 2013, pp. 688-689, for an example pertaining to fishes), more species are likely to be discovered (or recovered, paleontologically).

While reviewing cephalopod biodiversity and its influences, we draw attention to Fig. 7, which displays the mean standing diversity, 3T origination rates, and 3T extinction rates that we found for cephalopods using 50 iterations of shareholder-quorum subsampling based on a sample size of 107,273 cephalopod genus occurrences from the PBDB. Alroy (2008) demonstrated similar trends across all marine invertebrates (albeit without using three-timer rates) in origin, with peaks in origination rates around the end of the Devonian, early Triassic, and early Cretaceous. Our peaks reach values above 1.0, suggesting extraordinarily high origination of new genera, whereas Alroy (2008) shows more moderate origination rates. While our extinction rate magnitude matches that of Alroy (2008) fairly closely, the pattern itself does not. We show a pattern that is much more volatile, potentially resulting from our data being restricted to cephalopods rather than accounting for all marine invertebrates. Fig. 13 below shows an adapted plot from PBDB Navigator's, spanning from the Silurian to present.

Our graphic of mean sampled diversity demonstrates many stage-level fluctuations. The peaks of mean sampled diversity largely coincide with 3T origination rate peaks but also seem to occur where 3T extinction rates are high. However, our number of genera are significantly undercounted when compared to prior studies (see Kröger and Yun-Bai, 2009, for an example of Ordovician genera). We believe that the quorum value of 0.4 may largely underrepresent the number of genera in each time interval (see Fig. 14) but still shows overall trends. Lastly, across all SQS-derived values, we suggest that some degree of inaccuracy occurs due to some degree of bias within PBDB samples, as Mesozoic samples alone account for greater than 76.7% of total cephalopod occurrences.

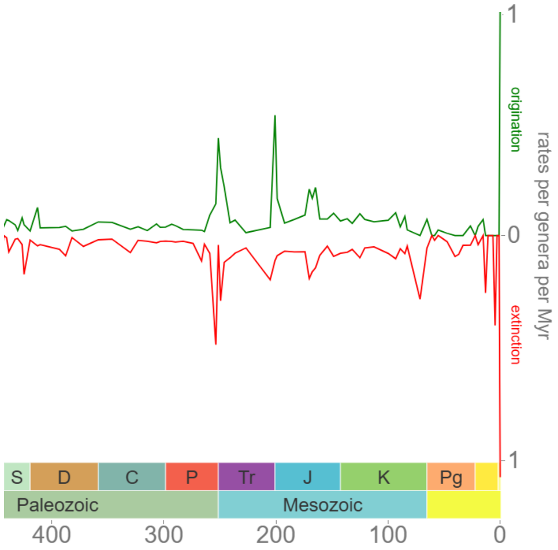

**Fig. 13.** Cephalopod origination and extinction rates based of PBDB data, estimated using methodology from Foote (2000). Figure adapted from plot generated in PBDB Navigator, with x-axis values in Ma.

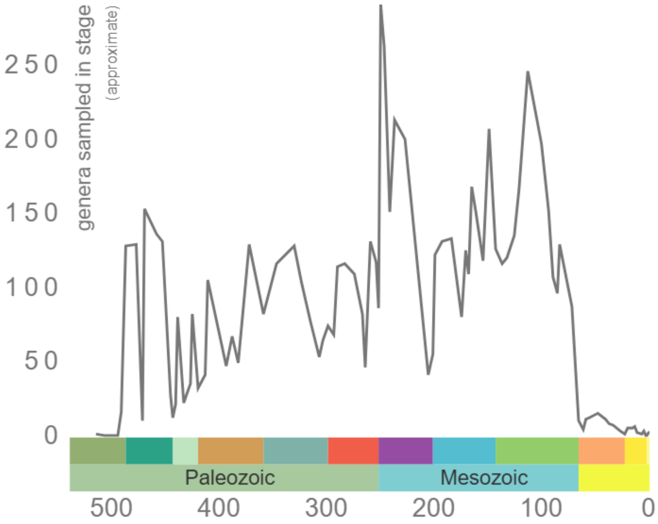

**Fig. 14.** Cephalopod genera diversity throughout the Phanerozoic, based on PBDB data. Plot generated in PBDB Navigator, with x-axis values in Ma.

