The Causes and Consequences of the Pliocene Marine Megafaunal Extinction Event

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I confirm that the work submitted is my own and that appropriate credit has been given where reference has been made to the work of others.

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Abstract

The late Pliocene marine megafaunal extinction event was a major episode of biodiversity loss for large-bodied marine vertebrates. The selective extinction of marine megafauna during this event is particularly relevant to modern ecosystems, as extant marine megafauna face increased extinction risk. However, the ecological consequences of the Pliocene marine megafaunal losses on ecosystem structure and function, and the primary extinction drivers behind them, remain unresolved. This thesis addresses these important knowledge gaps. Trait-based reconstructions of North Atlantic pelagic food webs were generated for pre- and post-extinction intervals. Despite substantial taxonomic losses, including the extinction of a giant apex predator, ecosystem structure, function and trophic organisation remained broadly stable across this event. Although minor structural shifts occurred, overall, food webs appeared to have been resilient to megafaunal losses, potentially due to trophic redundancy. Extinction rate analyses across the Neogene and Pleistocene were then used to examine regional variation in extinction rates across ocean basins. Significant spatial variation emerged, with the North Atlantic exhibiting comparatively lower extinction rates than other regions. Such spatial variation aligns with expectations for extinctions influenced by environmental factors. Palaeoclimate simulations were finally used to test whether continental shelf availability or changes in sea temperature explained extinction trends. These variables showed limited explanatory power across time, and the Pliocene extinction peak appears anomalous relative to background Neogene trends. This suggests that the drivers of the selective extinction of megafauna during the Pliocene were likely unique and multifactorial, potentially reflecting interacting climatic, tectonic, and ecological change. Overall, these findings provide new insight into an understudied extinction event, highlighting the resilience of past marine ecosystems and identifying promising directions for future research on extinction causes, mechanisms and outcomes.

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Abbreviations

BC	Boundary-crossover (extinction rate metric)
DEM	Digital elevation model
GCM	General circulation (climate) model
GLS	Generalised least squares
MME	Marine megafaunal extinction
MS	Mediterranean Sea
MST	Mean sea temperature
NA	North Atlantic
NP	North Pacific
PBDB	Paleobiology Database
PFIM	Paleo Food web Inference Model
SP	South Pacific
TL	Trophic level
3T	3-timer (extinction rate metric)

Chapter 1.

Introduction

1.1 The Importance of Marine Megafauna

1.1.1 Defining marine megafauna

The term marine megafauna is commonly used across ecological and palaeontological studies, yet precise definitions are rarely specified and can vary depending on contexts and disciplines (Authier *et al.*, 2017; Moleón *et al.*, 2020; Pereira *et al.*, 2023). Referring to large-bodied taxa, megafauna are predominantly defined by body mass or length thresholds (Moleón *et al.*, 2020). Estes *et al.*, (2016) proposed a maximum reported mass of >45kg for taxa to be considered marine megafauna and this definition has since been used widely (Pimiento *et al.*, 2020; Gaskins *et al.*, 2020; Pereira *et al.*, 2023). Falling within this category are species of marine mammals (including cetaceans, pinnipeds and sirenians), elasmobranchs, bony fish, reptiles, sea birds and molluscs. However, this body mass restriction may exclude taxa which are considered megafauna in many ecological studies, notably sea birds (with only one extant penguin species fitting this definition; Estes *et al.*, 2016) and even crustaceans (Pereira *et al.*, 2023). As such, other definitions instead focus on behavioural characteristics or ecological roles to determine marine megafauna. This can include having roles as ecosystem engineers (McIvor *et al.*, 2022), their ability to store nutrients (Tavares *et al.*, 2019) or even their trophic position, being generally positioned at the top of food webs (Authier *et al.*, 2017). These more flexible definitions incorporating ecological context allow for generally smaller taxa to be included within the term megafauna (Moleón *et al.*, 2020).

Defining marine megafauna in the fossil record presents further challenges. Using body mass to designate megafauna has been done in some palaeontological studies, mostly for Quaternary terrestrial taxa (for example Roberts *et al.*, 2001; Barnosky, 2008; Boulanger & Lyman, 2014). However, using these mass thresholds more widely and across deeper-time is difficult as body mass is not generally known for extinct taxa and the use of body mass estimates introduces additional biases and uncertainties (Gayford *et al.*, 2024). Similarly, ecological traits can also only be inferred for most taxa, making defining megafauna by ecological role equally challenging. Consequently, many studies do not provide a definition of extinct marine megafauna and instead some use modern analogues as benchmarks

(Pimiento *et al.*, 2017; Dominici *et al.*, 2018). This is also problematic as extinct marine megafauna are far more diverse than those currently extant (Estes *et al.*, 2016; Pimiento *et al.*, 2024). To address this, Pimiento *et al.*, (2024) proposed using a body length threshold instead, where marine megafauna are taxa equal to or >1m in length. This trait is easier to determine from the fossil record than mass and allows for a greater inclusion of extinct species. This value is still based upon modern marine megafauna, where the smallest extant species (as defined in Estes *et al.*, 2016 and Pimiento *et al.*, 2020) all exceed 1m and is acknowledged to be an arbitrary value (Pimiento *et al.*, 2024). Therefore, this definition may not be applicable to all studies, especially those in deeper-time, but provides an easy guideline that can be used in some palaeontological research.

1.1.2 The role of marine megafauna in ecosystems

Marine megafauna have been the focus of much ecological research due to their important roles in modern marine ecosystems (Tavares *et al.*, 2019; Moleón *et al.*, 2020). They often have disproportionate impacts on marine biodiversity (acting as keystone species; Cottee-Jones & Whittaker, 2012) and may even significantly influence habitat composition and community stability (acting as ecosystem engineers; Sanders & Frago, 2024). One key ecological role of marine megafauna is the transport and dispersal of nutrients. This occurs both vertically throughout the water column and laterally across ocean habitats, through the processes of feeding, defecation and death (Roman & McCarthy, 2010; Roman *et al.*, 2014). This process ensures vital nutrients (such as nitrogen, carbon and phosphorus) are recycled through ecosystems which boosts primary productivity, supports food webs and maintains ecosystem health (Gross, 2016; Doughty *et al.*, 2016; Quévreux *et al.*, 2021; Wang & Wang, 2024). In extant ecosystems, large whales are responsible for a significant proportion of nutrient transport, attributed to their size and migratory lifestyles (Gross, 2016; Doughty *et al.*, 2016; Pearson *et al.*, 2023), however sea birds also have major roles in connecting land and ocean nutrient concentrations (Doughty *et al.*, 2016). Long distance migration also aids in connecting ecosystems, creating wide reaching networks across multiple habitats (McCauley *et al.*, 2012; Estes *et al.*, 2016; Hammerschlag *et al.*, 2019). This not only distributes nutrients between systems, but also influences overall community functioning and stability (McCauley *et al.*, 2012).

Predatory marine megafauna are also influential in controlling populations through direct consumption (Estes *et al.*, 2011; Hammerschlag *et al.*, 2019; Pereira *et al.*, 2023). This is especially evident in apex predators which have notable influence over both predators and herbivores in marine ecosystems. Apex predators are defined by their position in a food web, occupying the highest trophic level, and experience little to no predation once reaching full maturity (Wallach *et al.*, 2015). Through exerting top-down pressure within communities, apex predators limit the population growth of mesopredators, drive prey behavioural patterns, alter herbivory intensity of habitats and thus even alter habitat composition (Estes *et al.*, 2011; Hammerschlag *et al.*, 2019; Hammerschlag *et al.*, 2022; Jordaan *et al.*, 2023). While not every marine apex predator may fall within all definitions of megafauna (Moleón *et al.*, 2020), most are large-bodied and macro-predatory. Their ability to regulate marine communities, providing stability to food web structure, makes them ecologically important and in some cases necessary for maintaining ecosystem health (Hammerschlag *et al.*, 2019; Hammerschlag *et al.*, 2022).

1.1.3 Current threats to marine megafauna

Despite the ecological importance of marine megafauna, this group is currently facing severe threats from anthropogenic impacts. Significant population declines have been recorded globally across elasmobranchs (Dulvy *et al.*, 2014; Pacoureau *et al.*, 2021; Sherman *et al.*, 2023), marine mammals (Avila *et al.*, 2018; Braulik *et al.*, 2023; Temple *et al.*, 2024; Authier, 2025) and sea birds (Dias *et al.*, 2019; Richards *et al.*, 2021), with large-bodied taxa suffering from disproportionate losses. These declines are predominantly attributed to impacts from fishing activities and climate change. Overfishing has negatively impacted marine megafauna populations indirectly through reducing abundance of their prey species and directly through accidental harvesting as bycatch (Bearzi *et al.*, 2006; Dulvy *et al.*, 2014; Temple *et al.*, 2024; Authier, 2025). Instead, anthropogenic-driven climate change has predominantly impacted marine megafauna through habitat alteration or loss, resulting in range shifts, prey scarcity and reproductive stress (Grose *et al.*, 2020; van Weelden *et al.*, 2021; Luo *et al.*, 2025). Further extreme temperature events have also been linked to sudden localised die-offs (Lubitz *et al.*, 2024). Other anthropogenic factors have also played a role in the declining megafauna populations, including the introduction of invasive species (Žydelis *et al.*, 2009; Dias *et al.*, 2019), pollution (Avila *et al.*, 2018) and direct hunting (Dulvy *et al.*, 2014; Dias *et al.*, 2019).

Marine megafauna often present greater extinction risk compared to smaller representatives of the same clades due to their ecological and life history traits. Taxa with slow growth rates and low fecundity (traits which most marine megafauna share) are limited in their ability to recoup population numbers following declines (Authier *et al.*, 2017).

Further, many marine megafauna reside near coastal habitats, with greater proximity to some anthropogenic threats increasing their vulnerability (Avila *et al.*, 2018; Sievers *et al.*, 2019; Sherman *et al.*, 2023). As many taxa exhibit migratory lifestyles, implementing conservation measures to reduce local threats has proved difficult (Lascelles *et al.*, 2014). Consequently, it is estimated that one third of all marine megafauna species are currently at risk of extinction (Pimiento *et al.*, 2020). Although much research has focussed on predicting future consequences or providing conservation action recommendations to prevent further declines (for example Pereira *et al.*, 2023; Zhang, X. *et al.*, 2024; Sequeira *et al.*, 2025), these studies often lack historical or palaeontological insight (Kiessling *et al.*, 2019; Pimiento & Antonelli, 2022; Kowalewski *et al.*, 2023). Previous extinctions of marine megafauna in recent human history provide little precedent to understand future marine megafauna losses of this magnitude. As such, deeper-time perspectives may provide additional and useful insight.

1.2 The Pliocene Marine Megafaunal Extinction Event

1.2.1 Taxonomic and functional impacts

The marine megafaunal extinction event which occurred at the end of the Pliocene was first identified in Pimiento *et al.*, (2017). Although patterns in large marine vertebrate extinctions during this period have previously been documented for localised regions (Villafaña & Rivadeneira, 2014) or within specific taxonomic groups (for example Uhen & Pyenson, 2007; Marx & Uhen, 2010; Sorbi *et al.*, 2012; Boessenecker, 2013; Pimiento & Clements, 2014), Pimiento *et al.*, were the first to link these to a global extinction event. They identified high extinction rates within marine megafauna in the late Pliocene, specifically the Piacenzian (~3.6-2.58 Ma), which were up to three times greater than rates seen in any other Epoch across the Cenozoic (Pimiento *et al.*, 2017). In this case, marine megafauna were not defined based upon specific size thresholds but as vertebrate genera from the largest marine vertebrate groups as designated in modern ecological research (Lewison *et al.*, 2004): marine mammals, seabirds, sea turtles, sharks and rays. Across these taxonomic groups, 36% of all genera went extinct (Figure 1.1). These losses were predominantly seen in marine mammals (which accounted for more than half of all extinctions), particularly within cetaceans, in line with other studies (Uhen & Pyenson, 2007; Marx & Uhen, 2010; Boessenecker, 2013). However, notable losses were also seen within turtles and seabirds, with lower proportional extinction within sharks (<10%).

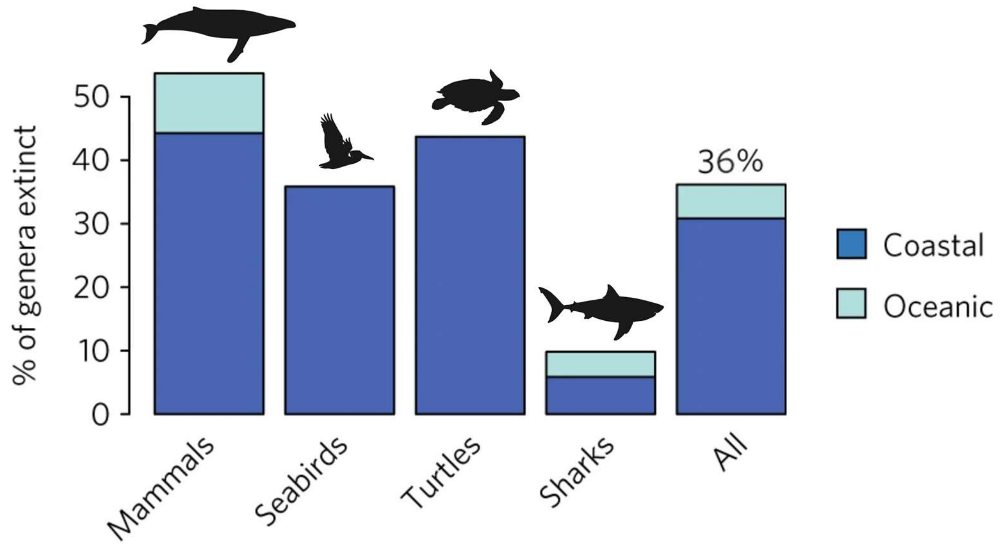

Figure 1.1 Proportional extinction of megafauna during the Pliocene marine megafaunal extinction, adapted from Pimiento *et al*. (2017). Silhouettes represent *Balaenoptera novaeangliae*, *Pelecanus occidentalis*, *Eretmochelys imbricata* and *Otodus megalodon*.

The megafauna that went extinct during this late Pliocene event presented a relatively wide diversity of ecological traits. For example, within feeding strategies losses were seen across herbivores (for example *Metaxytherium*; Sorbi *et al*., 2012) to the largest macropredators (for example *Otodus megalodon*; Pimiento & Clements, 2014). This is demonstrated well within cetaceans, with a wide array of predatory odontocetes and filter feeding mysticetes going extinct during this event. However, it was noted that the majority of extinctions (~86%) were associated with coastal habitats (Figure 1.1), though this trend may be impacted by preservation or sampling biases (Pimiento *et al*., 2017). As such, Pimiento *et al*. also assessed extinction selectivity, modelling five different ecological traits: maximum body size, ecological guild, vertical foraging position in the water column, thermoregulation and habitat. Interestingly, body size was not the best predictor of extinction risk, instead this was thermoregulation. Homeothermic taxa (endotherms and mesotherms), those that are able to regulate internal temperatures to differing degrees (Legendre & Davesne, 2020), had significantly higher chances of going extinct than those which do not (poikilotherms). While marine mammals and sea birds are exclusively endothermic, larger species of shark and turtles can be mesothermic (Pimiento *et al*., 2019; Legendre & Davesne, 2020).

In the Pleistocene, following the extinction event, origination of marine megafaunal genera occurred across the taxonomic groups. Therefore, despite over one third of genera going extinct in the Pliocene, the influx of new taxa resulted in the net generic loss across the Plio-Pleistocene boundary being considerably lower, at approximately 15% (Pimiento *et al*., 2017). However, taxonomic losses were not the only measured consequences of this extinction event. Pimiento *et al.*, also considered losses in functional diversity to assess how ecological roles may have changed following this event and thus the wider impacts on marine communities. Through identifying unique functional entities (taxa with unique trait combinations) and constructing a functional space (see Mouillot *et al.*, 2013) within coastal megafauna, a net loss of 16% in functional richness was found across the Plio-Pleistocene boundary. Further, many of the unique functional entities which survived the extinction were left with only a single genus representing these ecological roles, resulting in greater functional vulnerability. By not considering non-coastal taxa within this analysis, some further functional changes across this global event may be absent from these findings. However, it is clear that the extinction of marine megafauna at the end of the Pliocene had a notable impact on not only taxonomic losses, but also functional diversity.

1.2.2 The extinction of *Otodus megalodon*

During the Pliocene marine megafaunal extinction significant numbers of taxa went extinct including the well-known shark, *Otodus megalodon*. Considered a charismatic species (Pimiento & Clements, 2014), this shark is known for its giant size, macro-predatory lifestyle and abundant fossil record. Body size estimates of *O. megalodon* suggest this species potentially reached lengths of 16-24 metres (Cooper *et al.*, 2020; Perez *et al.*, 2021; Shimada *et al.*, 2025), larger than any other extant or extinct shark. Widely regarded as an opportunistic generalist preferentially preying upon cetaceans (McCormack *et al.*, 2022; Kast *et al.*, 2022; Benites-Palomino *et al.*, 2022; Cooper *et al.*, 2022), *O. megalodon* likely occupied a similar niche and transoceanic lifestyle as the extant great white shark, *Carcharodon carcharias* (McCormack *et al.*, 2022; Cooper *et al.*, 2022). At such a large size, *O. megalodon* was undoubtedly an apex predator within its marine communities, placing it among the largest apex predators to ever exist (Pimiento & Balk, 2015). It is expected this shark had notable impacts on marine ecosystems, controlling populations and even impacting global nutrient transfer (Cooper *et al.*, 2022). Further, the fossil record suggests *O. megalodon* was globally distributed (with teeth even found from deep-sea localities; Pollerspöck *et al.*, 2025).

Likely originating in the early Miocene (Pimiento *et al.*, 2016; Cooper *et al.*, 2022), *O. megalodon* occupied oceans for approximately 20 million years. Despite apparent success across this period, by the Pleistocene *O. megalodon* had gone extinct. While the timing of this extinction concurs with the late Pliocene marine megafaunal extinction (Pimiento *et al.*, 2017), the exact mechanism that drove this species' extinction have been highly debated (Pimiento & Clements, 2014; Boessenecker *et al.*, 2019). Abiotic causes proposed largely consist of changing climates across the Pliocene, notably global cooling and sea level drop over this period (Boessenecker *et al.*, 2019). This is supported by general trends across time where lamniform shark extinction rates increase during periods of cooling (Condamine *et al.*, 2019). It has also been suggested that the sea level drop may have resulted in a loss of nursery grounds for *O. megalodon*, and thus a key factor in this species' extinction (Herraiz *et al.*, 2020). However, evidence supporting climatic factors as the primary extinction driver for *O. megalodon* is currently limited (Pimiento *et al.*, 2016; Boessenecker *et al.*, 2019).

Conversely, several biotic causes have been put forward, notably changes in prey abundance or competition with other predators. The Pliocene decline in cetacean diversity in particular has been attributed to the loss of *O. megalodon*, with these taxa considered to have been a key prey source (Pimiento *et al.*, 2016; Cooper *et al.*, 2022). Potentially as a response to declining prey sources or as an evolutionary shift, some evidence suggests a change in *O. megalodon*'s diet led to feeding niche overlap with *Carcharodon carcharias*, the extant great white shark. As such, the larger *O. megalodon* with higher feeding requirements may have been outcompeted by the smaller *C. carcharias*. This is supported by tooth morphology analysis (Shimada *et al.*, 2025) and zinc isotope analysis (McCormack *et al.*, 2022) where diet and trophic feeding positions were inferred. The emergence of other predators, such as raptorial sperm whales (which likely occupied niches similar to those held by extant orcas, *Orcinus orca*) has also been suggested to have introduced competition (Pimiento *et al.*, 2016). However, how these hypotheses (both biotic and abiotic) relate to the Pliocene marine megafaunal extinction is unexplored and it is currently unclear what role this event played in the extinction of *O. megalodon*.

1.2.3 Knowledge gaps

Beyond the initial publication identifying the Pliocene marine megafaunal extinction by Pimiento *et al.* (2017), this event has remained largely unstudied. Questions remain regarding the long-term consequences of these global extinctions and the causes that led to such notable and selective losses. With high taxonomic and functional diversity losses, this event likely had significant implications for marine ecosystems, impacting community dynamics and function. Understanding the ecological consequences of such an event would provide a deeper understanding of how marine communities respond to global losses of large-bodied taxa, as well as provide insight into how modern ecosystems may respond to future predicted losses. As this event documents the extinction of a giant marine apex predator (*O. megalodon*), it also acts as a case study to assess the impacts of apex predator extinctions. Further, as extinction selectivity towards large body size is rare in the fossil record, unlike the trend seen in modern oceans (Payne *et al.*, 2016), exploring the primary drivers of this extinction event may uncover those stressors that marine megafauna taxa are most susceptible to.

1.3 Ecological Consequences

1.3.1 Community responses to marine megafauna losses

The removal of marine megafauna from ecosystems can have wide reaching ecological consequences. These consequences have predominantly been documented from localised extirpation events, where a single species of megafauna has gone extinct from a specific region (McCauley *et al.*, 2015; Estes *et al.*, 2016). Negative effects include the reduction in nutrient cycling efficiency, resulting in habitats to become less productive and less resilient to further perturbations (Roman & McCarthy, 2010; Doughty *et al.*, 2016). Community structure may also be impacted, where the balance of populations among trophic levels can be disrupted. In some cases this has led to significant changes to habitat composition either due to a reduction in predators keeping overgrazing at bay (Estes *et al.*, 1998; Estes *et al.*, 2011) or a reduction of herbivorous and filter feeders necessary for bioturbation and maintaining benthic community composition (Thrush & Dayton, 2002; Malhi *et al.*, 2022). Additional trophic cascades can occur when the megafauna lost are predatory (especially in the case of apex predators). Notably, without these predators to regulate populations, mesopredator release (where populations of smaller predators rapidly increase) can decimate local prey species, significantly impacting community stability (Heithaus *et al.*, 2008; Sherman *et al.*, 2020). In some cases, these cascades can even lead to secondary extinctions (Ebenman & Jonsson, 2005; Borrvall & Ebenman, 2006).

Despite well-studied regional examples of marine megafauna extirpation, modern and historical records offer limited insight into the ecological consequences of global extinction. Documented global extinctions of marine megafauna are rare, have occurred in isolation and are temporally staggered (Estes *et al.*, 2016; Pimiento *et al.*, 2020). They also only represent a portion of the taxonomic diversity exhibited by marine megafauna today. For example, the Steller's sea cow (*Hydrodamalis gigas*; Turvey & Risley, 2006), Caribbean monk seal (*Neomonachus tropicalis*; Baisre, 2013) and Great Auk (*Pinguinis impennis*;

Thomas *et al.*, 2019). Crucially, there has not been a global extinction of a marine apex predator in human history (Pimiento *et al.*, 2016). These constraints of recent analogues means it remains unclear what the ecological consequences would be if widespread losses across multiple taxonomic groups were to occur at once. As such the fossil record is vital for addressing such questions, providing records of metacommunity changes across long-term ecological timescales (Kowalewski *et al.*, 2023; Finnegan *et al.*, 2024). The Pliocene marine megafaunal extinction is a particularly relevant deep-time parallel to the current human-driven megafaunal losses, where the proportion of genera that went extinct (~36%) is comparable to the proportion of species currently at risk (~33%). Investigating the ecosystem changes which occurred following this event allows for insight into what trophic and functional restructuring can occur without the influence of anthropogenic pressure, as well as a better understanding of past marine ecosystems dynamics.

1.3.2 Measuring ecosystem changes in the fossil record

Extinction events are primarily considered from the perspective of taxonomic loss (Droser *et al.*, 2000; Christie *et al.*, 2013). While this metric is necessary for quantifying changes in biodiversity, on its own it provides limited insight into how ecosystem function and structure were affected. Taxonomic loss alone does not take into account the roles of species lost in ecological networks and how these losses translate into disruption of ecological interactions, niches and processes. Incorporating functional diversity allows for a more informative approach by assessing the conservation or loss of functional and ecological traits of taxa following extinction (Song *et al.*, 2018; Dunhill *et al.*, 2024; Liow & Quental, 2025). As such, the approach taken by Pimiento *et al.*, (2017) gives great insight into how the Pliocene marine megafaunal extinction event altered the functional space of global marine environments. However, this still does not take into account the impacts on overall ecosystem structure and function. Changes in taxonomic diversity may not directly correspond to changes in ecosystem dynamics (Droser *et al.*, 2000; Christie *et al.*, 2013; Song *et al.*, 2018). For example, loss of few keystone or functionally unique species may have significant impacts on community function, whereas greater taxonomic losses in ecosystems with high functional redundancy (where many species perform similar ecological roles) may have negligible impacts. Understanding the structure and function of these ecosystems is more informative of whole community impacts and allows for more applicable comparison to extant ecosystems.

Ecosystems can be reconstructed and analysed for past environments through food web modelling (Shaw *et al.*, 2021b; García-Girón *et al.*, 2022; Dunhill *et al.*, 2024). This is a growing field in palaeontology and food webs have been constructed for a wide range of environments (for example Roopnarine *et al.*, 2007 and Cortés & Larsson, 2023) and time periods (for example Dunne *et al.*, 2008 and Dunne *et al.*, 2014). Structural food webs are the most common, which depict the feeding interactions between taxa within a community in a static system. While structural food webs show the energy flow through an ecosystem, they do not quantify this energy, model populations or weight interaction strengths (Berg *et al.*, 2015). This is unlike dynamic food webs, which are less common in palaeontological studies due to their high data requirements (for example biomass data). Topological features of these feeding networks can be quantitatively measured, making them useful for comparing changes to structure and function before and after periods of perturbation or extinction. Multiple models have been used in previous palaeo food web studies, each with their own set of rules and assumptions (for example Dunne *et al.*, 2014; Shaw *et al.*, 2021b; García-Girón *et al.*, 2022; Huang *et al.*, 2025), and thus model choice does have a notable influence on network outputs. As such, these variations must be taken into consideration when making modelling decisions, for example choosing between a stochastic or deterministic model. Often model choice will depend upon data availability, with the fossil record presenting many limitations. Nevertheless, these methods allow for the integration of a functional approach (taking into account taxonomic diversity and their feeding niches) into a structural trophic network.

1.4 Extinction Drivers

1.4.1 Environmental context

The Pliocene Epoch (~5.3–2.58 Ma), and in particular the Piacenzian stage (~3.6–2.58 Ma), was a period of pronounced environmental change. Following the Mid-Piacenzian Warm Period (~3.3-3.0 Ma; Zhang, K. *et al.*, 2024), rapid and sustained global cooling occurred resulting in the glaciation of the Northern Hemisphere around 2.7-2.5 Ma (Lisiecki & Raymo, 2007; McClymont *et al.*, 2023). This has been well documented in benthic oxygen isotope records (McClymont *et al.*, 2023) and North Atlantic occurrences of ice-rafted debris (Jakob *et al.*, 2018). These tumultuous temperature changes resulted in large oscillations in global mean sea level across this period (Miller *et al.*, 2005), with a net decrease from the mid to end Piacenzian of approximately 20 metres, although some studies estimate decreases of over 50 metres (Schepper *et al.*, 2013; Tan *et al.*, 2017; Yang *et al.*, 2025). Other impacts on marine environments during the late Pliocene included shifting salinity patterns, with the onset of a stronger halocline and stratified upper water column (Swann *et al.*, 2006; McClymont *et al.*, 2023). The Piacenzian was also witness to significant tectonic shifts, notably the formation of the Isthmus of Panama (~3 Ma; O'Dea *et al.*, 2016). Closure of the Central American Seaway altered ocean circulation patterns, increased Atlantic salinity, strengthened the Gulf Stream and even enhanced heat transport to high latitudes (Haug *et al.*, 2001; Lunt *et al.*, 2008; Schepper *et al.*, 2013; Auderset *et al.*, 2019).

The culmination of these climatic and tectonic changes likely placed significant stress on marine ecosystems. The fluctuating temperatures, sea level oscillations and shifting ocean circulation patterns may have caused heightened levels of instability, making marine communities more susceptible to losses (Malanoski *et al.*, 2024; Kiessling *et al.*, 2025). However, whether any of these factors contributed to or were the primary drivers of the megafaunal extinctions during this period is unclear. The causes of the late Pliocene marine megafaunal extinction event have so far not been investigated and given other marine vertebrate taxa appeared unaffected by the shifting environmental conditions, this implies primary drivers differed from those responsible for other marine extinction events (Payne *et al.*, 2016; Malanoski *et al.*, 2024).

1.4.2 Neritic zone hypothesis

Currently, only one hypothesis for the primary drivers of the marine megafaunal extinction event has been proposed. Pimiento *et al.*, (2017) hypothesised that a substantial reduction in neritic zone area caused by falling sea levels led to the loss of productive coastal habitats, critical for marine megafauna. The neritic zone, defined as shallow marine environment above the continental shelf up to approximately 200 metres deep, lies within the photic zone and is among the most biologically productive marine habitats due to the high light availability and nutrient input from terrestrial environments (Mann & Lazier, 2005; Dolbeth & Arenas, 2021). Due to the high productivity of these habitats, many extant marine megafauna rely on these areas for foraging (Chatzimentor *et al.*, 2021; Bava *et al.*, 2022; Leurs *et al.*, 2023; Li *et al.*, 2023) and, in some cases, for reproduction and nursery habitats (Bost *et al.*, 2009; Guidino *et al.*, 2014; Li *et al.*, 2023). The availability of global neritic zone area is estimated to have decreased by 27% from the Pliocene to the Pleistocene (Figure 1.2), severely reducing this habitat availability for large marine vertebrates (Boer *et al.*, 2010; Pimiento *et al.*, 2017).

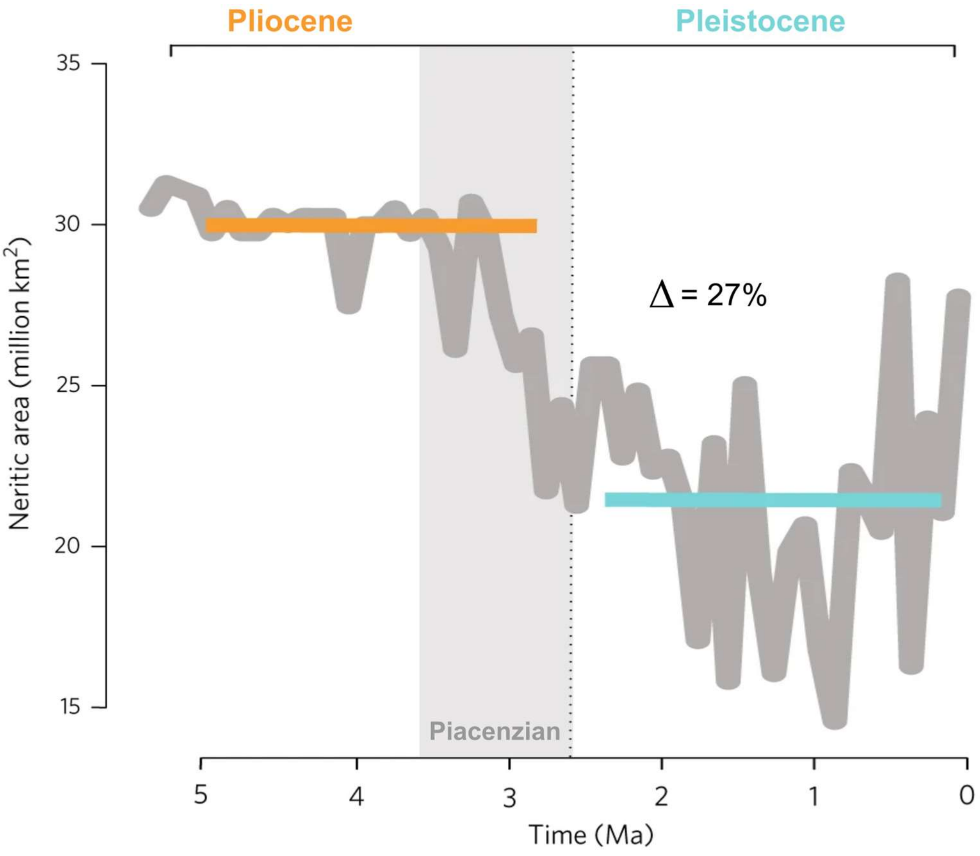

Figure 1.2 Global neritic zone area across the Pliocene and Pleistocene, adapted from Pimiento *et al.* (2017). Horizontal lines represent mean epoch values, with the Piacenzian highlighted.

The relationship between the reduction of shallow marine habitats (due to sea level drop) and biodiversity loss is complex and dependent upon several ecological, physiological and evolutionary factors (Holland, 2012). However, marine megafauna may be particularly sensitive to such habitat losses. This is particularly the case for homoeothermic taxa, which are more vulnerable to resource declines due to their narrow energetic constraints (Wright, 1983). As during the Pliocene marine megafaunal extinction event homeotherms exhibited the greatest extinction risk (Pimiento *et al.*, 2017), a reduction in productive foraging grounds may have had a disproportionate impact on the survival of this group which possess such high energetic demands (Boyles *et al.*, 2011). A loss in neritic zone area would have reduced prey availability and increased competition for prey within a reduced range. Additionally, species specific impacts may have further compounded extinction risk, such as a loss of specific-habitat requirements (for example seagrass dependency in sirenians; Sorbi *et al.*, 2012) or coastal nursery grounds (for example refugia for juvenile sharks; Herraiz *et al.*, 2020). In contrast, some homeothermic megafauna may have been less impacted by such habitat losses due to greater feeding plasticity (Pyenson & Lindberg, 2011; Pimiento *et al.*, 2017) or adaptations for deep-sea foraging (Watwood *et al.*, 2006).

Despite the rationale behind the neritic zone loss hypothesis, it has not been quantitatively tested. Given the heterogeneity of continental shelf area across ocean basins (Harris *et al.*, 2014), the contribution of neritic habitat loss to this extinction would have varied regionally if it did play a significant role. As this extinction event has only been considered on a global scale, regional analysis is needed to further address this hypothesis.

1.5 Aims and Structure

This thesis aims to broaden the current understanding of the Pliocene marine megafaunal extinction event and to address key questions relevant to extant ecological and conservation concerns. The three research chapters investigate both the ecological consequences and the potential causes of this extinction, providing insight into how large-bodied taxa influence marine ecosystem structure and how environmental change may shape extinction selectivity. Specifically, Chapter 2 quantifies how ecosystem structure and function changed following the megafaunal extinctions using food web modelling; Chapter 3 assesses whether the extinction event had varying regional impacts through spatial extinction rate analyses; and Chapter 4 tests hypotheses for the environmental drivers of the extinction using palaeoclimate simulations.

Chapter 2.

Trophic impacts of the Pliocene marine megafaunal extinction

2.1 Abstract

Marine megafauna are experiencing widespread population declines, yet the ecological consequences of their extinction are not well understood. Palaeoecology can provide useful insights into how ecosystems respond to taxonomic losses through studying past extinction events. This research investigates the ecological consequences of the Pliocene marine megafaunal extinction (~2.6 Ma) which saw the loss of over one third of marine megafaunal genera globally, including the apex predator *Otodus megalodon*. Here, the impact of these extinctions on food web structure and function is assessed alongside the consequences of apex predator loss on other top predator trophic positions. Using a trait-based model, food webs were reconstructed for North Atlantic marine communities in the Pliocene and Pleistocene. Despite substantial taxonomic loss, no major changes in structure or function were found and the relative trophic positions of top predators were unaffected by the extinction of *O. megalodon*. Minor shifts in food web structure suggest more densely connected post-extinction communities characterised by a larger proportion of generalist taxa. These findings show the loss of marine megafauna, including a cosmopolitan apex predator, did not significantly alter North Atlantic food web structure and function.

2.2 Introduction

Marine megafauna are currently experiencing significant population declines and are under increasing threat of extinction on a global scale (Malhi *et al.*, 2016; Payne *et al.*, 2016; Pimiento *et al.*, 2020). This is concerning as marine megafauna have important ecological impacts (Estes *et al.*, 2016; Hammerschlag *et al.*, 2019; Tavares *et al.*, 2019), such as modifying habitats, controlling prey populations and transporting nutrients. These declines have been driven by increasing anthropogenic activities, including overfishing (Dulvy *et al.*, 2014; Pacoureau *et al.*, 2021), and anthropogenic-driven climate change (Grose *et al.*, 2020; van Weelden *et al.*, 2021) with impacts disproportionately impacting predator populations (Estes *et al.*, 2011; Dulvy *et al.*, 2014). The loss of megafauna from marine ecosystems can trigger cascading impacts including mesopredator release (Heithaus *et al.*, 2008; Sherman *et al.*, 2020), prey behavioural shifts (Sherman *et al.*, 2020; Hammerschlag *et al.*, 2022), changes in habitat composition (Estes *et al.*, 2011; Estes *et al.*, 2016; Hughes *et al.*, 2024), and secondary extinctions (Borrvall & Ebenman, 2006). However, impacts are often documented from localised extirpations (Dulvy *et al.*, 2014; McCauley *et al.*, 2015; Estes *et al.*, 2016), and only a small number of global marine megafaunal species extinctions have been recorded throughout human history. Currently over one third of marine megafaunal species are at risk of global extinction (Pimiento *et al.*, 2020) and it is unclear how such large-scale losses may impact marine ecosystem structure and function.

A marine megafaunal extinction event at the end of the Pliocene (~2.6 Ma) resulted in ~36% of all marine megafauna genera going extinct globally (Pimiento *et al.*, 2017). This extinction is hypothesised to have been driven by global cooling, leading to sea level drop and a consequent loss of productive neritic habitats (Pimiento *et al.*, 2017). Whilst cetaceans suffered the most losses, these megafaunal extinctions include the giant shark *Otodus megalodon*. Estimated to have reached lengths of 16-24 metres (Cooper *et al.*, 2020; Perez *et al.*, 2021; Shimada *et al.*, 2025), *O. megalodon* inhabited the global ocean for approximately 20 million years and was one of the largest apex predators to ever exist. Apex predators occupy the highest trophic level in a food web and experience very little (if any) predation upon reaching full maturity (Wallach *et al.*, 2015). At such a large size, it is expected this shark had notable impacts on trophic interactions (including top-down predation pressure) and may have even impacted global nutrient transfer (Cooper *et al.*, 2022). Although the taxonomic and functional richness losses during this event are well understood, the ecological and trophic implications of these extinctions are not. Understanding how this geologically recent extinction event altered marine food web structure and function may provide useful insight into how extant ecosystems could respond in the future to similar megafaunal losses.

Research surrounding extinction events from the fossil record often focus solely on taxonomic diversity change. However, understanding the impacts on ecological interactions and trophic structure can provide a more complete picture as to how these events impacted overall ecosystem dynamics (Pimiento *et al.*, 2017; Song *et al.*, 2018; Dunhill *et al.*, 2024; Liow & Quental, 2025). The ecosystem structural and functional changes that occurred across extinctions are rarely considered yet may often be decoupled from the patterns seen in diversity changes alone (Song *et al.*, 2018). Reconstructing ecosystems in the form of food webs is a useful way to integrate a functional approach into a structural trophic framework (Roopnarine *et al.*, 2007; Dunne *et al.*, 2008; Dunne *et al.*, 2014; Roopnarine & Angielczyk, 2015; García-Girón *et al.*, 2022; Cortés & Larsson, 2023; Dunhill *et al.*, 2024). Structural food webs represent the interactions among taxa within a community through feeding links and can be informative in detangling the relationship between diversity loss and changes to ecosystem structure.

Here, the consequences of diversity loss on ecosystem structure and function following the Pliocene marine megafaunal extinction are assessed. Trait-based reconstructions of food webs were generated for pre- and post-extinction time periods for North Atlantic pelagic communities. First, metacommunity food webs were constructed, which record all possible feeding links. Then, the metacommunity webs were downsampled to produce 'realised' webs which have a reduced link distribution to align the networks with known levels of structural complexity. These realised webs ensure any structural changes over the extinction are not masked by the high link density of the metacommunity webs. Changes between pre- and post-extinction food webs were measured to quantify (1) ecosystem structure and functional shifts following the megafaunal extinctions, and, (2) the impact of marine apex predator (*Otodus megalodon*) extinction on the trophic positions of other top predators.