# CONCLUSION

In our meta-analysis of the interaction ecology of cephalopods throughout deep time, we have uncovered both temporally and environmentally dependent ecological patterns, as well as patterns that seem to reflect more about their taphonomy. Going from the Paleozoic to the post-Paleozoic, we have found an increase in overall parasitism prevalence and a decrease in overall predation frequency. However, these same trends are not reflected when considering the median values produced by in-taxon occurrences, suggesting that overall trends in interactions are not necessarily reflective of trends within any individual taxon. Still, we established strong relationships between environmental factors and in-taxon predation frequency across a wide range of cephalopods.

As in prevalence, we found significant relationships between environmental factors like carbon dioxide and equatorial (rather than local) temperatures and occurrences of single-taxon interaction traces. Additionally, we found that as continents broke apart further, it is more common to find these occurrences. In an examination of predictors of cephalopod mean sampled diversity, we determined that greater latitudinal homogeneity in temperature and a greater degree of continental fragmentation are both strong predictors.

Herein, we have established the important contribution that the environment plays in regulating cephalopod interactions and diversity but acknowledge that significantly more data would help elucidate trends further. In particular, we hope to encourage the examination of cephalopod fossils for interaction traces from temporally diverse geologic settings. We have discussed the lacking observations surrounding the Permian-Triassic extinction event but are still lacking data in other periods during which cephalopods existed (e.g., Cambrian, Ordovician). Many studies have reported an exceptional trace (or traces) on an individual fossil, but few have explored broader scale ecological interactions with fossil cephalopods as the focus. As many cephalopods tend to be in the middle trophic levels of their communities, their interactions can provide a wealth of information regarding trophic structures, both present and past. For that reason, exploring their fossil record informs us about their present ecology.

# APPENDIX A

## Prevalence, Occurrence, and Biodiversity R Script

```
library(tidyverse)
library(deeptime)
library(ggthemes)
library(car)
library(AER)
library(tweedie)
library(statmod)
library(ggeffects)
library(glmmTMB)
library(DHARMa)
library(mgcv)
library(MASS)
library(gratia)
library(patchwork)
library(ggsankey)
library(ggplot2)
library(purrr)

CephInt <- read.csv("C:/Users/zachm/Downloads/CephalopodInteractions03172025
    (1).csv", header = TRUE, sep = ",")
CephInt$Prevalence <- as.numeric(CephInt$Prevalence)
```

```
CephInt$Temp.Grad.North <- (Eq.Temp..Judd.et.al.. - NP.Temp..Judd.et.al..)

CephInt$Temp.Grad.South <- (Eq.Temp..Judd.et.al.. - SP.Temp..Judd.et.al..)

CephInt$Temp.Grad.Mean <- ((Temp.Grad.South + Temp.Grad.North)/2)

attach(CephInt)


CephPredPara <- CephInt %>%

  filter(Interaction == "predation" | Interaction == "parasitism") %>%

  filter(Victim.Class == "Cephalopoda")


CephPred <- CephPredPara %>%

  filter(Interaction == "parasitism")


CephPredParaN10 <- CephPredPara %>%

  filter(Sample.Size >= 10) %>%

  filter(!is.na(Prevalence))


CephPredParaN10Fossil <- CephPredParaN10 %>%

  filter(best.age > 0)


attach(CephPredParaN10Fossil)


attach(CephPredPara)
```

```
ggplot(data = CephPredPara, aes(best.age)) + geom_density(aes(fill=Interaction),
    alpha=0.5) + geom_rug(aes(color=Interaction), sides = "t", linewidth =0.5) +
    xlab("Ma") + ylab("Density") + scale_x_reverse() + scale_fill_colorblind() +
    scale_color_colorblind() + xlim(c(540,0)) + coord_geo() + theme_classic(base_size =
    15)

ggplot(data = CephPredParaN10, aes(best.age, Prevalence)) +
    geom_point(aes(fill=Interaction, size = Sample.Size), shape=21, color="black",
    alpha=0.5) + xlab("Ma") + ylab("Frequency") + scale_x_reverse() +
    scale_fill_colorblind() + scale_size(trans = "log10", breaks = c(100, 1000, 10000),
    labels = c("100", "1,000", "10,000")) + xlim(c(540,-10)) + ylim(c(-0.05, 1.05)) +
    coord_geo() + theme_classic(base_size = 15)

attach(CephPredParaN10)
nrow(subset(CephPredParaN10, Interaction == "predation" & Paleozoic=="Paleozoic"))
nrow(subset(CephPredParaN10, Interaction == "predation" &
    Paleozoic=="Post.Paleozoic"))
median(subset(CephPredParaN10$Prevalence, Interaction == "predation" &
    Paleozoic=="Paleozoic"))
median(subset(CephPredParaN10$Prevalence, Interaction == "predation" &
    Paleozoic=="Post.Paleozoic"))
```

```
wilcox.test(subset(CephPredParaN10$Prevalence, Interaction == "predation" &
    Paleozoic=="Paleozoic"), subset(CephPredParaN10$Prevalence, Interaction ==
    "predation" & Paleozoic=="Post.Paleozoic"))

ggplot(data = subset(CephPredParaN10, Interaction=="predation")) +
    geom_boxplot(aes(Paleozoic, Prevalence))

attach(CephPredParaN10)
nrow(subset(CephPredParaN10, Interaction == "parasitism" & Paleozoic=="Paleozoic"))
nrow(subset(CephPredParaN10, Interaction == "parasitism" &
    Paleozoic=="Post.Paleozoic"))
median(subset(CephPredParaN10$Prevalence, Interaction == "parasitism" &
    Paleozoic=="Paleozoic"))
median(subset(CephPredParaN10$Prevalence, Interaction == "parasitism" &
    Paleozoic=="Post.Paleozoic"))

ggplot(data = CephPredParaN10) + geom_boxplot(aes(Interaction, Prevalence,
    fill=Paleozoic), alpha=0.5) + xlab("") + ylab("Frequency") + ylim(c(0,1.05)) +
    scale_fill_colorblind() + theme_classic(base_size = 20) + theme(legend.title =
    element_blank())

attach(CephPredParaN10Fossil)
```

```
PrevalenceGAM <- gam(Prevalence ~
                    s(MeanSampledDiversity) +
                    s(X3TOriginationRate) +
                    s(X3TExtinctionRate) +
                    s(Loc.Temp..Judd.et.al..) +