2.3 Methods

2.3.1 Fossil occurrence data

Taxon occurrence data were compiled from the North Atlantic for the Pliocene (5.2-2.58 Ma) and Pleistocene (2.58-0.012 Ma) to represent pre- and post-extinction marine metacommunities. This region was chosen due to better sampling in the North Atlantic compared to other ocean basins across this time period. Vertebrate taxa were collected at genus level from fossil occurrence data sourced from literature (Ray, 1983; Emslie, 1995; Bianucci, 1996; Stringer, 1998; Ray & Bohaska, 2001; Tiwari & Ralte, 2012) and the

Paleobiology Database (PBDB). From the PBDB, genera were downloaded from North American and European marine sediments for the taxonomic groups of Actinopterygii, Chondrichthyes and Sarcopterygii (see Supplementary Material). The Sarcopterygii were subsequently split into the groups of Aves, Reptilia (non-avian) and Mammalia as the PBDB includes all tetrapod descendants in this clade. The dataset was cleaned to remove any terrestrial taxa and those that were not found in the North Atlantic.

Incompleteness of fossil datasets is an endemic problem faced by all palaeontological researchers, with the fossil record not only being incomplete but also exhibiting sampling bias (Lloyd *et al.*, 2012; Benson *et al.*, 2021), which can vary both temporally and spatially (Vilhena & Smith, 2013; Dunhill *et al.*, 2014; Benson *et al.*, 2021). To account for this, the dataset was expanded to include ranged-through occurrences based on first and last occurrence data as well as knowledge of extant species ranges. By ranging-through occurrences this regional study is making the assumption that taxa did not become extirpated from the North Atlantic for a period of time and were present in this area across both epochs as extirpation is assumed to be less likely than the absence of taxa being the result of a sampling failure. These ‘inferred occurrences’ are denoted in each dataset and make up 5% of the Pliocene and 21% of the Pleistocene datasets (Supplementary Material).

Invertebrate taxa are represented initially in the dataset by two nodes, one to represent microinvertebrates (e.g. plankton and larvae) and one to represent macroinvertebrates (e.g. crustaceans and molluscs). Individual invertebrate genera were not included as many invertebrates represented by these nodes are not found in the fossil record (Shaw *et al.*, 2021a), such as plankton. Also, the focus of this study is on changes within pelagic communities with most macroinvertebrates being benthic and not interacting with these vertebrate species other than as a prey source. However, squids are an exception to this assumption as it is known from extant pelagic ecosystems that squid play important ecological roles as both predators and prey within these marine communities (Coll *et al.*, 2013), with several vertebrate genera in the dataset interpreted to be specialist cephalopod consumers. Due to their predominantly soft-bodied nature, Cenozoic squids have a poor fossil record and no fossil occurrences have been recorded in the North Atlantic for either the Pliocene or Pleistocene. To address this data gap, 19 nodes were added to represent each of the unique feeding guilds of modern North Atlantic squids (see Supplementary Material). These guilds were identified based on the traits detailed below. As the food webs in this research are structural, only showing presence/absence of taxa without consideration of abundance, the amount of primary productivity entering the web does not need to be quantified. Consequently, primary productivity is represented as just a single node to root the web, an approach previously used in palaeo food web reconstructions (Dunhill *et al.*, 2024).

2.3.2 Ecological trait data

Functional trait data was assigned to each node in each community and consisted of body size, vertical position in the water column, depth distribution and feeding habits. These traits were selected as they are informative of feeding interactions in modern pelagic systems and represent predator ability to subdue and consume prey, predator-prey encounter rates, and predator foraging choice. Trait data was primarily sourced from the published literature, however, if little or no information could be found for a particular fossil organism, traits for extant species of the same genus that presently reside in the North Atlantic were used, sourced from extant species databases (Froese & Pauly, 2023; IUCN, 2023). Trait data for all categories could not be found for every genus in the dataset and these genera were thus removed from the analysis as the model framework requires a complete set of trait data for each taxon.

Body size is arguably the most important trait in determining trophic interactions in marine communities, underpinning much modern ecology theory, such as optimal foraging theory (Petchey *et al.*, 2008). Here body size refers to the maximum length of the largest known specimens. In the case of birds, this was taken as the distance from head to tail as opposed to wingspan and for turtles this was taken as the carapace length due to the poor preservation and lack of size estimates which include head and neck length (Weems, 1980; Dodd & Morgan, 1992; Weems & Brown, 2017). These lengths were taken from direct measurements of fossil specimens or body size estimates from published literature. If no size estimate for fossil specimens was given, the length of the largest extant North Atlantic member of the genus was used. Taxa were then placed into discrete body size categories: tiny (<1m), small (1-3m), medium (3-6m), large (6-9m), giant (9-12m) and mega (>12m). Suspension feeders within Mammalia and Chondrichthyes were separated into their own size categories: medium suspension (3-6m), large suspension (6-9m), giant suspension (9-12m) and mega suspension (>12m). It was necessary to differentiate this group due to these predators operating under different size feeding rules than other taxa (see Model Framework). Body size was also used to define the marine megafauna in the dataset, with all vertebrates with a body length >1m considered megafauna based upon Pimiento *et al.* (2024).

The traits of vertical position and depth distribution were selected to cover all spatial aspects of the marine taxa in order to parameterise encounter likelihood within the modelling framework. The vertical position of where a taxon is found in the water column was classified as being either close to the bottom of the ocean floor (benthic), out in the open ocean (pelagic) or a combination of the two (benthopelagic). Similarly, depth distribution corresponds to the maximum depth at which a genus would usually reside, split into three broad categories of neritic (<200m), twilight (200-1000m) and midnight (>1000m). A genus can be assigned a combination of any of these three.

The preferred diet of taxa (the usual feeding behaviour of adult individuals) is accounted for by feeding habit. Feeding habits were restricted to what classes of organism a taxon could feed on: Actinopterygii, Chondrichthyes, Mammalia, Aves, Reptilia, Cephalopoda, macroinvertebrates and microinvertebrates. Feeding interactions were determined using fossil evidence such as tooth morphology, gut contents or predation marks and inferences from modern taxa. Herbivores were assigned to feed directly on the primary productivity node.

2.3.3 Model framework

Food webs were reconstructed using the Paleo Food web Inference Model (PFIM), a model which has been successfully applied in other palaeontological studies (Shaw *et al.*, 2024; Dunhill *et al.*, 2024). This trait-based model was designed specifically for the reconstruction of ancient food webs using only fossil data. In addition to a list of taxa and associated traits, the model requires defined rules specifying which traits are ‘compatible’ and allow one taxon to feed upon another. These rules are grounded in optimal foraging theory (Beckerman *et al.*, 2006; Pyke & Starr, 2021), where links are assigned based on whether taxa are likely to interact and if it is energetically beneficial for a consumer to feed on a resource. The original framework used traits and rules based on Bambach’s ecospace cube (Roopnarine, 2006; Bambach *et al.*, 2007) used to establish potential modes of life of marine fauna, predominantly invertebrates. As this study focusses on pelagic vertebrates, this prior framework was not appropriate as it does not allow for sufficient separation between the diverse modes of life of pelagic marine vertebrates. Consequently, the traits and rules used here are tailored to these pelagic marine communities.

The rules assigned in this study firstly consist of a size hierarchy. For body size, it is generally not beneficial nor often physically possible for taxa to hunt and feed on resources larger than themselves as they will often expend more energy than they recoup from eating that prey item. Similarly feeding upon a prey item too small will also result in an energetic imbalance. While some extant species engage in cooperative hunting to take down larger prey (for example Pitman & Durban, 2012), here only individual behaviours are considered.

As such, consumers are assigned to only feed upon taxa which are in the same size category or up to three sizes smaller. This size restriction means that while any taxon within the category ‘large’ can feed on any resource smaller than themselves, the bigger predators are restricted to how small their prey can be. The three category limit was chosen based upon the feeding range of modern top predators, in addition to the known feeding range of *O. megalodon* (Lucifora *et al.*, 2008; Collareta *et al.*, 2017). Suspension feeders have been incorporated separately in this rule. Regardless of size, all chondrichthyan and mammalian filter feeders are only permitted to feed on taxa in the ‘tiny’ size category, due to their ecological lifestyle.

For the traits of vertical position and depth distribution the rules dictate that a consumer must share spatial distribution with its prey; they must co-occur together in the same location, water depth and position in the water column. The strict feeding habits assigned to each genus finally dictate which classes of organism they can feed upon.

All modelling was performed in R (R Core Team, 2021) version 4.3.1. The PFIM generates pairwise combinations between all taxa in the community. This includes combinations between two of the same genera to allow for the possibility of cannibalism. For a feeding link to then be assigned for each combination, all the rules stated above must be satisfied. The PFIM then returns an edge-list of all feasible interactions and constructs a network, assigning each genus a trophic value (based upon the average node length to reach the primary node). These networks are then plotted as metacommunity food webs, showing all feasible interactions, using the R package igraph (Csárdi *et al.*, 2024). Metacommunity food webs were constructed for the Pliocene and Pleistocene North Atlantic.

As this research is interested in the trophic position of *O. megalodon* yet some of the functional traits of this shark are subject to speculation, the metacommunity webs for the Pliocene were run several times with different trait combinations. The fossil record gives little indication of the depth range of *O. megalodon*, with fossils sourced predominantly from shallow, coastal habitats. Research hypothesising a similar ecology to extant great white sharks, *Carcharodon carcharias* (Cooper *et al.*, 2022), would imply migration to deeper oceanic regions with depths beyond the neritic zone and this is supported by the recent discovery of a fossil tooth from a deep-sea locality in the Pacific Ocean (Pollerspöck *et al.*, 2025). Isotopic studies also indicate a generalist feeding habit (McCormack *et al.*, 2022; Kast *et al.*, 2022; McCormack *et al.*, 2025), suggesting a greater prey breadth than recorded by feeding traces in the fossil record. Thus different traits for depth distribution and feeding habit were trialled to determine whether these returned different outcomes (see Supplementary Material). Additionally, to further assess the trophic role and impact of *O.*

megalodon in these marine communities, an additional Pleistocene metacommunity food web was constructed including the presence of this shark post-extinction.

2.3.4 Food web downsampling

The metacommunity food webs modelled for the Pliocene and Pleistocene show every feasible feeding interaction. In actuality, it is unlikely that all of these interactions would have occurred, thus meaning the metacommunity webs are likely over connected with regard to what would be expected. It is possible that a high density of interactions could mask any changes detected when analysing the food webs, potentially underestimating the extent of community change following the extinction event. To account for this possibility, 'realised' webs were also modelled which exhibit a reduced link distribution.

The realised webs were constructed using a downsampling function which sets a target degree (link) distribution based on the mixed-exponential power law found to represent the structure of modern and some extinct communities (Dunne *et al.*, 2002b; Roopnarine, 2006; Roopnarine *et al.*, 2007; Shaw *et al.*, 2024). During downsampling, links are removed randomly, where feeding links attached to more highly connected nodes have a higher probability of removal. While this method relies on the assumption of consistency of food web degree distribution through time, this Pliocene extinction is relatively recent in geological terms and, therefore, modern marine communities are likely to have exhibited a similar pattern to these earlier Neogene communities.

Initially, 1000 iterations of realised webs were generated for each time bin. Due to the random removal of links, downsampling resulted in multiple web topologies with two or more primary nodes. This occurred when taxa with few feeding links (notably squid) had all of their prey links removed and were thus moved to the base of the webs. These webs were removed from the dataset as they do not represent realistic food web structures. As with the metacommunity food webs, an additional sample of realised webs were also generated simulating the presence of *O. megalodon* in the post-extinction Pleistocene communities. A further 1000 iterations of the realised webs were generated and those without realistic food web structures removed, as described above.

2.3.5 Food web analysis

The metacommunity and realised food webs were analysed to assess changes in structure and function across the extinction event. Commonly used network-level and node-level metrics and motifs (patterns of interaction between three connecting nodes; Giling *et al.*, 2019) were calculated in R (Table 2.1). Additionally, effect size was calculated for each of the metric and motif values from the realised webs using the Cohen's d measure (Cohen, 2013) where values <0.49 signify a small effect size, 0.5-0.79 a medium effect size and >0.8 a large effect size. As the realised food webs were downsampled to achieve a target connectance, effect size for this metric is considered with caution.

Table 2.1 Structural metrics and functional motifs used in the food web analysis, detailing what they measure and how they are calculated. Table modified from Shaw *et al.* (2024).

Metric/Motif	Description	Explanation
Connectance	Realised feeding links expressed as a proportion of all links in a completed network	Measure of connectivity, often used as a proxy for ecosystem complexity
Normalised in-degree i.e. generality	Average number of resource nodes a consumer node is linked to	Measure of the range of prey items consumed by predators in the community
Normalised out-degree i.e. vulnerability	Average number of consumer nodes a resource node is linked to	Measure of the range of predators that feed upon prey taxa within the community
Number of linear chains i.e. linearity (motif)	Normalised number of linear three-node chains in the network	Measure of linear energy pathways, often used as a proxy for vertical complexity
Omnivory (motif)	Normalised number of three-node chains with a consumer feeding on two resources at different trophic levels	Measure of predation across trophic levels, an indicator of specialism
Apparent competition (motif)	Normalised number of three-node chains where a consumer is linked to two resource nodes	Measure of predator choice
Direct competition (motif)	Normalised number of three-node chains where two consumers share a resource node	Measure of competition between predators

2.4 Results

2.4.1 North Atlantic food webs

The trait-based Paleo Food web Inference Model (PFIM) constructed metacommunity food webs (showing all feasible feeding links) for Pliocene and Pleistocene North Atlantic pelagic communities (Figure 2.1),consisting of 267 and 242 individual vertebrate genera respectively, as well as 21 invertebrate nodes and a primary productivity node. The magnitude of marine megafauna extinction in these communities is close to the taxonomic loss found in global assemblages albeit with slightly lower overall generic losses (~25% in the North Atlantic vs 36% globally).

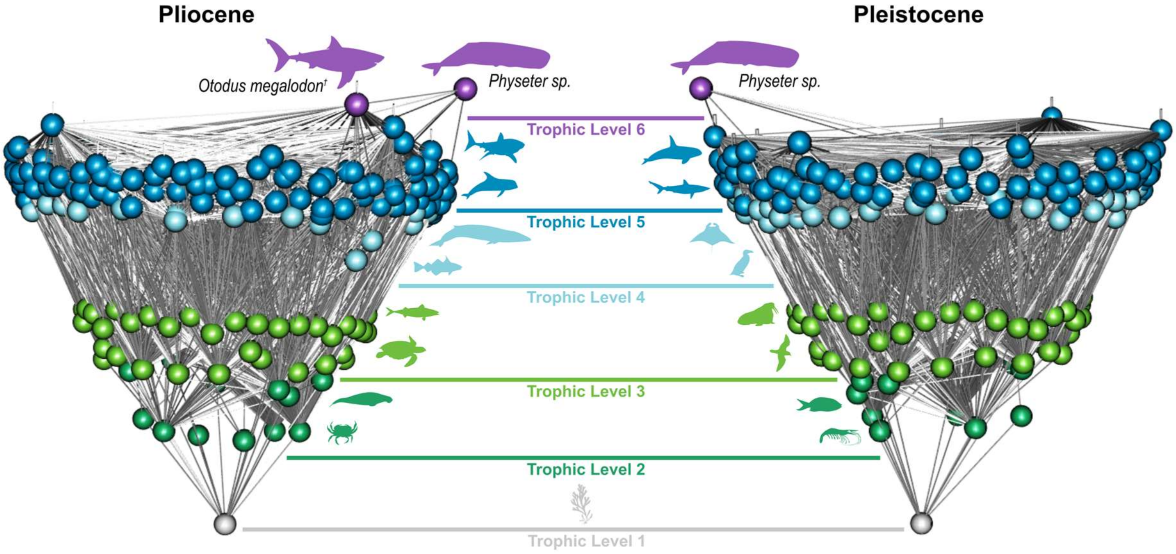

Figure 2.1 Metacommunity food webs of North Atlantic marine communities for the Pliocene (left) and Pleistocene (right). Nodes represent individual vertebrate genera, the primary productivity node (in trophic level 1) and the invertebrate nodes. Different node colours denote different trophic levels. Example taxa are presented for each trophic level, with silhouettes representing *Fucus serratus* for trophic level 1; *Metacarcinus magister*, *Metaxytherium*, *Caridea* and Acanthuridae for trophic level 2; *Eretmochelys imbricate*, *Scomber scombrus*, *Pachyptila* and *Odobenus rosmarus* for trophic level 3; *Melanogrammus aeglefinus*, *Balaenoptera physalus*, *Pinguinis impennis* and *Mobula alfredi* for trophic level 4; *Grampus griseus*, *Carcharodon carcharias*, *Carcharhinus obscurus* and *Orcinus orca* for trophic level 5; *Otodus megalodon* and *Physeter microcephalus* for trophic level 6.

The distribution and position of taxa in the metacommunity food webs are similar before (i.e. Pliocene) and after the extinction event (i.e. Pleistocene). Further, the extant taxa present in these ancient food webs occupy trophic level positions comparable to those seen in modern ecosystems. Genera that fall within the same trophic levels mostly occupy the same broad ecological guilds. Herbivores and the macroinvertebrate and microinvertebrate nodes are the sole occupants of trophic level two. Mesopredators of various sizes are spread between trophic levels three and four, with these genera largely being piscivorous, durophagous, or filter-feeders. Taxa that would be considered top predators in extant ecosystems, mostly larger sharks and toothed cetaceans, are positioned in trophic level five (i.e. with trophic levels of 5.0 to 5.9) alongside the largest predatory fish and cephalopods and consist of both specialist and generalist feeders. In the Pliocene, trophic level six (i.e. with trophic levels 6.0 to 6.9) consists of *O. megalodon* and the extant sperm whale, *Physeter* (see Top predator changes below; Figure 2.4). In the Pleistocene, following the extinction of *O. megalodon*, *Physeter* solely occupies trophic level six.

To account for uncertainties in *O. megalodon* palaeoecology, the Pliocene model was constructed several times with variable feeding and depth distribution traits for *O. megalodon* yet found these had negligible impacts on trophic positioning and structure (see Supplementary Material). The Pliocene food webs displayed here are based upon the recent interpretations of *O. megalodon* (Cooper *et al.*, 2022; McCormack *et al.*, 2025) as a transoceanic generalist with the broadest feeding habit and a depth distribution up to 1000m.

As the metacommunity food webs exhibit all feasible feeding links, the connectance of the webs (the proportion of expressed links out of all possible links in a network) at ~0.2 is higher than would be expected in most observed modern communities, which usually fall within the range of 0.01 and 0.1 (Dunne *et al.*, 2004; Marina *et al.*, 2018), potentially masking structural signals. Consequently, these webs were downsampled to produce realised webs with a target mixed exponential-power law in-degree distribution (Roopnarine, 2006; Shaw *et al.*, 2024) by randomly removing links to reach this desired link distribution. Of the 1000 realised webs generated for each epoch, 858 and 834 iterations recovered realistic web structures (see Methods) for the Pliocene and Pleistocene respectively. These realised webs exhibit a wide range of structure with connectance values close to those observed in modern communities, ranging from 0.030 to 0.048 (Figure 2.2).

The realised webs follow a similar pattern of taxa distribution to the metacommunity webs, with the ecological guilds shifting from herbivores to mesopredators to top predators with increasing trophic level. However, the removal of a significant number of feeding links in the realised webs results in longer pathways to the primary node, thus these webs have a greater number of trophic levels reaching a maximum of 8.7 (Figure 2.2). This is reflected in a greater spread of the guilds across the trophic levels; herbivores and invertebrates are still restricted to trophic level two, however, mesopredators are now present from trophic levels three to five (and occasionally six) and top predators from levels five to eight.