                    s(Temp.Grad.Mean) +
                    s(CO2) +
                    s(best.age),
                  family = betar(link = "logit"),
                  data = CephPredParaN10Fossil,
                  method = "REML")

summary(PrevalenceGAM)

plot(PrevalenceGAM, pages = 7, shade = TRUE, rug = TRUE, scale = 0)

gam.check(PrevalenceGAM)

summary(PrevalenceGAM)$dev.expl

plot(PrevalenceGAM, pages = 1, shade = TRUE, terms="CO2", rug = TRUE, scale = 0)

PrevalenceGAMPlots <- draw(PrevalenceGAM, select = NULL)
```

```
CustomPrevalenceGAMPlots <- lapply(seq_along(PrevalenceGAMPlots), function(i) {
  PrevalenceGAMPlots[[i]] +
    theme_classic() +
    scale_fill_viridis_c(option = "C") +
    ylim(c(-6,6))
})

combined_plot <- wrap_plots(CustomPrevalenceGAMPlots) + plot_layout(nrow = 3)

ggsave("PrevalenceGAM.pdf", plot = combined_plot, dpi = 300, width = 12, height = 8,
      units = "in")

attach(CephPredPara)
OccurrenceSummary <- CephPredPara %>%
  filter(first.stage == last.stage) %>%
  group_by(first.stage) %>%
  # filter(!is.na(CO2) & !is.na(Eq.Temp..Judd.et.al..) & !is.na(Temp.Grad.Mean) &
      !is.na(MeanSampledDiversity) & !is.na(X3TOriginationRate) &
      !is.na(X3TExtinctionRate) & !is.na(FI)) %>%
  reframe(nOccurrences = n(),
          Sample.Size = sum(Sample.Size, na.rm = TRUE),
          CO2 = unique(CO2),
```

```
        EquatorTemp = unique(Eq.Temp..Judd.et.al..),
        MeanTempGrad = unique(Temp.Grad.Mean),
        MeanSampledDiversity = unique(MeanSampledDiversity),
        OriginationRate = unique(X3TOriginationRate),
        ExtinctionRate = unique(X3TExtinctionRate),
        Fragmentation = unique(FI)
  )

ggplot(data = OccurrenceSummary) +
    geom_histogram(aes(MeanSampledDiversity),fill="darkgrey", color="black")

glm_tweedie_2 <- glm(MeanSampledDiversity ~ nOccurrences + CO2 + EquatorTemp +
    MeanTempGrad + Fragmentation,
                data = OccurrenceSummary,
                family = statmod::tweedie(var.power = 2, link.power = 0),
                weights = Sample.Size)

summary(glm_tweedie_2)

plot_nOcc <- plot(ggpredict(glm_tweedie_2, terms = "nOccurrences"))
plot_CO2 <- plot(ggpredict(glm_tweedie_2, terms = "CO2"))
plot_Temp <- plot(ggpredict(glm_tweedie_2, terms = "EquatorTemp"))
plot_Grad <- plot(ggpredict(glm_tweedie_2, terms = "MeanTempGrad"))
```

```
plot_Frag <- plot(ggpredict(glm_tweedie_2, terms = "Fragmentation"))


plot_nOcc

plot_CO2

plot_Temp

plot_Grad

plot_Frag


glmnOccur <- ggpredict(glm_tweedie_2, terms = "nOccurrences")

glmCO2 <- ggpredict(glm_tweedie_2, terms = "CO2")

glmEqTemp <- ggpredict(glm_tweedie_2, terms = "EquatorTemp")

glmMeanTempGrad <- ggpredict(glm_tweedie_2, terms = "MeanTempGrad")

glmFrag <- ggpredict(glm_tweedie_2, terms = "Fragmentation")



pnOccur <- ggplot(data = glmnOccur) + geom_line(aes(x=x, y=predicted), size=1.2) +
    geom_ribbon(aes(x=x,ymin = conf.low, ymax = conf.high), alpha = 0.2) +
    ylim(c(0,90)) + labs(x = "Number of Occurrences of Predation or Parasitism", y =
    "Mean Sampled Diversity", title = "Partial Effect of Interaction Occurrences") +
    theme_classic(base_size = 15)
pCO2 <- ggplot(data = glmCO2) + geom_line(aes(x=x, y=predicted), size=1.2) +
    geom_ribbon(aes(x=x,ymin = conf.low, ymax = conf.high), alpha = 0.2) +
```

```
    ylim(c(0,90)) + labs(x = "CO2 (ppm)", y = "Mean Sampled Diversity", title = "Partial
    Effect of CO2 Concentration") + theme_classic(base_size = 15)
pEqTemp <- ggplot(data = glmEqTemp) + geom_line(aes(x=x, y=predicted), size=1.2) +
    geom_ribbon(aes(x=x,ymin = conf.low, ymax = conf.high), alpha = 0.2) +