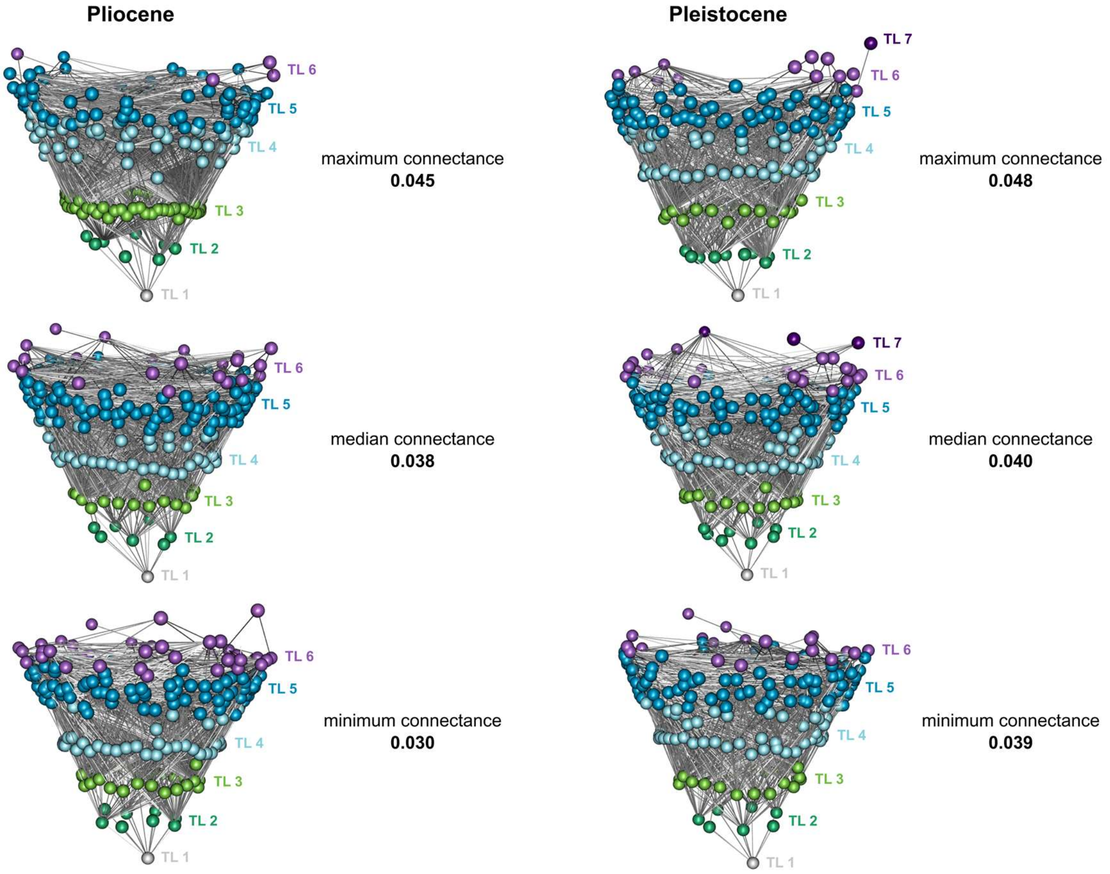

Figure 2.2 Iterations of the realised webs representing the range of connectance for the Pliocene (left) and Pleistocene (right). Nodes represent individual vertebrate genera, the primary productivity node (in trophic level 1) and the invertebrate nodes. Different node colours denote different trophic levels (TL).

2.4.2 Changes to food web structure and function

Despite the loss of 25% of megafaunal genera, including apex predator *O. megalodon*, these results suggest there was only minimal change in North Atlantic food web structure following the extinction event. This was found for both the metacommunity and realised food webs when metrics (measuring overall structural properties) and motifs (measuring functional changes through specific interactions between three connected nodes) were assessed across the Plio-Pleistocene boundary (Table 2.2). Although the wide range of food web structures generated for the realised webs is reflected in the calculated metrics and motifs (Figure 2.3), the measure of effect size allows for the strength of the changes over the boundary to be quantified. The overall directional change seen across the extinction event in the realised webs match that of the metacommunity webs, with the exception of omnivory.

Table 2.2 Calculated metrics and motifs for the metacommunity and realised food webs. Mean values are provided for the realised webs alongside the calculated Cohen's *d* value and associated effect size. Definitions for the metrics and motifs are found in Table 2.1.

Metric/Motif	**Metacommunity webs**		**Realised webs (means)**			
	Pliocene	Pleistocene	Pliocene	Pleistocene	*Cohen's d*	*Effect size*
Connectance	0.22	0.23	0.038	0.040	0.79	medium
Mean trophic level	4.62	4.54	4.637	4.536	0.42	small
Maximum trophic level	6.31	6.22	6.885	6.721	0.37	small
Generality	0.17	0.18	0.048	0.050	0.54	medium
Vulnerability	0.24	0.24	0.045	0.046	0.62	medium
Linearity	1.24	1.05	0.212	0.207	0.20	small
Omnivory	4.62	4.53	0.064	0.065	0.03	small
Apparent competition	3.53	3.56	0.427	0.433	0.08	small
Direct competition	6.78	6.49	0.384	0.383	0.03	small

The most notable shift seen in the metrics is that of connectance, which increases across the extinction and exhibits a borderline large effect size (Cohen's *d* of 0.79). This signifies an increase in the density of links amongst the surviving taxa and corresponds to increases seen in both generality (more feeding links per predator taxa) and vulnerability (more feeding links per prey taxa). Despite the generality and vulnerability metrics showing little change in the metacommunity webs, they both exhibit medium effect sizes (Cohen's d values of 0.54 and 0.62 respectively) for the realised webs. Although these effect sizes indicate differences over the extinction boundary, shifts in these three metrics are still no greater than 15%, highlighting that the changes, whilst significant directional signals, are only minor in terms of magnitude of change.

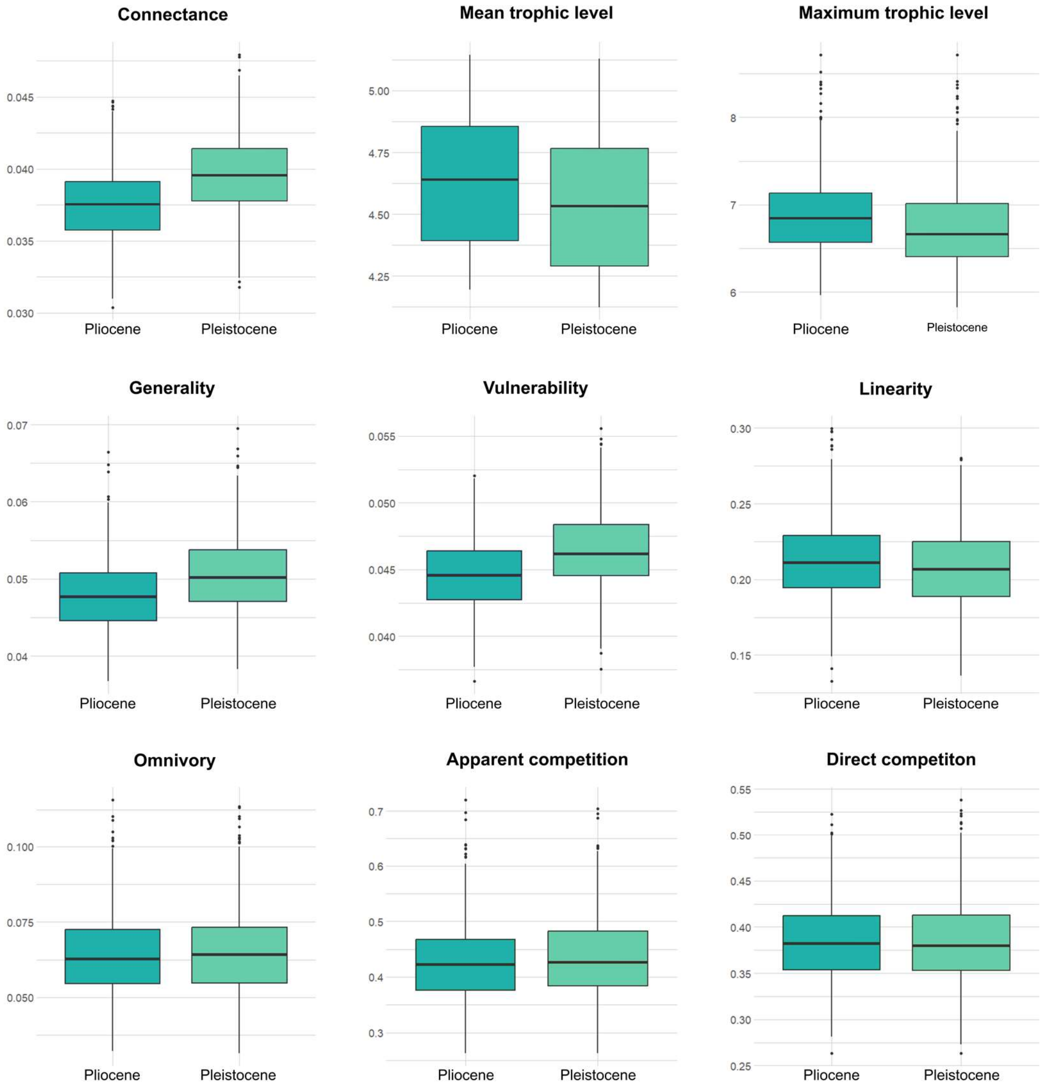

Figure 2.3 Realised food web metrics and motifs variation across the extinction event. Boxplots show the range in values recovered across the 858 Pliocene and 834 Pleistocene realised webs.

Both mean and maximum trophic level decrease over the extinction in the metacommunity and realised food webs, although this is only a marginal shift with a low effect size. Interestingly, the largest shift seen in the metacommunity webs is that of a decrease in the linearity motif which signifies a decrease in the number of linear feeding chains. However, a small effect size (Cohen's d value of 0.2) reflects a weaker signal and thus a smaller sign of change in the realised food webs. Both apparent and direct competition show very small effect sizes, suggesting overall little change in either direct or indirect competition occurred from the Pliocene to the Pleistocene. Finally, the omnivory motif presents a contrary pattern, decreasing in the metacommunity webs and increasing in the realised webs.

However, with a very small effect size, there was likely very little change, if any at all, in the levels of feeding from predators across different trophic levels following the extinction.

2.4.3 Top predator trophic changes

Both the metacommunity and realised food webs record no major shifts in the trophic positions of the top predators following the marine megafaunal extinction, despite the extinction of *O. megalodon* (Figure 2.4). In the Pliocene metacommunity food web, *O. megalodon* holds the position of apex predator being in the highest trophic level (with a trophic value of 6.19) and is not predated upon (aside from cannibalism). Surprisingly, the sperm whale *Physeter* is also positioned in the highest trophic level with a value even higher than that of *O. megalodon* (at 6.31). Despite this slightly higher position in the food web, *Physeter* is not considered an apex predator due to predation from *O. megalodon*, as seen in the feeding links. The other top predators (taken here as trophic value 5.7 and above) in the Pliocene metacommunity web consist of the extant predators *Carcharodon* (great white shark), *Orcinus* (orca) and *Grampus* (Risso's dolphin) alongside the lamniform shark *Parotodus* which went extinct in the marine megafauna extinction event.

In the Pleistocene metacommunity food web, the extinction of *O. megalodon* leaves *Physeter* as the sole occupant of trophic level six with a trophic level of 6.22. The lack of predation from *O. megalodon* or any other predator now results in *Physeter* positioned as the apex predator in the Pleistocene. The other surviving top predators hold similar trophic positions following the extinction event, though with the predatory cetacean *Grampus* now occupying the highest position in trophic level five, above *Carcharodon*. Overall, all predators undergo a slight decline in trophic level, corresponding to the drop in mean and maximum trophic level mentioned previously.

The realised food webs record a wide range of trophic levels for the top predators identified in the metacommunity webs (Figure 2.4). The highest trophic positions recovered by these predators are due to the longer pathways to the primary node, a facet of downsampling the metacommunity webs. While *Physeter* still maintains an average trophic level higher than *O. megalodon* in the Pliocene, the range of *Physeter* trophic levels now fits more closely within the extant sperm whale range (see Discussion). Overall, the average trophic levels of the individual taxa and their relative positions to each other before and after the extinction event in the realised webs fit closely to that seen in the metacommunity webs. This suggests top predator trophic levels were not affected by the high connectance of the metacommunity food webs.

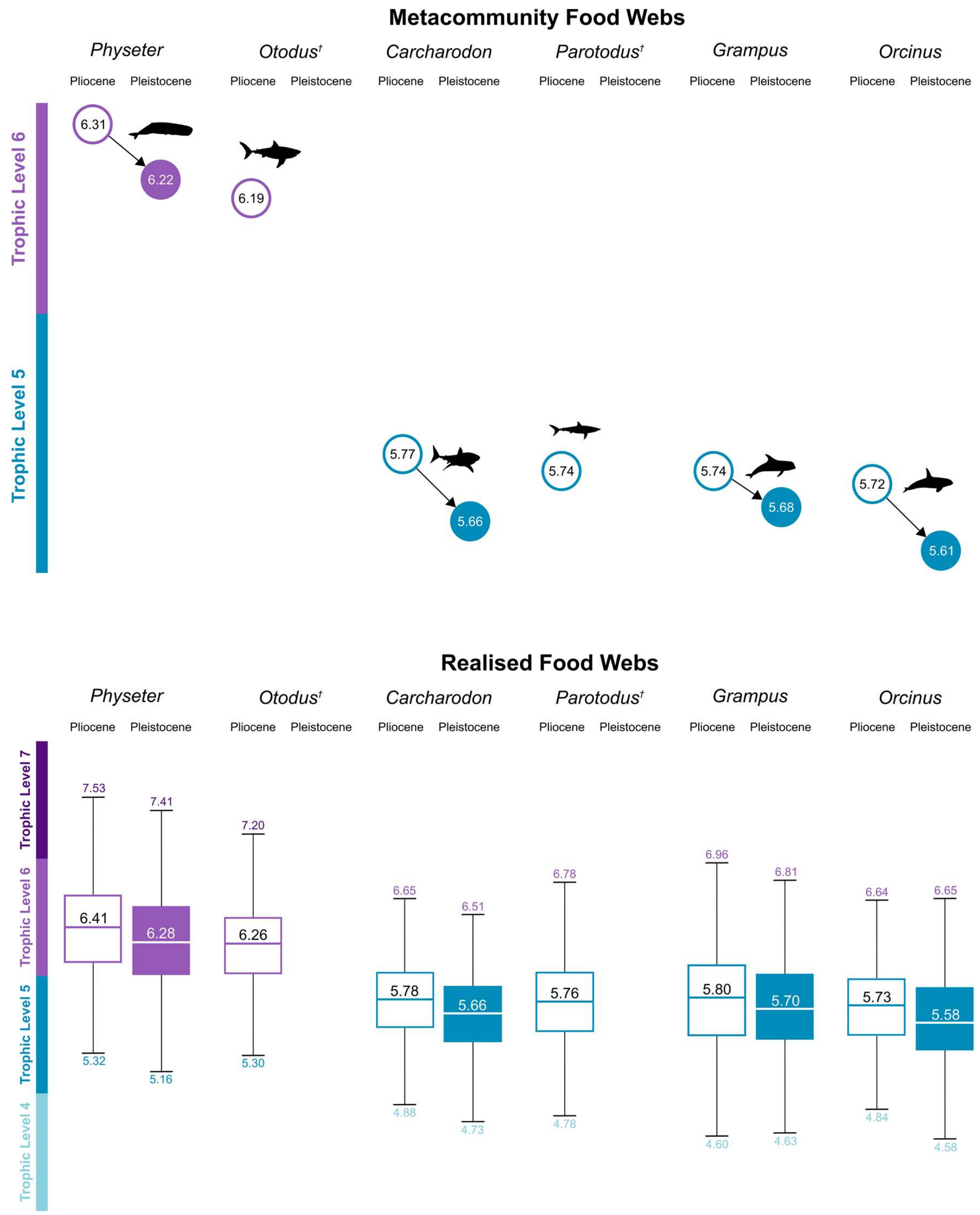

Figure 2.4 Trophic value changes in top predators for the metacommunity (top) and realised (bottom) food webs. For the metacommunity webs, arrows show directional shift of trophic value of surviving top predators from the Pliocene to the Pleistocene. For the realised webs, boxplots show the range of trophic values recovered. Outliers have been removed with the maximum, minimum and median values labelled. Colours denote different trophic levels and representative silhouettes consist of *Physeter microcephalus*, *Otodus megalodon*, *Carcharodon carcharias*, *Carcharhinus obscurus* (used to represent *Parotodus*), *Grampus griseus* and *Orcinus orca.*

Simulating the presence of *O. megalodon* post-extinction allowed for the impact of this apex predator in these marine communities to be assessed. Additional metacommunity and realised Pleistocene food webs were constructed, for which 867 iterations of 1000 recovered realistic food web structures. The trophic value of *O. megalodon* did decrease from the Pliocene, from 6.19 to 6.09 in the metacommunity webs and from a median of 6.26 to 6.14 in the realised webs. These shifts are in line with the decreases in trophic level seen amongst the other surviving predators over this boundary. The key metrics and motifs also did not significantly change following the inclusion of *O. megalodon* in the Pleistocene.

2.5 Discussion

Food webs were reconstructed for Pliocene and Pleistocene North Atlantic marine communities to assess structural and functional change following the Pliocene marine megafaunal extinction event. Analysis and comparison of the food webs before and after the extinction finds only minor shifts in structure and function. Post-extinction Pleistocene communities are more densely connected, characterised by more generalist taxa and exhibit a decrease in mean trophic level. However, despite these minor changes, food web structure remains fairly consistent across the Pliocene and Pleistocene, lacking any of the major shifts that may be expected across a major extinction boundary.

The minor shifts exhibited in food web structure are predominantly seen in the metrics of connectance, generality and vulnerability which exhibited large and medium effect sizes. Increases in these three metrics in modern ecological theory are often attributed to more robust and stable ecosystems (Dunne *et al.*, 2002b; Landi *et al.*, 2018), which is perhaps contrary to what would be expected of communities following a major faunal turnover. However, these increases in connectance, generality, and vulnerability are comparable to patterns exhibited following other extinction events in the fossil record which, rather than corresponding to increasing ecosystem stability and robustness, reflect extinction selectivity against specialist species and increased survivorship of opportunist generalists (Clavel *et al.*, 2011; Dunhill *et al.*, 2024). This is likely the case in these Pleistocene communities where approximately two thirds of the genera lost from the Pliocene food web had a narrow diet breadth, feeding on only one or two feeding categories. Predators with a broader diet breadth are more likely to retain sufficient prey options across periods of perturbation when extinction rates are high (Clavel *et al.*, 2011). Thus, this concept of increased survivorship of generalists supports the increase seen in generality and connectance here, as surviving predators each feed upon a broader range of prey which results in more feeding links per node across the community. The increase in vulnerability can similarly be explained due to the increase in predation pressure on the lower trophic level prey, where a larger proportion of generalist predators are feeding upon more of these prey nodes. These justifications do not preclude the inferences from modern ecology and it is possible these more densely connected Pleistocene communities may have been more stable following the extinction. As there is still some debate around what inferences can be made from these metrics, particularly connectance (Dunne *et al.*, 2002a; van Altena *et al.*, 2016; Landi *et al.*, 2018), these minor shifts could reflect varying ecosystem dynamics.

Further structural shifts were detected in the metacommunity food webs, however, given the small effect sizes observed for these metrics and motifs in the realised webs, these results should be interpreted with caution. The decline in mean and maximum trophic levels likely reflects the loss of high trophic level prey, resulting in top predators having shorter feeding chains connected more directly to the primary node. The observed increase in the apparent competition motif may align with the increase in generality (i.e. broader diet breadth among surviving taxa thus increased predator choice and competition between surviving prey to avoid being predated). However, this pattern is plausibly driven by the disproportionate loss of predators relative to prey. Direct competition also decreases across the extinction boundary in the metacommunity webs, suggesting a drop in competition between predators for the same prey; an expected outcome in communities with fewer predators following the extinction. The most pronounced change in the metacommunity webs is seen in linearity, which declines substantially across the extinction boundary. This indicates that Pleistocene food webs became less vertically complex, with fewer linear feeding chains reflecting the loss of nodes and connections at higher trophic levels. Consequently, potential energy pathways through the web were curtailed, reducing the overall vertical structure of the community.

The loss of vertical complexity across the Plio-Pleistocene boundary may offer support for the hypothesis that neritic zone loss was a primary driver of these extinctions (Pimiento *et al.*, 2017). A reduction in productive shelf habitats would be expected to create more energetically constrained ecosystems, limiting energy transfer through the food web. The observed decline in vertical complexity, inferred through reduced linearity, can therefore act as a proxy for these energetic constraints (France, 2012), with fewer taxa able to persist at the highest trophic levels. However, this decrease in linearity may instead simply reflect the loss of *O. megalodon* and other high trophic level predators from the Pleistocene webs, rather than a basin-wide reduction in energy availability. The removal of these predators eliminates pathways to trophic levels five and six, thereby reducing the number of possible linear chains. Nevertheless, because the effect size of this motif was small in the realised webs, any ecological inferences drawn from this metric must be treated with caution.

As marine megafauna fulfil important ecological roles in marine ecosystems (Estes *et al.*, 2016; Hammerschlag *et al.*, 2019; Tavares *et al.*, 2019), it may be expected the high taxonomic loss during the extinction would result in various cascading impacts and be reflected in significant structural and functional changes in the food web. The lack of major changes may be partly due to the conservative nature of topological structural food webs (Berlow *et al.*, 2004; O'Gorman *et al.*, 2019). Topological food webs will intrinsically underestimate certain elements of ecosystem structural change, as they only consider the presence/absence of taxa and interactions without the nuances of changing population sizes, biomass or interaction strength between nodes. However, in general, extant marine food webs are found to be particularly resilient to losses of both well-connected and random taxa (Dunne *et al.*, 2004).

The resilience of these ecosystems may be linked to high levels of redundancy. Trophic redundancy (where multiple taxa in one ecosystem fulfil the same broad feeding niche), buffers against extinction cascades making an ecosystem less vulnerable to further secondary extinction cascades (Sanders *et al.*, 2018). The Pliocene food web contains high levels of trophic redundancy, likely contributing to the preservation of ecological roles through feeding links and thus preserving food web structure across the extinction event despite high generic losses. Also, despite the Pliocene marine megafaunal extinction being one of the biggest marine extinction events of the Cenozoic, it is of relatively small magnitude compared to major mass extinction events in the fossil record. Therefore, while other more significant marine extinctions have resulted in larger changes in trophic structure (as seen in Early Toarcian Extinction Event food webs; Dunhill *et al.*, 2024), this extinction may be too small to drive such significant shifts in ecosystem structure.

The impact of the extinction of *Otodus megalodon*, a marine predator, on the trophic positions of other top predators was also considered. As apex predators are known to exert top-down predation pressure (Baum & Worm, 2009; Steneck, 2012; Hammerschlag *et al.*, 2022), it may be expected the extinction of this shark would cause trophic shifts in the other top predators. However, the negligible relative shifts in top predator trophic levels that are seen in both the metacommunity and realised food webs may be due to any resultant cascading effects (such as mesopredator release) primarily impacting population dynamics, which cannot be interpreted from structural webs alone (Berg *et al.*, 2015). This is similarly the case when further analysis simulating the presence of *O. megalodon* in the Pleistocene food webs found the positions of the predators to be comparable regardless of *O. megalodon* being present or absent in these post-extinction Pleistocene food webs.

These findings also have implications for hypotheses concerning the extinction mechanisms of *O. megalodon*. It has been proposed that *O. megalodon* experienced intensified direct competition with other top predators, particularly *Carcharodon carcharias* (the great white shark), for remaining prey resources following the decline of its primary prey, mostly large-bodied mysticetes (Pimiento *et al.*, 2016; Collareta *et al.*, 2017; McCormack *et al.*, 2022). If competitive displacement was a key extinction driver, the simulated Pleistocene food webs would be expected to show a marked decrease in the trophic position of *O. megalodon*, reflecting a shift toward feeding interactions more similar to those of *C. carcharias* as both taxa targeted smaller prey (McCormack *et al.*, 2022). However, this pattern is not observed in the simulated Pleistocene webs. Although *O. megalodon*'s trophic level does decrease in the simulations, the magnitude of this decline is comparable to the general drop in trophic level exhibited by all top predators across the extinction boundary. This suggests a broad restructuring of prey availability rather than a competitive shift specific to *O. megalodon*. Importantly, this species remains at trophic level six in the simulated post-extinction webs, indicating that prey were still present, albeit likely at reduced abundances insufficient to sustain viable *O. megalodon* populations. Such energetic limitations cannot be conclusively assessed using topological food webs alone; evaluating whether prey biomass was adequate to support *O. megalodon* would require dynamic food web modelling capable of incorporating energy flow and population biomass (Curtsdotter *et al.*, 2011).

The reconstructed food webs also present further interpretation of the trophic positions of all top predators during the Pliocene and Pleistocene. Most interpretations of extinct predator trophic levels are derived from stable isotope analysis on fossil samples (usually teeth), where diet is inferred from isotope ratios and thus provides a measure of a taxon's position in a food web (for example Martin *et al.*, 2015; McCormack *et al.*, 2022; Kast *et al.*, 2022). Trophic levels derived from food web reconstructions are instead measured by the length of the multiple chains (the number of nodes) required to reach the base of the food web from the taxa. Therefore, the differences in these approaches may give differing insights into the trophic positions of key species. In the Pliocene food web, *O. megalodon* is positioned as the apex predator in trophic level six, a level higher than apex predators in modern marine communities where pelagic systems only consist of four to five trophic levels (Dunne *et al.*, 2004; Hussey *et al.*, 2014; Blanchet *et al.*, 2019). The trophic level of 6.19 for *O. megalodon* aligns with isotopic analyses which also place this species in trophic level six or above (Kast *et al.*, 2022). The trophic level six assignment of *Physeter,* the sperm whale, in our modelled food webs, is perhaps surprising as this genus is usually positioned in trophic level five in modern ecosystems (Blanchet *et al.*, 2019; Guerra *et al.*, 2023). However, research using stable isotope analysis (Wild *et al.*, 2020) estimates an extant trophic value of 5.7 ± 0.4, close to its position in the metacommunity webs, and falls well within the realised webs range. The positioning of *Physeter* above *O. megalodon* (despite being predated upon by the shark) is due to the sperm whale's prey being positioned solely in trophic level five, albeit the lower end of this level, whereas *O. megalodon* has feeding links for a broader range of prey which span multiple trophic levels, predominantly baleen whales (Pyenson & Koch, 2022).

In the Pleistocene food web, following the extinction of *O. megalodon*, *Physeter* is now positioned as the apex predator, facing no predation. In modern ecosystems, the sperm whale is not an apex predator as it is predated upon by orcas through pack hunting, a feeding method this food web model does not account for. However, there is currently no fossil evidence to support such predation in the fossil record and the feeding behaviour of *Orcinus* is known to have changed within the last million years (Bianucci *et al.*, 2022). The trophic positioning of the other top predators during both epochs are in line with their ecological lifestyles. The extant *Carcharodon*, *Grampus* and *Orcinus* are macropredators in modern ecosystems and also positioned in the higher trophic levels (in most cases trophic level five). Understanding of the ecology of the extinct shark *Parotodus* is limited (Collareta *et al.*, 2023), though it likely had similar macropredatory feeding preferences to the other top predators, supporting its position in this high trophic level.

The end Pliocene marine megafaunal extinction event saw only minor shifts in North Atlantic food web structure and function, with negligible impacts on the relative trophic positions of top predators. The post-extinction communities are more highly connected and characterised by an increase in generalist taxa, however, overall marine ecosystems remained structurally stable and robust to losses of large-bodied taxa, including a marine apex predator. As the food web reconstructions of the Pliocene and Pleistocene are comparable to modern ecosystems, in terms of the ecological guilds present and the trophic positioning of taxa, some inferences may be made from this extinction event. Future marine megafaunal extinctions to the extent recorded in the Pliocene may have similarly minimal impacts on future marine ecosystem structure and function, especially if a level of trophic redundancy is retained. However, the ongoing and multifactorial anthropogenic pressures (Dulvy *et al.*, 2014; Grose *et al.*, 2020; Pacoureau *et al.*, 2021; van Weelden *et al.*, 2021), not present in the Pliocene and Pleistocene, may intensify the impacts of future extinctions. Therefore, even if overall ecosystem structure remains intact, severe changes to populations and marine biomass could still occur.

Chapter 3.

Regional variation of the Pliocene marine megafaunal extinction

3.1 Abstract

The Pliocene marine megafaunal extinction was a major episode of biodiversity loss, yet although previous studies have quantified its global magnitude, the extent of spatial variability and the underlying drivers remain insufficiently understood. The late Pliocene was characterised by climatic instability and if environmental factors played a significant role in driving megafaunal extinctions, regional difference in extinction severity would be expected. Here, global and basin-specific extinction dynamics of marine megafauna across the Neogene to early Pleistocene were assessed. Extinction rates were estimated at both global and regional scales for five ocean basins using three complimentary extinction rate metrics, allowing for correction of sampling inconsistencies and biases. All three metrics revealed a clear global peak in extinction rates during the Piacenzian, coinciding with the timing of the marine megafaunal extinction. However, regional patterns demonstrated marked spatial heterogeneity. The North Pacific, South Pacific and Mediterranean basins exhibited substantial Piacenzian peaks, whereas the North Atlantic showed notably lower extinction rates, indicating comparatively reduced extinction impacts in this region. This pattern persisted when marine mammals and sharks were analysed separately. These findings provide partial support for the previously proposed neritic zone hypothesis, which infers that basins with larger continental shelf areas would be expected to have experienced buffered extinction impacts. While the North Atlantic broadly conforms to this expectation, high extinction rates exhibited in the Mediterranean suggest that additional environmental or ecological stressors likely contributed to the regional variation observed.

3.2 Introduction

The marine megafaunal extinction event at the end of the Pliocene is a relatively understudied period of significant biodiversity loss in the Cenozoic. Occurring just prior to the Plio-Pleistocene boundary (approximately 2.6 Ma), 36% of large-bodied marine genera were lost, including marine mammals, seabirds, sharks and turtles (Pimiento *et al.*, 2017). Functional diversity of marine ecosystems was also affected, with megafaunal functional richness loss of up to 17% (Pimiento *et al.*, 2017). Despite the considerable taxonomic and functional losses that occurred during this extinction event, there are substantial gaps in our understanding of the underlying mechanisms of these faunal extinctions. The magnitude of these marine megafauna losses have previously only been quantitatively measured on a broad global scale (Pimiento *et al.*, 2017) and it is not known how this event varied spatially.

Extinction events in the fossil record rarely exhibit uniform global impacts (for example MacLeod & Keller, 1994; Krug & Patzkowsky, 2007; Edie *et al.*, 2018; Danise *et al.*, 2019). Even the most severe biotic crises, such as the end Permian mass extinction, displayed regional variability in extinction magnitude and ecological consequences (Davydov *et al.*, 2021; He *et al.*, 2025). This variability is often attributed to spatial heterogeneity in environmental pressures. These can include latitudinal climate gradients impacting temperature stressors (Song *et al.*, 2020; Pohl *et al.*, 2023), ocean circulation patterns varying nutrient availability and oxygen levels (Clarkson *et al.*, 2016; Brugger *et al.*, 2021; Foster *et al.*, 2024) and suitable habitat availability including the presence or absence of refugia (Pohl *et al.*, 2023; Peng *et al.*, 2025). Although marine megafaunal extinction rates during the Pliocene have been quantified and found to be significantly elevated compared to the other epochs in the Cenozoic (Pimiento *et al.*, 2017), it remains unclear whether these rates are globally uniform. Assessing any potential regional variability in extinction magnitude could provide valuable insights into the drivers of this event.

The primary drivers of the megafaunal extinctions during the end Pliocene are currently not well understood. However, it is hypothesised that a reduction in neritic zone area may have been a key ecological stressor (Pimiento *et al.*, 2017). The neritic zone is shallow marine habitat, up to 200m in depth, situated above the continental shelf (Boaden & Seed, 1985; Dolbeth & Arenas, 2021). This habitat is among the most biologically productive marine environments (Boaden & Seed, 1985), maintaining diverse and complex communities and is crucial for supporting extant marine megafauna (for example Bost *et al.*, 2009; Guidino *et al.*, 2014; Chatzimentor *et al.*, 2021; Bava *et al.*, 2022; Leurs *et al.*, 2023; Li *et al.*, 2023). During the late Pliocene, a transition to global cooling resulted in glaciation of the Northern

Hemisphere and subsequent sea level fall (Miller *et al.*, 2005; Lisiecki & Raymo, 2007; Miller *et al.*, 2020). This drop in sea level exposed large areas of the continental shelf, reducing the neritic zone area by ~27% (Pimiento *et al.*, 2017). Therefore, the marine megafauna that would have relied on this habitat for foraging and reproduction could have faced heightened extinction risk due to decreased resource and habitat availability. This is supported by some apparent extinction selectivity towards coastal and homeothermic taxa (species with high metabolic demands and thus high feeding requirements; Boyles *et al.*, 2011).

Neritic zone area is not homogenous across ocean basins. The extent of continental shelf varies substantially, both in the present and throughout geological time. Although a drop in global sea level would reduce the area of shallow marine habitats, basins with relatively large continental shelves would have retained more neritic zone habitat, potentially buffering the marine megafauna there from the full ecological impact of the extinction event. Conversely, ocean basins with narrow continental shelves would have undergone proportionally greater neritic zone habitat loss under equivalent sea-level changes. However, neritic zone area is not the only potential extinction driver that would lead to regional variation in extinction impacts. As the late Pliocene was a period of significant climatic change, other environmental variables, such as a decrease in sea temperature (McClymont *et al.*, 2023; Partarrieu *et al.*, 2025) or shifting salinity patterns (Swann, 2010), may have also been influential in driving the megafaunal losses and would similarly exhibit non-uniform global patterns. Therefore, if environmental pressures were responsible for the extinction selectivity during the extinction event, regional variation would be expected.

Here, extinction rates of marine megafauna are quantified across the Neogene and Pleistocene to assess the impact of the Pliocene marine megafaunal extinction event on a global and a regional scale. Three different extinction rate metrics are used to account for inconsistencies and biases in fossil sampling and thus improve confidence in estimated patterns. Extinction rates are quantified across the extinction event in different ocean basins and between different taxonomic groups to test the hypothesis that extinction impacts exhibited regional variation.

3.3 Methods

3.3.1 Data collection

The marine megafauna considered in this study are marine mammals, sharks, reptiles and sea birds greater than 1m in length (based on Pimiento *et al.*, 2024). Although other taxonomic groups, particularly ray-finned fish (Actinopterygii), reached such lengths (e.g. *Thunnus*), these were excluded to be consistent with the marine megafauna considered in the original study defining this extinction event (Pimiento *et al.*, 2017). Further, Actinopterygii do not appear to have been significantly impacted by this event, with only one genus extinction recorded in the North Atlantic (see Chapter 2).

Occurrence data was sourced from the Paleobiology Database (PBDB) for each stage from the Miocene (23.03Ma) through to the Pleistocene (0.0117Ma). Data was collected at genus level for Chondrichthyes, Mammalia and Reptilia from marine sediments only (see Supplementary Material). Species occurrences were also collected however were not used in the analyses due to poor taxonomic resolution and inconsistency between different taxonomic groups.

To assess regional variation in marine megafaunal extinction rates, fossil occurrence data were sorted into ocean basins; the North Pacific, South Pacific, North Atlantic, South Atlantic and Mediterranean Sea. Six ocean basins were originally chosen to provide reasonable global coverage, however due to lack of occurrence data in the Indian Ocean (with only 11 genera recorded across the entire time period), this basin was removed. Palaeo-latitudes and longitudes of fossil collections were used to separate genera into the respective basins.

3.3.2 Extinction rate analysis

Extinction rates for marine megafauna were calculated using three commonly-used metrics: raw, boundary-crossover (BC; Foote, 1999) and three-timer (3T; Alroy, 2008). This approach differs from that in Pimiento *et al.* (2017), where Pyrate was applied to estimate rates across the entire Cenozoic by epoch. While Pyrate often outperforms other methods when used on well-sampled datasets, its accuracy decreases when fossil occurrence data is sparse (Flannery-Sutherland *et al.*, 2022), as is the case for the spatially restricted datasets here. As sampling varies considerably among ocean basins, these traditional methods (raw, BC and 3T) were selected instead.

To apply the extinction rate metrics to spatially restricted regions, the framework outlined in Allen *et al.* (2023) is used. In this original approach, fossil occurrences were subset into latitudinal bins prior to evolutionary rate estimation using raw, BC and 3T metrics, enabling the assessment of latitudinal variation in taxonomic turnover. Here, this framework was modified to assign occurrences to the five selected ocean basins instead. These methods require a minimum of five genera per regional time bin to calculate a rate for that period and extinction rates are represented as a proportion.

It is recommended to calculate and compare all three of these extinction metrics as they represent a trade-off between robustness to sampling bias and data requirements (Allen *et al.*, 2023). While raw rates can be estimated from relatively sparse datasets, BC and 3T require larger sample sizes to produce rate estimates, as each additional correction for sampling bias places further constraints on the taxa that can be included. This is particularly noticeable in regionally subsampled data where occurrence counts can be low. Rate estimates from the 3T metric are overall more accurate, presenting less bias than when calculated using BC or raw (Alroy, 2008). However, this is heavily dependent upon the sampling of the time slices used in each calculation, and in some circumstances raw or BC may perform better (Allen *et al.*, 2023). As such, comparing the three methods may be valuable when interpreting extinction rate analysis results.

Extinction rates were calculated for all three metrics for each geological stage from the Aquitanian to the Calabrian, globally and for each of the five ocean basins. Rates were further calculated separately for all marine megafauna taxa and then individually for sharks and marine mammals. The other megafaunal taxonomic groups (sea birds and reptiles) did not have sufficient sample sizes to also calculate these rates individually. All analyses were performed in R (R Core Team, 2021) version 4.4.0 using the tidyverse package (Wickham *et al.*, 2019).

3.4 Results

3.4.1 Global and regional marine megafauna extinction rates

The three extinction rate metrics estimate a similar global pattern of rates (represented as proportion of genera extinction) from the Aquitanian to the Calabrian (Figure 3.1). The metrics vary in rate magnitude, with the raw data consistently calculating the highest rate values for each stage, followed by the boundary-crossover (BC) and the three-timer (3T) which presents notably lower rates. All three metrics exhibit a clear peak in extinction rates during the Piacenzian, the final stage of the Pliocene during which the marine megafaunal extinction occurred. Following the marine megafaunal extinction there is a clear drop in extinction rates into the Gelasian. Prior to this extinction, another clear peak is seen in the Tortonian by all three metrics, and the raw and BC metrics present another earlier peak in the Burdigalian.

On a regional scale, the South Atlantic basin was too poorly sampled across the time period for rates to be calculated for the majority of stages, regardless of the metric. Thus a clear pattern of extinction rates across time could not be deduced for this region, particularly over the Plio-Pleistocene boundary. As such these rates are not presented here but can be found in the Supplementary Material. For the other basins, in each case sampling was too inconsistent for the 3T metric to estimate a continuous pattern however rates are mostly complete for both the raw and BC (Figure 3.1). For the raw data and BC metrics, the North Pacific presents extinction rates which most closely follow those presented globally compared to the other ocean basins. The increase in extinction rates during the marine megafaunal extinction (in the Piacenzian) is present, with rates peaking even higher than those globally for all three metrics. The South Pacific presents a less comparable pattern of rates to the global. Notable differences include contrasting shifts in the raw and BC rates in the Burdigalian (with the former increasing and the latter decreasing) and a sizeable decrease in 3T rates during the Zanclean. However, all three metrics peak in the Piacenzian for the marine megafaunal extinction, though sampling is too poor in the early Pleistocene to estimate post-extinction rates. Similarly to the South Pacific, the Mediterranean Sea presents some differences to the global pattern, such as decreasing rates in the Burdigalian and much lower rates in the Serravallian. This basin is notable for exhibiting more exaggerated peaks and troughs than the other regions, particularly in the Tortonian and from the Messinian to the Piacenzian. Post-extinction rates were also not able to be calculated for neither the Gelasian nor the Calabrian due to sampling.

The North Atlantic presents a very similar pattern of rates to the global throughout the Miocene, with the exception of a lack of peak in the Burdigalian from the BC metric (Figure 3.1). However, the North Atlantic differs from all ocean basins and the global pattern in the Pliocene as it does not exhibit the sizeable peak characteristic of the marine megafaunal extinction in the Piacenzian. Although the BC metric does show a slight increase in this stage, it is only a minor change and the raw data actually decreases in extinction rate instead. Unfortunately there is no value calculated for the 3T metric in the Piacenzian. Post-extinction rates also show a more gradual change compared to the other regions.