    ylim(c(0,90)) + labs(x = "Temperature at the Equator (C)", y = "Mean Sampled
    Diversity", title = "Partial Effect of Equator Temperature") + theme_classic(base_size
    = 15)
pMeanTempGrad <- ggplot(data = glmMeanTempGrad) + geom_line(aes(x=x,
    y=predicted), size=1.2) + geom_ribbon(aes(x=x,ymin = conf.low, ymax = conf.high),
    alpha = 0.2) + ylim(c(0,90)) + labs(x = "Mean Latitudinal Temperature Gradient (C)",
    y = "Mean Sampled Diversity", title = "Partial Effect of Mean Latitudinal
    Temperature Gradient") + theme_classic(base_size = 15)
pFrag <- ggplot(data = glmFrag) + geom_line(aes(x=x, y=predicted), size=1.2) +
    geom_ribbon(aes(x=x,ymin = conf.low, ymax = conf.high), alpha = 0.2) +
    ylim(c(0,90)) + labs(x = "Fragmentation Index", y = "Mean Sampled Diversity", title
    = "Partial Effect of Continental Fragmentation") + theme_classic(base_size = 15)

MeanSampledDiversityGLMplot <- wrap_plots(pnOccur, pCO2, pEqTemp,
    pMeanTempGrad, pFrag, nrow = 3)

ggsave("MeanSampledDiversityGLMPlot.pdf", plot = MeanSampledDiversityGLMplot,
    dpi = 300, width = 12, height = 8, units = "in")
```

```
attach(OccurrenceSummary)

gam_poissonk12 <- gam(nOccurrences ~ s(CO2) + s(EquatorTemp) +
                        s(MeanSampledDiversity, k=12) +
                        s(OriginationRate) +
                        s(ExtinctionRate) +
                        s(Fragmentation),
                      data = OccurrenceSummary,
                      family = poisson, weights = Sample.Size)
summary(gam_poissonk12)

plot(gam_poissonk12, pages = 6, all.terms = TRUE, shade = TRUE, rug = TRUE, scale = 0)



gam_poissonk12Plots <- draw(gam_poissonk12, select = NULL)

Customgam_poissonk12plots <- lapply(seq_along(gam_poissonk12Plots), function(i) {
  gam_poissonk12Plots[[i]] +
    theme_classic() +
    scale_fill_viridis_c(option = "C") +
    ylim(c(-6,6))
})
```

```
combinedgam_poissonk12_plot <- wrap_plots(Customgam_poissonk12plots) +
    plot_layout(nrow = 3)

ggsave("OccurrenceGAMpoissonk12.pdf", plot = combinedgam_poissonk12_plot, dpi =
    300, width = 12, height = 8, units = "in")

countpred <- matrix(c(318,3116,
                      1723, 122685),
                    nrow=2, byrow=TRUE)
chisq.test(countpred)

countparus <- matrix(c(256,13956,
                       669, 17283),
                     nrow=2, byrow=TRUE)
chisq.test(countparus)

result_pred <- chisq.test(countpred)
result_parus <- chisq.test(countparus)

result_pred
result_parus
```

```
sankey <- read.csv("C:/Users/zachm/OneDrive/Documents/Sankeydiagram.csv")
attach(sankey)


sankey_expanded <- sankey[rep(1:nrow(sankey), sankey$Count), ]
attach(sankey_expanded)


sankey_long <- sankey_expanded %>%
  make_long(step1, step2, step3, step4)


terminal_labels <- sankey_long %>%
  filter(x == "step4") %>%
  group_by(node) %>%
  summarise(count = n(), .groups = "drop")


final_labels <- sankey_long %>%
  filter(x == "step4") %>%
  left_join(terminal_labels, by = "node")


sankey_long$flow <- rep(sankey$Count, times = 420)


ggplot(sankey_long, aes(x = x,
                        next_x = next_x,
                        node = node,
```

```
                    next_node = next_node)) +
  geom_sankey(color = "black", size = 0.2, alpha = 1, fill = "skyblue") +
  geom_sankey_label(data = final_labels,
                  aes(label = paste0(node, "\n(n = ", count, ")")), size = 3) +
  geom_sankey_label(data = sankey_long %>% filter (x != "step4"), aes(label = node),
    size = 3) +
  theme_void(base_size = 16)


ggsave("C:/Users/zachm/Downloads/sankey_plot.png",
       width = 10,
       height = 6,
       dpi = 600)
```