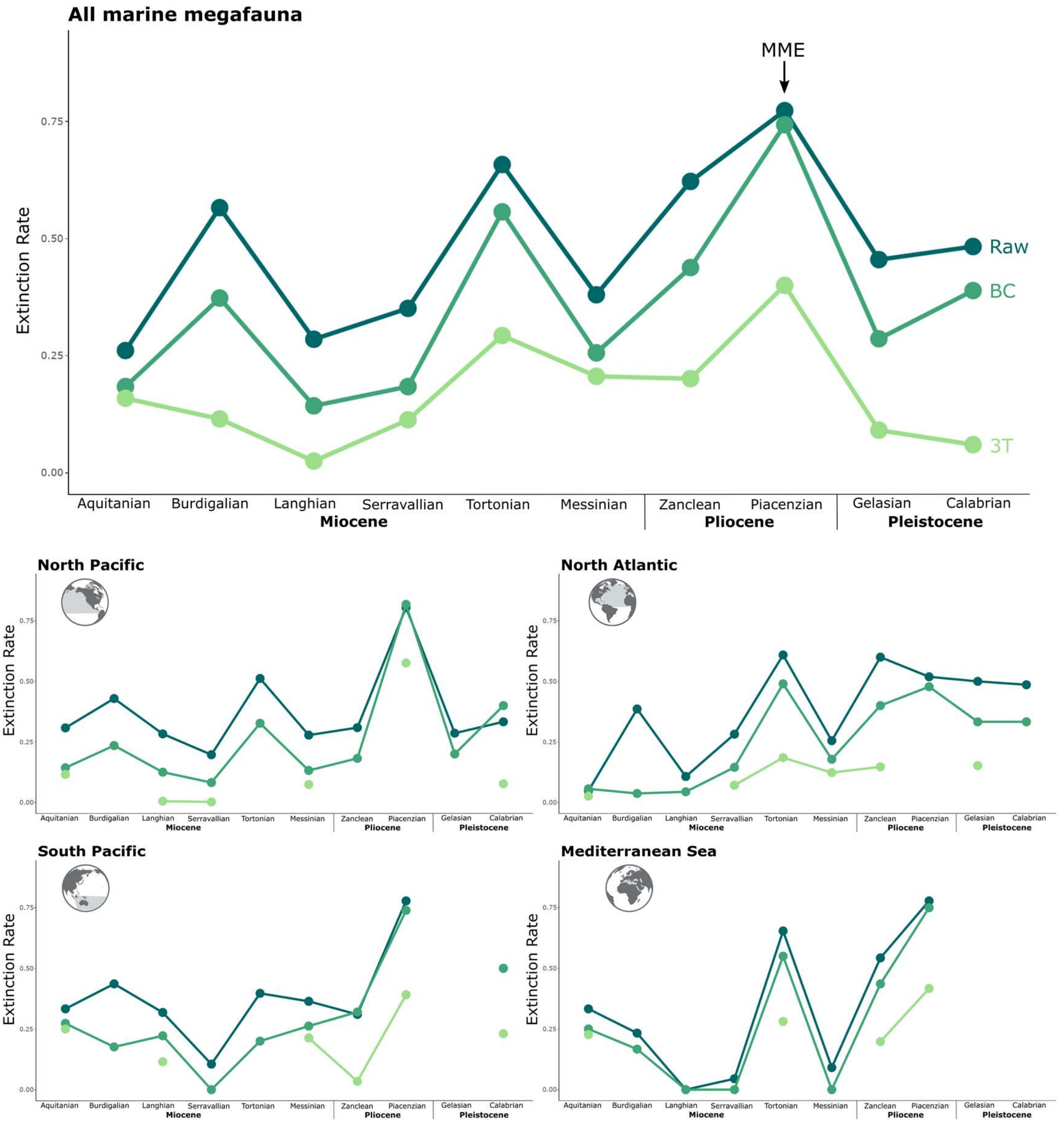

Figure 3.1 Estimated extinction rates for marine megafaunal genera for each stage from the Aquitanian to the Calabrian for global (top) and regional (bottom) occurrence data. The marine megafaunal extinction (MME) in the Piacenzian is labelled on the global extinction rates. The three extinction rate metrics raw, BC and 3T are labelled and differentiated by colour. Missing points for periods and regions are due to insufficient data availability to calculate an estimate.

3.4.2 Megafaunal mammal and shark extinction rates

When the extinction rates of megafaunal mammals (Figure 3.2) and sharks (Figure 3.3) are considered individually, different patterns across time emerge. Overall, for both the global data and at regional scales, the sampling is more inconsistent for these groups, thus there are fewer data points for all three metrics, though most notably within the 3T metric.

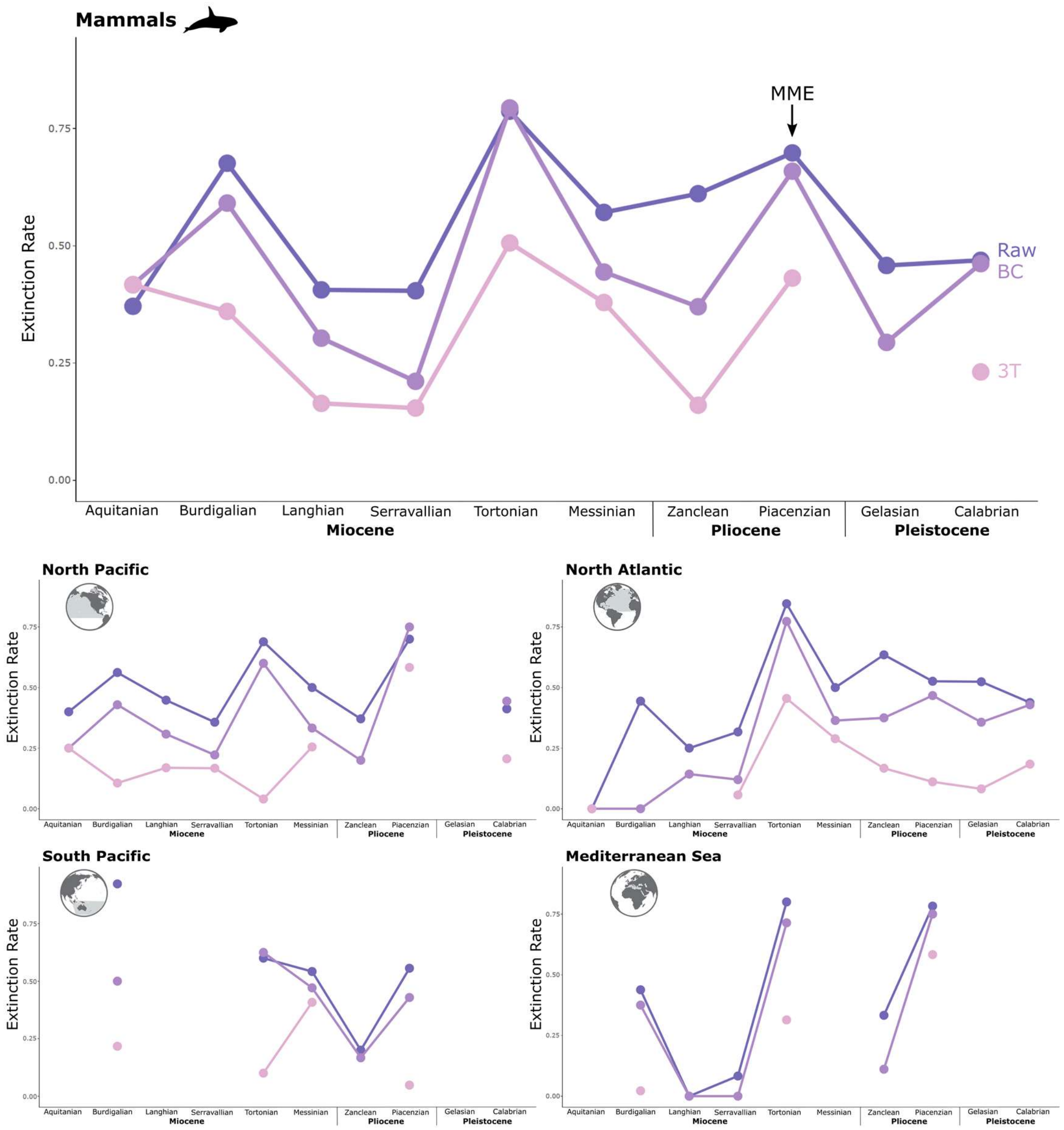

Figure 3.2 Estimated extinction rates for megafaunal mammal genera for each stage from the Aquitanian to the Calabrian for global (top) and regional (bottom) occurrence data. The marine megafaunal extinction (MME) in the Piacenzian is labelled on the global extinction rates. The three extinction rate metrics raw, BC and 3T are labelled and differentiated by colour. Missing points for periods and regions are due to insufficient data availability to calculate an estimate.

On a global scale, mammals present a pattern similar to that seen when all marine megafauna are considered (Figure 3.2). Notably the same peaks in extinction rates are seen in the Burdigalian, Tortonian and Piacenzian. However, the mammals differ in that the

Tortonian peak is higher than that seen in all marine megafauna and is higher than the peak present during the marine megafaunal extinction. The increase in rates in the Piacenzian is not only lower than the Tortonian but is also smaller in magnitude than that seen when all marine megafauna are considered. Following the marine megafaunal extinction, a notable decline in post-extinction rates for the raw and BC metrics is seen.

Sharks differ from mammals in presenting overall much lower extinction rates across the entire Miocene (Figure 3.3). The greatest peak during this epoch is seen in the Burdigalian with the raw metric, although this is a more minor shift in the BC metric. However, there is a significant increase in rates in the Pliocene. For the raw data this jump is seen in the Zanclean with a further increase again in the Piacenzian, but in the BC and 3T metrics, this initial increase is only seen in the Piacenzian. Although for the 3T metric, sharks exhibit an extinction rate lower than that seen in mammals during the Piacenzian, for the raw and BC metrics sharks present rates comparable to that seen in all megafauna, greater than the mammals. Similarly to mammals, a post-extinction decline in rates is seen, exhibited in all three extinction rate metrics.

Sampling across the different ocean basins was very variable for both groups across time, with this being evident in the inconsistency of representation in the metrics, especially 3T, with the North Pacific and North Atlantic showing the clearest patterns. There are also more instances of missing stage data for all three metrics than seen in the cumulative marine megafauna rates. This in particular makes it hard to determine post-extinction rate patterns, with the exception of the North Atlantic for mammals and the North Pacific for sharks.

The pattern of extinction rates across the marine megafaunal extinction in the different regions for these separate groups largely matches that seen in the rates for all megafauna. Peaks in extinction rates during the Piacenzian (where the metrics are available) are clearly seen for both sharks and mammals for the North Pacific and South Pacific. However, the 3T metric in the mammal data shows particularly low rates (especially compared to the raw and BC metrics) in the South Pacific, this is likely due to small sample sizes, with no 3T rates reported for either the Zanclean or Gelasian (the prior and subsequent stages). Mammals also see a significant peak in Piacenzian extinction rates in the Mediterranean Sea, however sampling of shark occurrences in this region were too poor to recover a rate estimate for any of the three metrics.

As with the regional rates calculated for all marine megafauna, the North Atlantic does not present a notable peak in extinction during the Piacenzian for either the mammals or sharks. In mammals, the raw metrics shows a slight decrease in extinction rate during this period and BC as slight increase whereas the 3T metric (which was missing from the cumulative megafaunal rates) shows a continuous decline from the Messinian. The 3T metric is not available for this period and region in the sharks, however, the raw and BC metrics both report declines in extinction rate.

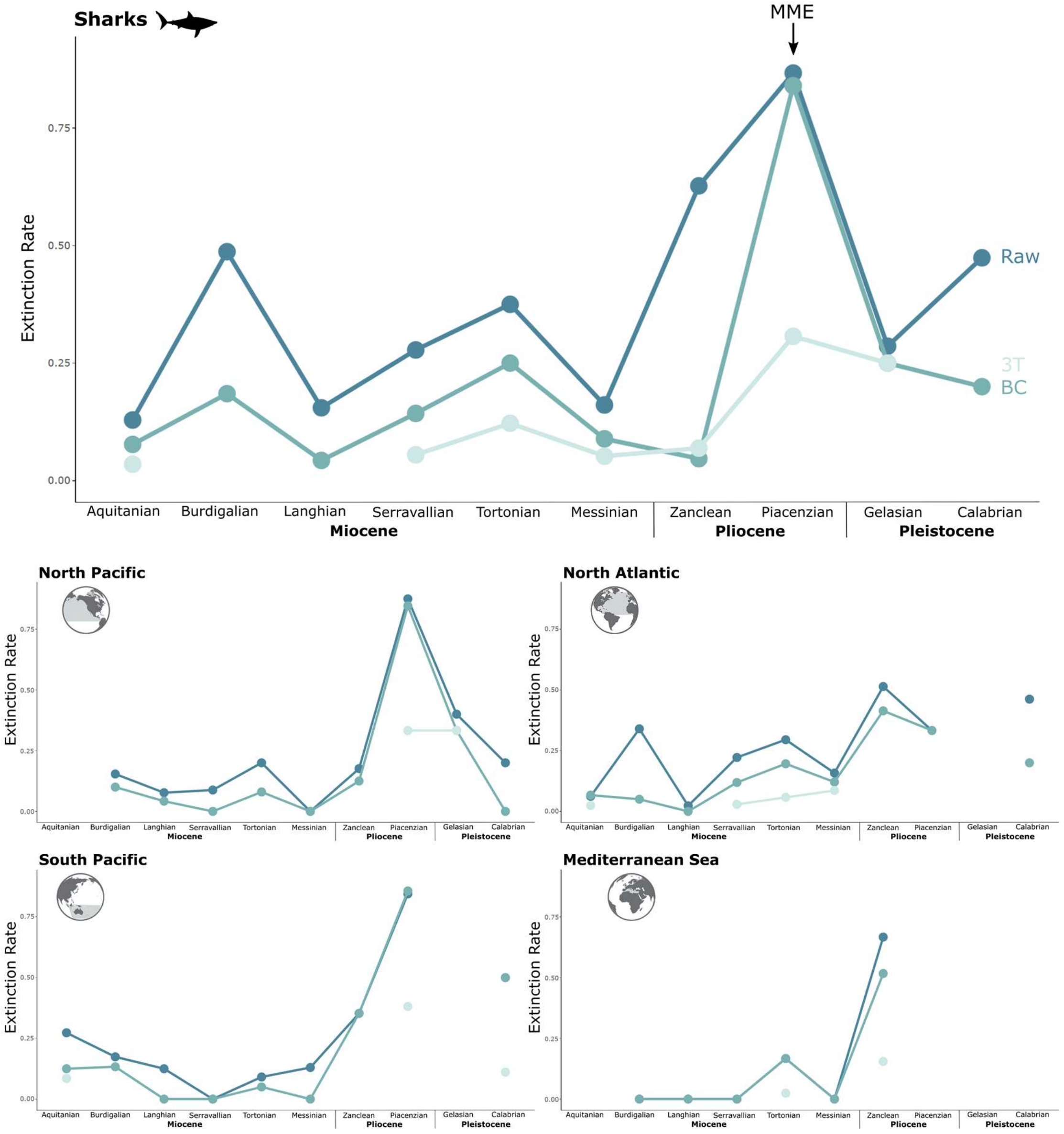

Figure 3.3 Estimated extinction rates for megafaunal shark genera for each stage from the Aquitanian to the Calabrian for global (top) and regional (bottom) occurrence data. The marine megafaunal extinction (MME) in the Piacenzian is labelled on the global extinction rates. The three extinction rate metrics raw, BC and 3T are labelled and differentiated by colour. Missing points for periods and regions are due to insufficient data availability to calculate an estimate.

3.5 Discussion

The end Pliocene marine megafaunal extinction event, though not a mass extinction, was a time of significant loss in marine megafauna (Pimiento *et al.*, 2017). This is reflected in the notable peak in extinction rates of megafaunal sharks, mammals, reptiles and birds in the Piacenzian, when this extinction event occurred. As all three extinction rate metrics calculated here exhibit a persistent global peak, this suggests the rise in extinction rates is a true signal that is robust to sampling biases. Prior extinction rate analysis using Pyrate identified higher rates across the entire Pliocene compared to other Cenozoic epochs (Pimiento *et al.*, 2017) and the analysis here supports this on a higher-resolution temporal and regional scale, further solidifying the timing of this event in the latter stage of the Pliocene. Similarly to the Pyrate analysis, when analysing all marine megafauna genera, extinction rates during the extinction interval are greater in magnitude than any other rates during the period considered here (from the Miocene to the Pleistocene). Sharks, assessed independently, likewise exhibit elevated extinction rates in the Piacenzian, however, these even more significantly exceed rates in other periods. Although this may suggest a disproportionately severe impact on this group, the small number of genera lost during the extinction implies megafaunal sharks were already low in diversity and thus extinction had a larger proportional impact. In mammals, a Piacenzian peak is also evident, but it does not exceed the proportional extinction seen in the Tortonian. This does not diminish the impact of the Pliocene extinction however, with substantially high proportional generic losses in this period, but instead reinforces the Tortonian as another critical interval for megafaunal mammal losses. As such, globally, this end Pliocene extinction presents a robust signal across taxonomic groups. However, regional patterns do not uniformly reflect this trend.

Here, regional variation in the extinction impacts of the Pliocene marine megafaunal extinction event are identified for the first time. While the North Pacific, South Pacific and Mediterranean Sea exhibit notable peaks in extinction rates during the Piacenzian, the North Atlantic shows only modest changes. This is consistent across both the complete dataset and individual taxonomic group analyses, with most metrics reporting a decline in rate as opposed to an increase. Although there are some missing values for the 3T metric for this period, it is reasonable to assume a large peak would be unlikely even if this data was present as 3T is the most conservative of the metrics. This suggests there were lower extinction impacts in the North Atlantic compared to the other ocean basins examined. These findings align with research on other environmental-driven marine extinction events, where regional disparity in extinction magnitude or effects is common.

Spatial variation during marine extinction events is often linked to environmental stressors which are heterogeneous between ocean basins. In larger-scale extinction events, this regional heterogeneity is reflected predominantly in the timing of extinction as opposed to intensity (for example Algeo *et al.*, 2012; Li *et al.*, 2022; Sahoo *et al.*, 2023), however it is not uncommon for whole regions to experience more limited impacts for the whole duration of the event (Payne *et al.*, 2023). This has been well reported in non-vertebrate marine taxa, where lower extinction rates may be exhibited in specific ocean basins (as is the case here) or across a whole hemisphere. For example, across the Cretaceous-Paleogene extinction, extinction rates of deep-sea benthic foraminifera were notably lower (at 3% compared to ~10%) in the Southern Ocean than in other regions (Alegret & Thomas, 2013), whereas calcareous nannoplankton underwent notably less extinction in the entire Southern Hemisphere (followed by a quicker recovery) than in the Northern Hemisphere (Jiang *et al.*, 2010). Conversely, extinction can be localised to one specific basin or region (Di Martino *et al.*, 2018; Mondanaro *et al.*, 2024), however, this is less relevant to the findings here. While fewer studies address the regional disparity in extinction rates of marine vertebrate taxa, it is expected similar regional variation would have occurred due to the heterogeneity of environmental stressors.

The pattern of regional variation reported during this Pliocene extinction, with lower extinction impacts in the North Atlantic, has not previously been linked to other marine taxonomic extinction events. Differences between Atlantic and Pacific Ocean basins have however been found in regards to non-uniform environmental stressors. As ocean circulation currents differ markedly between the Atlantic and Pacific and these currents strongly influence extinction stressors such as acidification, anoxia and nutrient cycling, contrasts between these basins are often pronounced (for example Ilyina & Heinze, 2019; Braaten *et al.*, 2023). Interestingly, in extant ecosystems it is the North Atlantic basin which sees greater local extinction in marine taxa, including vertebrates, compared to other basins (Nikolaou & Katsanevakis, 2023), contrary to what occurred in the Piacenzian.

The regional variation in extinction rates identified here, neither fully support nor disagree with the patterns that would be expected given the proposed neritic zone hypothesis (Pimiento *et al.*, 2017). If neritic zone area was a primary extinction driver, ocean basins with a greater proportional extent of continental shelf area would likely experience lower extinction impacts as less neritic habitat would be lost, allowing for the maintenance of productive foraging habitats relied on by many marine megafauna (Bost *et al.*, 2009; Guidino *et al.*, 2014; Chatzimentor *et al.*, 2021; Bava *et al.*, 2022; Leurs *et al.*, 2023; Li *et al.*, 2023). Currently, the North Atlantic Ocean basin does contain notably more continental shelf area proportional to basin size compared to both the North and South Pacific (IHO, 2008; Harris *et al.*, 2014). This was likely consistent in the Pliocene, given minimal shelf-area changes across the last three million years. In contrast to the Atlantic, which consists predominantly of passive continental margins, the Pacific has a high proportion of active margins (Harris *et al.*, 2014). These active margins and subduction zones (where oceanic crust moves beneath the continental crust) in both of the Pacific Ocean basins result in steep shelf slopes, with narrow shallow shelf area. Therefore, a drop in sea level would have more significant implications for the neritic zone area in these basins. This so far supports the neritic zone hypothesis as higher extinction rates were exhibited in the Pacific.