# APPENDIX B

## PBDB-based Diversity, 3T Origination Rates, and 3T Extinction Rates R Script

```
library(tidyverse)
library(paleobioDB)
library(divDyn)
library(iNEXT)
library(deeptime)

ceph_data <- pbdb_occurrences(limit="all", vocab="pbdb", base_name = "Cephalopoda",
show = c("phylo", "ident", "time", "coords", "classext"))
attach(ceph_data)

data(stages)
attach(stages)

stages$mid_age <- ((stages$max_age + stages$min_age)/2)

ceph_data$stage <- cut(
  ceph_data$max_ma,
  breaks = rev(stages$max_age),
  labels = rev(stages$name)[-1],  # Ensure labels match breaks
```

```
  right = FALSE
)


ceph_data_subset <- ceph_data[, c("stage", "genus")]


ceph_data_subset$genus <- as.character(ceph_data_subset$genus)


ceph_data_subset$stage <- factor(ceph_data_subset$stage, levels = stages$name)
ceph_data_subset$stage_bin <- as.numeric(ceph_data_subset$stage)


stgFreq <- divDyn(ceph_data_subset, tax="genus", bin="stage_bin")


missing_bins <- setdiff(1:95, stgFreq$stage_bin)


# If any bins are missing, append them with NA values
if (length(missing_bins) > 0) {
  missing_rows <- data.frame(stage_bin = missing_bins)
  missing_rows[, setdiff(names(stgFreq), "stage_bin")] <- NA
  stgFreq <- rbind(stgFreq, missing_rows)
}


stgFreq <- stgFreq[order(stgFreq$stage_bin), ]
```

```
stages$stage_bin <- as.numeric(factor(stages$name, levels = stages$name))


stgFreq <- merge(stgFreq, stages[, c("stage_bin", "name", "mid_age")], by = "stage_bin",
all.x = TRUE)
stgFreq <- stgFreq[, c("name", setdiff(names(stgFreq), "name"))]


ceph_data_clean <- ceph_data_subset[!is.na(ceph_data_subset$genus), ]


sqs_results <- subsample(ceph_data_clean, tax="genus", bin="stage_bin", type = "sqs",
q=.9)
sqs_results <- merge(sqs_results, stages[, c("stage_bin", "name", "mid_age")], by =
"stage_bin", all.x = TRUE)


attach(sqs_results)
ggplot(sqs_results, aes(x = mid_age, y = divSIB)) +
  geom_line() +
  geom_point() +
  ylab("SQS Mean Standing Diversity") +
   scale_x_continuous(name = "Geologic Time", trans = "reverse", limits = c(538.8,0)) +
  coord_geo(ylim = c(0, max(sqs_results$divSIB, na.rm = TRUE)),
            pos = "bottom", dat = list("periods", "epochs")) +
  theme_classic()
```

```
ggplot(sqs_results, aes(x = mid_age, y = ori3t)) +
  geom_line() +
  geom_point() +
  ylab("Three Timer Origination Rate") +
  scale_x_continuous(name = "Geologic Time", trans = "reverse", limits = c(538.8,0)) +
  coord_geo(ylim = c(0, max(sqs_results$ori3t, na.rm = TRUE)),
            pos = "bottom", dat = list("periods", "epochs")) +
  theme_classic()

ggplot(sqs_results, aes(x = mid_age, y = ori3t-ext3t)) +
  geom_line() +
  geom_line(y=0)+
  geom_point() +
  ylab("Net Biodiversification Rate") +
  scale_x_continuous(name = "Geologic Time", trans = "reverse", limits = c(538.8,0)) +
  coord_geo(ylim = c(-2, max(sqs_results$ori3t, na.rm = TRUE)),
            pos = "bottom", dat = list("periods", "epochs")) +
  theme_classic()

ggplot(sqs_results, aes(x = mid_age, y = ext3t)) +
  geom_line() +
  geom_point() +
```

```
  ylab("Three Timer Extinction Rate") +
  scale_x_continuous(name = "Geologic Time", trans = "reverse", limits = c(538.8,0)) +
  coord_geo(ylim = c(0, max(sqs_results$ext3t, na.rm = TRUE)),
            pos = "bottom", dat = list("periods", "epochs")) +
  theme_classic()

NewDiversityCephalopods <- write.csv(sqs_results, "NewDiversityCephalopods.csv")
```

# APPENDIX C

## Condensed Dataset

Authors, Year, Title, Journal, Interaction, Victim.Genus, Victim_Genus_species, Prevalence, n.victims.w.traces, Sample.Size, first.stage, last.stage, max.age, min.age, best.age, FI, Paleozoic, MeanSampledDiversity, 3TOriginationRate, 3TExtinctionRate, PeriodMidPointAge, Latitude (modern; deg,min,sec), Longitude (modern; deg,min,sec), Paleolatitude (via Gplates 2.5), Paleolongitude (via Gplates 2.5), CO2, Loc Temp (Judd et al.), NP Temp (Judd et al.), Eq Temp (Judd et al.), SP Temp (Judd et al.)