The high extinction rates exhibited during the Piacenzian in the Mediterranean Sea, however, do not support the proposed neritic zone hypothesis. Unlike the North Atlantic, the taxonomic data for this region was sufficient for all three metrics to calculate an estimated rate for this basin and in each case a notable Piacenzian peak is found. The Mediterranean Sea actually has a higher proportion of continental shelf area than the North Atlantic (IHO, 2008; Harris *et al.*, 2014) which according to the hypothesis would imply this region would instead have lower extinction rates than those presented. This suggests that either continental shelf area was not a primary driver of these megafaunal extinctions and the low extinction impacts in the North Atlantic are due to another cause, or other drivers resulted in greater extinction in the Mediterranean Sea despite having large extents of continental shelf area. The Mediterranean is unique compared to the Atlantic and Pacific in that it is relatively isolated, with limited connectivity to other ocean basins. Further, delayed recolonization following the Zanclean flood post Messinian desiccation (Garcia-Castellanos *et al.*, 2009; Bulian *et al.*, 2022; Agiadi *et al.*, 2024) may have heightened the vulnerability of marine taxa which were recovering from low richness (Agiadi *et al.*, 2024). A concurrent extinction of bivalves in the Mediterranean (Mondanaro *et al.*, 2024), despite this group not facing similar losses in other basins, may support this as a time of low resilience in this region. Alternatively, it is possible that there is a threshold of proportional neritic zone loss, below which energetic demands of megafauna cannot be met and the Mediterranean could have crossed this. Overall, while these results may provide some support for the neritic zone hypothesis, further investigation is needed to fully assess the role of this variable in driving the extinction event.

Concurrent to the marine megafaunal extinction, the Isthmus of Panama fully formed approximately three million years ago (O'Dea *et al.*, 2016), though some models suggest an even earlier formation (Bacon *et al.*, 2015). While this event likely impacted marine megafauna less than the climatic changes during this period, it is important to consider the impact this may have had on a regional scale. The Isthmus of Panama isolated the Atlantic and Pacific Ocean basins, resulting in intensification of the Gulf Stream and the redirection of ocean currents and changing circulation patterns (Haug & Tiedemann, 1998; Haug *et al.*, 2001; Lunt *et al.*, 2008; Auderset *et al.*, 2019). The increased oxygenation and cooling of the Atlantic has been proposed to be linked to some marine extinctions (O'Dea *et al.*, 2007; O'Dea *et al.*, 2016). Further, this change has been attributed to modern differences in diversity in the Caribbean and the Pacific Coral Triangle, with higher extinction rates in the Atlantic following the Isthmus formation (Di Martino *et al.*, 2018). However, these findings are contrary to what is presented here. Previous studies do not solely consider marine megafauna, and while it is possible this formation may have played some role in the extinction, the cooling of the North Atlantic does not appear to elevate extinction rates.

Additionally, the global and regional extinction rate analyses also provide insight into the extinction dynamics of marine megafauna across the entire Neogene and indicate overall resilience to other key climatic, tectonic and oceanographic events. As some of these events are known to have negative impacts on marine taxa, this is perhaps unexpected. A notable example includes the Middle Miocene Climate Transition, which marked a period of global warming from the Burdigalian, followed by rapid cooling in the Langhian (Holbourn *et al.*, 2005; Hamon *et al.*, 2013). While it could be argued that the initial warming oceans may have coincided with the slight peak in extinction rates during the Burdigalian (most notable in mammals), this event has not previously been linked to species turnover of any kind. Conversely, the subsequent icehouse conditions are linked to some declines in marine taxa (Böhme, 2003; Torfstein & Steinberg, 2020; Harzhauser *et al.*, 2024), yet no such increases in extinction rates of marine megafauna are seen in the Langhian here.

Even more significant to altering marine ecosystems were the consequences of the progressive closure of the Tethys Ocean throughout the Miocene which resulted in the isolation of the Mediterranean and changes in Indian Ocean circulation (Hou & Li, 2018; Bialik *et al.*, 2019; Podder *et al.*, 2024). This ultimately drove the subsequent evaporation and the desiccation of the Mediterranean Sea during the Messinian Salinity Crisis (Hou & Li, 2018; Krijgsman *et al.*, 2024) which led to widespread extinctions of marine taxa in the basin (Agiadi *et al.*, 2024). The absence of a peak in extinction rates in marine megafauna in the Mediterranean during the Messinian is arguably one of the most unexpected results of this analysis. The drop in extinction rate seen instead is nearly certainly due to sampling issues, with mammals in particular being so poorly sampled in this basin during this period and the surrounding time bins, preventing any of the metrics from estimating rates. Further, all fossil occurrence data in the Messinian Mediterranean basin are sourced from only three collections. Given these limitations in available localities and the broad temporal time bins used here, it is most likely the full consequences of the Messinian Salinity Crisis were not recorded in this dataset.

Megafaunal sharks and mammals were also analysed separately to discern whether group-specific extinction dynamics occurred across the Pliocene marine megafaunal extinction. Despite some minor global and regional differences in Piacenzian extinction rates, overall the patterns were broadly consistent with all megafaunal genera. However, across the entire Neogene there are clear disparities between these taxonomic groups. Mammals almost always exhibited higher rates than sharks, suggesting greater extinction vulnerability over this period. This could reflect their shorter evolutionary history (Uhen, 2007) or even physiological traits, where mammals are solely endothermic. Being endothermic, mammals have much higher energetic demands (Bennett & Ruben, 1979), higher than that required by most sharks, though there are notable exceptions (for example Watanabe *et al.*, 2019; Griffiths *et al.*, 2023). As such, mammals may have been more sensitive to shifts in ocean circulation, temperature and foraging habitat availability. This is in line with the neritic zone hypothesis, as it was suggested the reason the end Pliocene marine megafaunal extinction saw predominantly high-energy-dependent taxa go extinct was because they were more proportionally affected by neritic habitat loss (Pimiento *et al.*, 2017). The higher rates in mammals is perhaps most evident in the Tortonian. Despite being present in the complete dataset, this Tortonian extinction peak is predominantly driven by the losses seen in marine mammals. This trend has previously been noted in Cetacea (Uhen & Pyenson, 2007), but remains largely undiscussed with the cause unclear and would benefit from further study.

The lower extinction rates exhibited in sharks is perhaps most notable for the lack of significant peak in rates during an early Miocene pelagic shark extinction in the Burdigalian (Sibert & Rubin, 2021). Although the raw metric does show a peak in the Global and North Atlantic rates, this is very modest compared to the Piacenzian extinction, and other metrics and regions show low proportional rates. Therefore, despite a decrease in morphological diversity by over 70% during this event (Sibert & Rubin, 2021), this is not reflected here. Perhaps this loss of diversity does not correlate to direct extinction of whole genera, or these losses were predominantly seen in smaller sharks, not recorded in this megafaunal dataset. However, any interpretations made for both sharks and mammals individually should account for limitations in sampling. Although the methods used here do account for sampling biases (Allen *et al.*, 2023), low taxonomic counts, especially when the data is not only split by region but also by clade, may reduce confidence in the patterns presented.

The extinction rate analyses presented here advance current understanding of the Pliocene marine megafaunal extinction by revealing regional variability in extinction impacts that has been hypothesised but not quantitatively tested. These findings also help contextualise potential drivers of the event, particularly in relation to the neritic zone hypothesis. The comparatively lower extinction rates exhibited in the North Atlantic relative to the higher rates in the Pacific provide some support for the idea that basins with more extensive neritic habitats experienced buffered extinction impacts. However, the elevated extinction rates in the Mediterranean stand in contrast to this expectation, indicating that neritic habitat loss alone is insufficient to explain the spatial patterns observed. Instead, a more complex interplay of environmental and ecological pressures likely contributed to megafaunal extinction selectivity. Further work incorporating a broad range of environmental variables will be essential for resolving the primary drivers of this understudied event.

Chapter 4.

Environmental drivers of the Pliocene marine megafaunal extinction

4.1 Abstract

The Pliocene marine megafaunal extinction represents one of the most significant losses of large marine vertebrates in the past 66 million years, yet its primary drivers remain unresolved. While past and present declines in megafauna are often attributed to human impacts, the Pliocene marine megafaunal extinction occurred in absence of anthropogenic influence, offering a valuable opportunity to assess natural environmental controls on the extinction of large-bodied taxa. This study addresses two hypotheses: that megafaunal losses were driven by (1) contraction of neritic zone habitats resulting from sea-level fall and reduced continental shelf area, and/or (2) global cooling that increased metabolic demands and altered foraging dynamics. To test these hypotheses, generalised least squares regression is used to model global and regional extinction rates of marine megafauna against palaeoclimate simulations of sea surface temperature and continental shelf availability from the Miocene to the Pleistocene. Across all extinction metrics and spatial scales, the null model consistently provided the best fit, indicating that neither temperature nor continental shelf availability exerted significant control on extinction rates. Continental shelf proportion showed weak and spatially inconsistent correlations with extinction, while temperature had negligible explanatory power. These findings suggest that the Pliocene marine megafaunal extinction event was not driven by gradual Neogene environmental trends but by more complex, regionally variable processes. The anomalously high extinction rates during the Piacenzian likely reflect major oceanographic and ecological reorganisations, rather than single abiotic drivers.

4.2 Introduction

The Pliocene marine megafaunal extinction event represents a major turnover in Cenozoic oceanic ecosystems, during which numerous large-bodied marine vertebrates disappeared from the fossil record (Pimiento *et al.*, 2017). Occurring during the Piacenzian, prior to the Plio-Pleistocene boundary, over one third of marine megafaunal genera went extinct, predominantly homeothermic taxa, and this was accompanied by a notable reduction in functional richness (Pimiento *et al.*, 2017). Despite its apparent significance as one of the largest extinction events of the last 66 million years, the primary drivers of this event remain unresolved. Understanding the environmental and ecological factors behind these taxonomic losses is particularly important, as this extinction pattern, restricted primarily to marine megafauna, differs from most other past extinction events (Payne & Heim, 2020), suggesting a unique combination of underlying drivers.

Although the relationship between body size and extinction vulnerability is complex, selective extinction towards large-bodied taxa is generally rare in the fossil record (Payne *et al.*, 2016; Payne & Heim, 2020; Malanoski *et al.*, 2024). Only a few past events have exhibited a positive relationship between elevated extinction rates and increased body size (Smith *et al.*, 2018; Monarrez *et al.*, 2021). Notably, this includes the well-known losses of Pleistocene terrestrial megafauna, however, these extinctions are primarily attributed to increasing interactions with human populations compounded by changing climates (Stewart *et al.*, 2021; Bergman *et al.*, 2023; Svenning *et al.*, 2024). Similarly, the declining megafauna populations seen today are predominantly driven by anthropogenic impacts (Estes *et al.*, 2011; Pimiento *et al.*, 2020; He *et al.*, 2021; Pacoureau *et al.*, 2021). In the absence of any anthropogenic influences, the drivers of the Pliocene marine megafaunal extinction are unclear, yet could provide useful insight into which environmental stressors have high impacts on marine megafauna, a group currently facing significant extinction threats (Pimiento *et al.*, 2020).

Spatial analysis of extinction rates found that different ocean basins exhibited varying magnitudes of extinction impacts during the Pliocene marine megafaunal extinction (Chapter 3). While extinction rates were elevated during the Piacenzian extinction interval for the North Pacific, South Pacific and Mediterranean Sea, the North Atlantic exhibited relatively low rates during this period. These findings indicate that the drivers of these megafaunal losses likely also varied regionally, and the North Atlantic basin may have undergone less environmental change or been buffered from the most severe effects. Most environmental variables inherently vary across space (for example Song *et al.*, 2020; Foster *et al.*, 2024; Peng *et al.*, 2025), however, this pattern of extinction impacts, with high rates exhibited in all but the North Atlantic basin, has not previously been linked to past extinction events. Thus, these findings alone do not provide sufficient evidence to determine the primary drivers of the megafaunal losses.

The original hypothesis proposed for the primary extinction driver suggests that megafaunal losses were driven by a reduction in neritic zone habitat caused by a global drop in sea-level (Pimiento *et al.*, 2017). The neritic zone occurs on the continental shelf at depths shallower than ~200m (Dolbeth & Arenas, 2021) and loss of this productive habitat would have reduced energy availability within these marine ecosystems. The cascading impacts from these environmental changes would have had a disproportionate impact on homeothermic megafauna, taxa which have high metabolic requirements (Boyles *et al.*, 2011). Further, because ocean basins vary in the extent of their continental shelf area, regional variation in extinction severity would be expected if neritic habitat loss was a primary driver.

Here, an additional hypothesis is proposed, theorising that a primary extinction driver of marine megafauna was significant global cooling. Temperature change during the end Piacenzian represents one of the most substantial climatic stressors during this geological stage (Ravelo *et al.*, 2004; Dolan *et al.*, 2015) and may have had physiological and ecological impacts on megafaunal taxa. Colder environments increase metabolic costs for many marine megafauna, particularly homeotherms (John *et al.*, 2021; Williams, 2022), where more energy must be dedicated to thermoregulation. To compensate, these taxa must increase prey consumption to meet their energetic requirements (for example Rojano-Doñate *et al.*, 2024). Additionally, ectothermic taxa have more restricted tolerances to temperature change (Seibel & Birk, 2022; Fusi *et al.*, 2024), likely resulting in notable range shifts. Consequently, large predators that primarily rely on smaller ectothermic prey may have experienced reduced foraging opportunities within their habitat ranges. Similarly to neritic zone habitat, the impacts of temperature would have varied spatially depending upon climate gradients and species range shifts.

Both a loss of neritic zone and a decrease in temperature could have introduced significant stress to megafaunal taxa, particularly those with high energetic requirements, and would have exhibited spatial variation. However, the influence of either environmental factor during the Pliocene marine megafaunal extinction has not been quantifiably tested. The extinction mechanisms underlying this event were likely complex and multifactorial, and it is possible that both variables contributed to the observed extinction patterns. To fully understand the selective nature of megafaunal losses in the Piacenzian, changes in environmental conditions must be quantifiably examined at both global and regional scales.

This study investigates the environmental factors driving regional and global extinction rates of marine megafauna from the Miocene to the Pleistocene. Multiple linear regression analyses are used to test the relationship between modelled sea temperature, continental shelf extent and megafaunal extinction rates. These analyses test the hypotheses that the peak in megafaunal extinction during the Piacenzian was driven by (1) loss of continental shelf neritic habitat leading to subsequent energy constraints for high-metabolism taxa, and, (2) declines in sea surface temperature, which may have increased metabolic demands and altered foraging ranges.

4.3 Methods

4.3.1 Extinction rate data

The marine megafaunal extinction rates used in this analysis were those presented in Chapter 3. These rates were calculated from marine megafauna occurrence data sourced from the Paleobiology Database (PBDB) for each stage from the Aquitanian (23.03 Ma) to the Calabrian (0.774 Ma). Marine megafauna were defined as taxa equal to or >1m in length (as per Pimiento *et al.*, 2024), and were collected at genus level for Chondrichthyes, Mammalia and Reptilia from marine sediments only. Occurrences were subsequently subset into the ocean basins of the North Atlantic, South Atlantic, North Pacific, South Pacific and Mediterranean Sea using palaeo-latitudes and longitudes.

Extinction rates were calculated globally and for each of the ocean basins for each time bin using the framework presented in Allen *et al.*, (2023), however, owing to data limitations the South Atlantic basin was excluded. Extinction rate estimates using all three metrics, raw, boundary-crossover (BC) and 3-timer (3T), were included in the linear regression analyses. In addition, the number of unique collections from the PBDB for all megafaunal occurrences included in the extinction rate analysis was quantified at both global and regional scales and included in the analyses here as a simple measure of sampling intensity (Reijenga & Close, 2025).

4.3.2 Environmental data

Palaeoclimate model simulations were used to estimate environmental conditions for each geological stage from the Aquitanian to the Calabrian, both globally and for the North Atlantic, North Pacific, South Pacific and Mediterranean. Boundary conditions were defined using the Getech palaeogeographic digital elevation models (DEMs) for each geological stage. These reconstructions provide higher temporal resolution than most other palaeogeographic models (Chiarenza *et al.*, 2019). Climate simulations were generated using the HadCM3L general circulation model (GCM) version 4.5 at a spatial resolution of 3.75° longitude x 2.75° latitude. This coupled atmosphere-ocean model incorporates 20 oceanic vertical depth levels (see Valdes *et al.*, 2017, for model details). Both the Getech DEMs and HadCM3L have been successfully used to reconstruct environmental conditions across a variety of temporal and spatial scales (for example Chiarenza *et al.*, 2019; Farnsworth *et al.*, 2019; Witkowski *et al.*, 2025; Goodman *et al.*, 2025).

Climatic variables were extracted from the model outputs for mean sea temperature (MST) at depths of 5m, 95.75m, and 203.7m below sea level. Values represent mean annual temperatures across each geological stage and further averaged globally and within each ocean basin.

Continental shelf area was derived from the Getech DEMs (where oceanic depth refers to metres below sea level) and used to calculate shelf extent for each 3.75 x 2.5 grid cell. To account for depth averaging within spatial cells, two thresholds of continental shelf were defined: a strict measure (depth ≤ 200m) and a generous measure (depth ≤ 400m). The generous threshold was selected under the assumption that grid cells with depths up to 400m would contain continental shelf habitat over at least half of their total area. Grid cells were converted into absolute areas to estimate strict and generous continental shelf extent (km^2), and shelf area was also expressed as a proportion of the total basin area. While absolute shelf area captures total habitat availability, proportion measures reflect relative changes in habitat extent across time.

4.3.3 Linear regression analysis

Generalised least squares (GLS) models were used to test for relationships between the environmental variables of temperature and continental shelf extent and marine megafaunal extinction rates at global and regional spatial scales. Log^{10}-transformed unique collection counts were included in all the models to account for variation in sampling intensity.

Collinearity among predictor variables was assessed using Pearson correlation coefficients. High levels (>0.8 Pearson's *r*) of collinearity were observed between each of the temperature variables and each of the continental shelf variables for most ocean basins. Exceptions were identified between MST at 5m and MST at 203.7m in the North Atlantic ($r=0.78$), and between the proportions of generous shelf and strict continental shelf area in the South Pacific ($r=0.046$). Models containing combinations of highly collinear variables were excluded from further analyses.

Remaining models incorporated all combinations of MST at 5m, 95.75m, and 203.7m, strict and generous shelf proportions and collection counts for each ocean basin and the global dataset. Alternative models substituting shelf proportions with absolute shelf area were also tested; however, absolute area measures exhibited limited explanatory power for extinction trends. Model fit was evaluated for each of the three extinction rate metrics (raw, BC and 3T) using the corrected Akaike Information Criterion for small sample sizes (AICc; Hurvich & Tsai, 1989).

To account for potential temporal autocorrelation, analyses were repeated using a first-order autoregressive model (AR-1), assessing whether extinction rates within a given stage were dependent on rates in the preceding stage. All analyses were conducted in R using the packages nlme (Pinheiro *et al.*, 2025) and MuMIn (Bartoń, 2025).

4.4 Results

4.4.1 Spatial and temporal environmental trends

Previous analyses indicate that marine megafaunal extinction rates varied markedly through time at both global and regional scales (for full description and interpretation see Chapter 3). Globally, extinction rates show broadly consistent temporal trends across the three metrics used, despite differences in magnitude (Figure 4.1). All metrics identify a major peak in the Piacenzian, corresponding to the marine megafaunal extinction, followed by a sharp decline in the Gelasian. An earlier peak is also evident in the Tortonian, with the raw and BC metrics additionally recording a rise in the Burdigalian. At regional scales, the North Pacific basin most closely mirrors the global pattern, including an amplified Piacenzian peak (Figure 4.2). The South Pacific and Mediterranean show similar Piacenzian peaks but diverge from global trends in earlier intervals, while poor early Pleistocene sampling prevented the estimation of post-extinction rates (Figures 4.3-4.4). The North Atlantic generally aligns with global patterns throughout most of the Miocene but uniquely lacks the pronounced Piacenzian peak observed elsewhere in the Pliocene (Figure 4.5).