Andrew, Howe, & Paul,2014,Fatally bitten ammonites from septarian concretions of the ‘Marston Marble’ (Lower Jurassic, Sinemurian), Somerset, UK, and their taphonomy,Proceedings of the Geologists' Association,predation,Promicroceras,NA,0.090909091,2,22,Sinemurian,Sinemurian,199.5,192.9,196.2,0.316572006,Post.Paleozoic,18.54,0.856034405,0.851296587,NA,51.278014,-2.547031,38.0935,3.1773,1065.773,26.1375,-0.306,32.5983,9.6124

Andrew, Howe, & Paul,2014,Fatally bitten ammonites from septarian concretions of the ‘Marston Marble’ (Lower Jurassic, Sinemurian), Somerset, UK, and their taphonomy,Proceedings of the Geologists' Association,predation,Asteroceras,NA,0.6,3,5,Sinemurian,Sinemurian,199.5,192.9,196.2,0.316572006,Post.Paleozoic,18.54,0.856034405,0.851296587,NA,51.278014,-2.547031,38.0935,3.1773,1065.773,26.1375,-0.306,32.5983,9.6124

Andrew, Howe, & Paul,2014,Fatally bitten ammonites from septarian concretions of the ‘Marston Marble’ (Lower Jurassic, Sinemurian), Somerset, UK, and their taphonomy,Proceedings of the Geologists' Association,predation,NA,NA,0.6,3,5,Sinemurian,Sinemurian,199.5,192.9,196.2,0.316572006,Post.Paleozoic,18.54,0.856034405,0.851296587,NA,51.278014,-2.547031,38.0935,3.1773,1065.773,26.1375,-0.306,32.5983,9.6124

Andrew, Howe, & Paul,2010,Fatally bitten ammonites from the lower Lias Group (Lower Jurassic) of Lyme Regis, Dorset,Proceedings of the Yorkshire Geological Society,predation,NA,NA,0.2265625,29,128,NA,NA,201.4,145,173.2,NA,Post.Paleozoic,NA,NA,NA,NA,50.730185,-2.92531,38.6737,8.4725,NA,NA,NA,NA,NA

Bockwinkel, Becker,& Ebbighausen,2013,Late Givetian ammonoids from Hassi Nebech (Tafilalt Basin, Anti?Atlas, southern Morocco),Fossil Record,parasitism,Pseudoprobeloceras,Pseudoprobeloceras_pernai,0.004,1,250,Givetian,Givetian,387.7,382.7,385.2,0.422950843,Paleozoic,7.9,0.34657359,0,388.4,NA,NA,NA,NA,1004.462,NA,7.3719,31.7206,-0.3403

Böttcher,1989,Über die Nahrung eines Leptopterygius (Ichthyosauria, Reptilia) aus dem süddeutschen Posidonienschiefer (Unterer Jura) mit Bemerkungen über den Magen der Ichthyosaurier,Stuttgarter Beiträge zur Naturkunde Serie B (Geologie und Paläontologie),predation,NA,NA,NA,NA,NA,Toarcian,Toarcian,184.2,174.7,179.45,0.316572006,Post.Paleozoic,17.04,0.529675638,1.443115459,NA,48.646988,9.554873,37.7647,18.9766,797.0936,27.3276,6.2086,32.314,15.5132

Bromley,1993,Predation habits of octopus past and present and a new ichnospecies, Oichnus ovalis,Bull. geol. Soc. Denmark,predation,Nautilus_pompillius,NA,NA,NA,NA,modern,modern,0,0,0,NA,Post.Paleozoic,NA,NA,NA,1.3,-27.4403133,153.1769528,-27.4403133,153.1769528,400,NA,NA,NA,NA

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