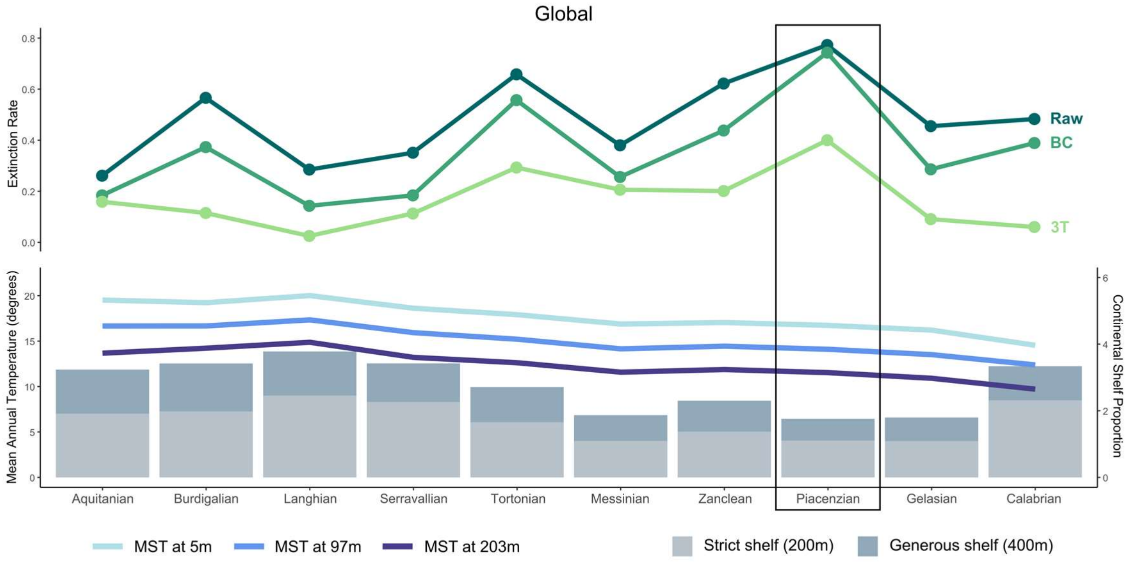

Figure 4.1 Global extinction rates of marine megafauna, mean sea temperature and continental shelf proportion from the Aquitanian to the Calabrian. The Piacenzian extinction time bin is outlined.

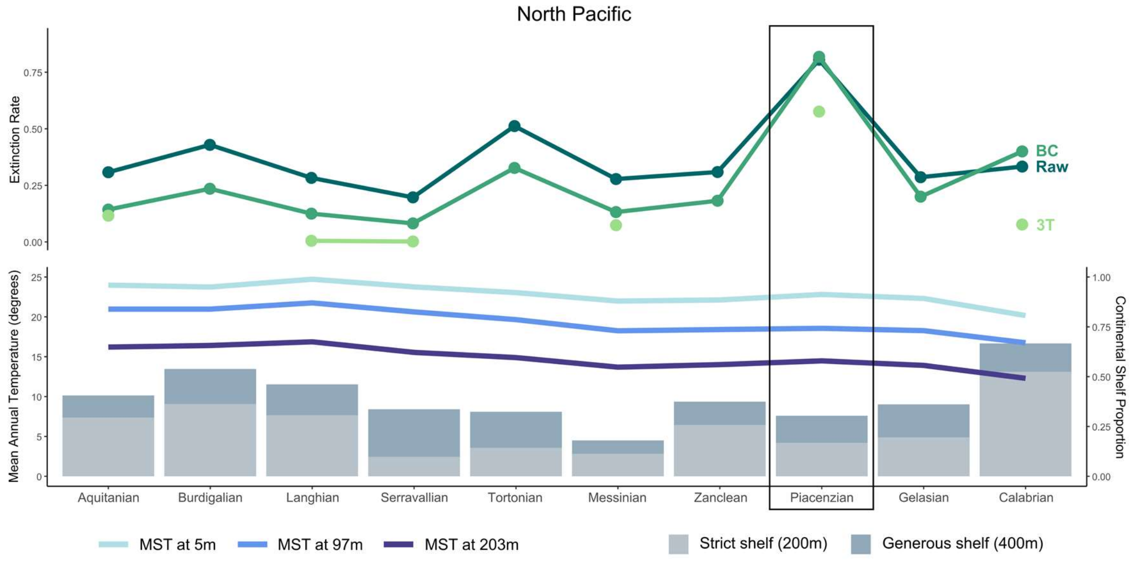

Figure 4.2 North Pacific extinction rates of marine megafauna, mean sea temperature and continental shelf proportion from the Aquitanian to the Calabrian. The Piacenzian extinction time bin is outlined.

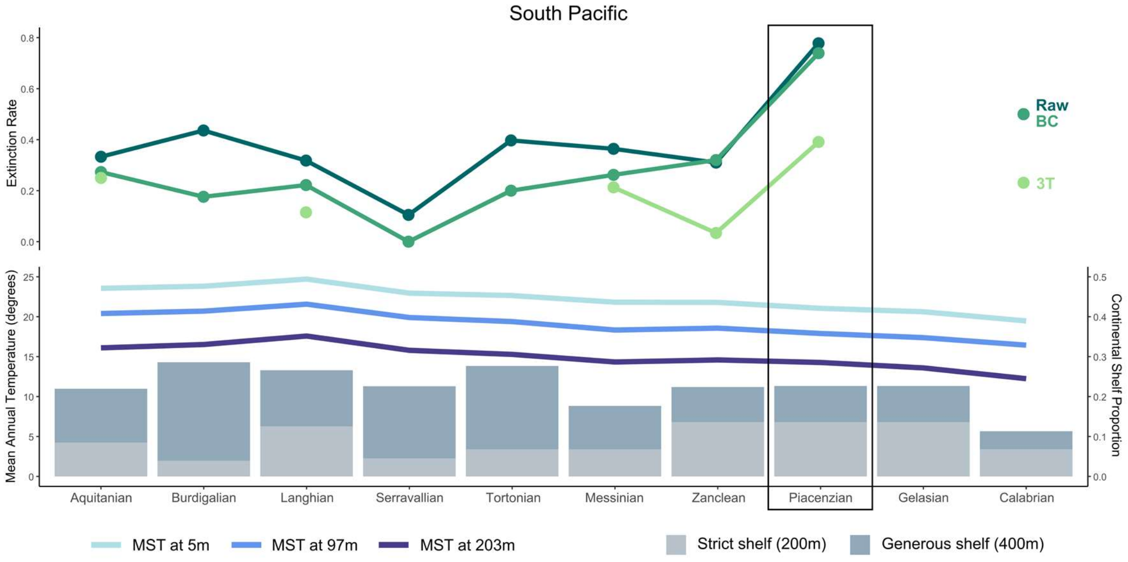

Figure 4.3 South Pacific extinction rates of marine megafauna, mean sea temperature and continental shelf proportion from the Aquitanian to the Calabrian. The Piacenzian extinction time bin is outlined.

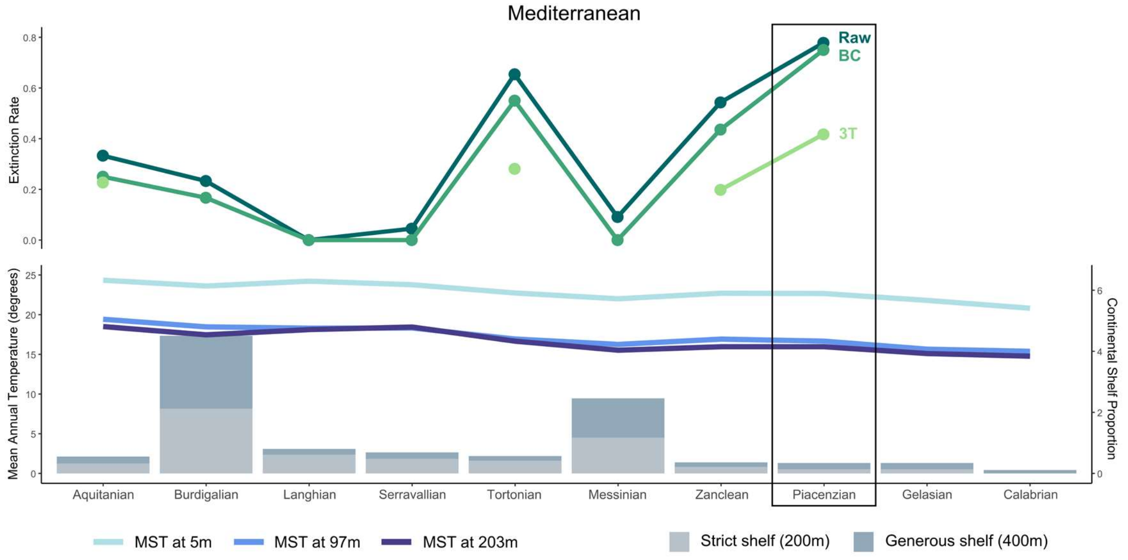

Figure 4.4 Mediterranean extinction rates of marine megafauna, mean sea temperature and continental shelf proportion from the Aquitanian to the Calabrian. The Piacenzian extinction time bin is outlined.

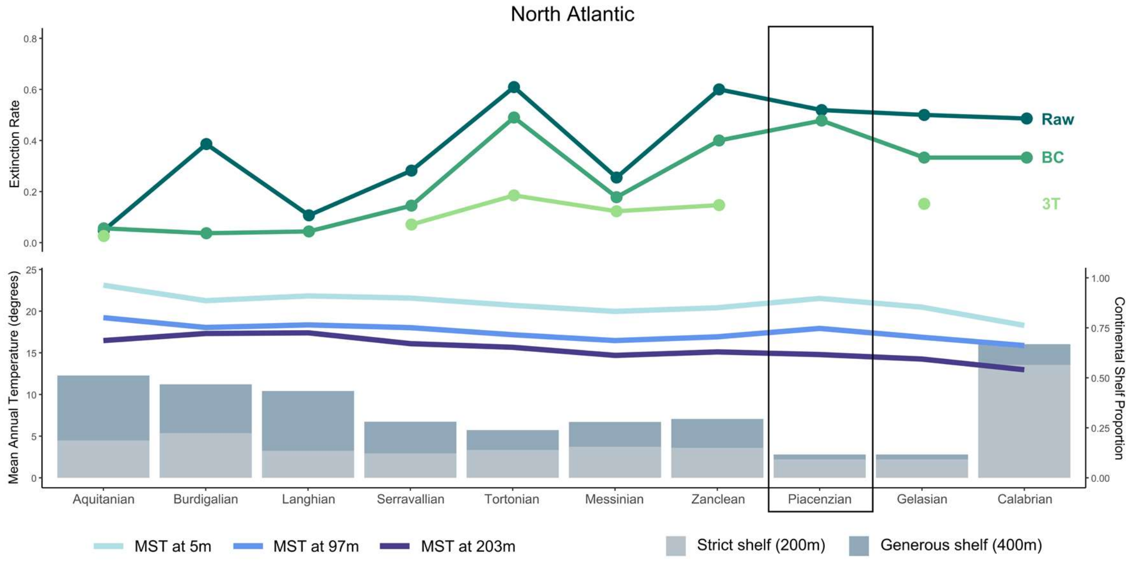

Figure 4.5 North Atlantic extinction rates of marine megafauna, mean sea temperature and continental shelf proportion from the Aquitanian to the Calabrian. The Piacenzian extinction time bin is outlined.

4.4.2 Drivers of marine megafaunal extinction

The five best-fitting models for global drivers of marine megafaunal extinction rates across the Neogene were identical across all three extinction rate metrics (Table 4.1). Ranked by AICc, the model order was consistent for the raw and BC metrics, with the 3T metric showing only minor variation in ranking. Incorporating an AR-1 structure did not improve model fit for any GLS models and among AR-1 analyses only the null model ranked within the five best-fitting models for the global dataset. Further, no multivariate models were included among any of the best-fitting models.

For all three extinction metrics, the null model was the best-fitting model, with the lowest AICc, indicating that none of the explanatory variables substantially improved model fit. The difference in AICc between the null model and the second best models, in each case, was considerable (Table 4.1), confirming the superior fit of the null model. Among the top five models for each metric, both strict (≤200m) and generous (≤400m) continental shelf proportions were consistently included, whereas no temperature variables appeared. In these low-support models, shelf proportion was negatively associated with extinction rates, indicating lower shelf availability corresponded to greater extinction. Unique collection counts consistently ranked as the fifth best-fitting model and were positively associated with extinction rates, although this association was not significant at $p<0.05$ (Table 4.2), suggesting the influence of sampling on observed extinction rates is small.

Table 4.1 Top five best-fitting models, ranked by AICc, globally for all three extinction rate metrics. The relationship between the extinction rates and each environmental variable is stated in bold, being either a positive (+ve) or a negative (-ve) correlation.

Metric	Regression model	R^2	Log like.	AICc	Weight
Raw	Null model	<0.00001	2.05820	1.597894	0.76429
	Null model + AR1	0.00677	2.06154	5.876914	0.72144
	Strict shelf prop. **-ve**	0.23304	1.81760	6.364793	0.07049
	Generous shelf prop. **-ve**	0.24414	1.50591	6.988185	0.05161
	Collections **+ve**	0.12644	1.48239	7.035222	0.05042
BC	Null model	<0.00001	1.12563	3.46303	0.75143
	Null model + AR1	-0.00097	1.12573	7.74855	0.74591
	Strict shelf prop. **-ve**	0.22742	0.95944	8.08112	0.07466
	Generous shelf prop. **-ve**	0.25411	0.73006	8.53988	0.05936
	Collections **+ve**	0.07511	0.42501	9.14999	0.04375
3T	Null model	<0.00001	5.66300	-5.61172	0.72661
	Strict shelf prop. **-ve**	0.41399	6.09828	-2.19656	0.13174
	Null model + AR1	-0.00219	5.89441	-1.78881	0.87199
	Generous shelf prop. **-ve**	0.39381	5.59283	-1.18566	0.07947
	Collections **+ve**	0.09669	4.55267	0.89466	0.02808

Table 4.2 Summary of explanatory variables for the best-fitting models in Table 4.1. Null models are excluded due to the absence of any explanatory variables.

Metric	Regression Model	Intercept			Variable		
		Estimate	SE	p-value	Estimate	SE	p-value
Raw	Strict shelf prop.	0.7467	0.1761	0.0028	-0.1527	0.0979	0.1576
	Generous shelf prop.	0.7817	0.1920	0.0036	-0.1080	0.0672	0.1466
	Collections	0.1986	0.2699	0.4828	0.1354	0.1258	0.3133
BC	Strict shelf prop.	0.6438	0.1960	0.0111	-0.1673	0.1090	0.1634
	Generous shelf prop.	0.6928	0.2116	0.0113	-0.1222	0.0740	0.1374
	Collections	0.1119	0.3081	0.7259	0.1157	0.1436	0.4435
3T	Strict shelf prop.	0.4014	0.1031	0.0046	-0.1364	0.0574	0.0447
	Generous shelf prop.	0.4201	0.1152	0.0065	-0.0919	0.0403	0.0521
	Collections	-0.0005	0.1839	0.9978	0.0793	0.0857	0.3818

At the global level, models including explanatory variables generally found that these predictors did not have a significant effect on extinction rates (Table 4.2), with the exception of the 3T metric model incorporating strict shelf proportion. Although strict shelf proportion was a statistically significant predictor ($p<0.05$), this model had an AICc difference relative to the null model which exceeded 3, suggesting it does not provide a substantially improved fit. It is possible the non-significance exhibited by most variables could be an artefact of small sample sizes, however, the results collectively indicate that while shelf availability shows some relationship with global extinction rates, overall, the explanatory environmental variables contribute only marginally to the observed patterns of global marine megafaunal extinction through the Neogene.

For the spatial analysis of individual ocean basins, the 3T metric contained too few extinction rate estimates across the Neogene to support the GLS analysis. As the BC metric is generally considered more reliable than raw rates (Allen *et al.*, 2023), only the BC results are presented here (Table 4.3), with raw rate analyses provided in the Supplementary Material.

The null model is the best-fitting model for the North Atlantic, North Pacific and Mediterranean Sea, with AICc values substantially lower than those of the second-ranked models, consistent with the global results (Table 4.3). In the South Pacific, the best-fitting model was strict shelf proportional area, with a notable AICc difference relative to the null model (second best-fitting). Similar to global analyses, inclusion of an AR-1 structure did not improve model fit in any basins. However, for the South Pacific, strict shelf proportion with AR-1 ranked among the top five models, alongside the null model. Again, no multivariate models ranked within the top five in any basin.

Continental shelf proportion appeared in the top five models for each basin and generally ranked higher than temperature variables where both were present (in the North Atlantic and Mediterranean). The relationship between shelf proportion and extinction rates varied by basin: negative correlations in the North Atlantic and Mediterranean, a positive correlation in the North Pacific and contrasting effects in the South Pacific, where strict shelf proportion and generous shelf proportion showed positive and negative correlations, respectively. Mean annual sea temperature, when included in top models, consistently displayed a negative relationship with extinction rates, while unique collection counts were positively associated.

Across all ocean basins, only one predictor, mean annual sea temperature at 203m in the North Atlantic, was statistically significant (Table 4.4). Nevertheless, this model was not strongly supported by model selection criteria, with an AICc difference exceeding 4 relative to the best-fitting null model. Overall, these results indicate that environmental variables have limited explanatory power for regional extinction patterns, with continental shelf availability showing the strongest, though variable, associations across basins.

Table 4.3 Top five best-fitting models, ranked by AICc, for each ocean basin for the BC metric. Ocean basins abbreviated as NA (North Atlantic), NP (North Pacific), SP (South Pacific) and MS (Mediterranean Sea). The relationship between the extinction rates and each environmental variable is stated in bold, being either a positive (+ve) or a negative (-ve) correlation.

Basin	Regression model	R^2	Log like	AICc	Weight
NA	Null model	<0.00001	1.57504	2.56421	0.55101
	Null model + AR1	0.13886	2.98181	4.03638	0.84413
	Generous shelf prop. **-ve**	0.25105	2.59042	4.81916	0.17844
	Strict shelf prop. **-ve**	0.00021	1.67684	6.64632	0.07157
	MAT at 203.7m **-ve**	0.42773	1.60191	6.79618	0.06640
NP	Null model	<0.00001	-0.18956	6.09340	0.67277
	Strict shelf prop. **+ve**	0.00445	0.17883	9.64234	0.11408
	Generous shelf prop. **+ve**	0.00147	0.14338	9.71323	0.11011
	Null model + AR1	0.01467	-0.17497	10.3499	0.82711
	Collections **+ve**	0.02006	-0.93146	11.8629	0.03759
SP	Strict shelf prop. **+ve**	0.33400	3.04749	4.70501	0.47612
	Null model	<0.00001	-0.00944	6.01888	0.24684
	Generous shelf prop. **-ve**	0.15758	1.87524	7.04952	0.14744
	Null model + AR1	0.15508	1.6101	7.57981	0.73119
	Strict shelf prop. + AR1 **+ve**	0.36506	3.82397	10.3521	0.18283
MS	Null model	<0.00001	-2.16991	10.7398	0.81772
	Null model + AR1	-0.03223	-2.10644	16.2129	0.967
	Collections **+ve**	0.18848	-2.19013	16.3808	0.04873
	Strict shelf prop. **-ve**	0.21605	-2.30189	16.6038	0.04358
	MAT at 5m **-ve**	0.14606	-2.80317	17.6064	0.02640

Table 4.4 Summary of explanatory variables for the best-fitting models in Table 4.3. Null models are excluded due to the absence of any explanatory variables. Ocean basins abbreviated as NA (North Atlantic), NP (North Pacific), SP (South Pacific) and MS (Mediterranean Sea).

Basin	Regression Model	Intercept			Variable		
		Estimate	SE	p-value	Estimate	SE	p-value
NA	Generous shelf prop.	0.4218	0.1174	0.0070	-0.5060	0.3090	0.1401
	Strict shelf prop.	0.2529	0.1037	0.0407	-0.0186	0.4547	0.9684
	MAT at 203.7m	1.5460	0.5322	0.0197	-0.0838	0.0343	0.0402
NP	Strict shelf prop.	0.2373	0.1609	0.1785	0.1102	0.5284	0.8547
	Generous shelf prop.	0.2399	0.2366	0.3403	0.0619	0.5697	0.9161
	Collections	0.1499	0.2920	0.6216	0.0723	0.1787	0.6963
SP	Strict shelf prop.	0.0217	0.1603	0.8963	3.2354	1.7268	0.1031
	Generous shelf prop.	0.6496	0.3140	0.0774	-1.5663	1.3688	0.2901
	Strict shelf prop. + AR1	0.1874	0.1803	0.3332	1.8999	1.294	0.1847
MS	Collections	-0.0566	0.2928	0.8531	0.2312	0.1958	0.2825
	Strict shelf prop.	0.4057	0.1433	0.0300	-0.1995	0.1552	0.2459
	MAT at 5m	3.2557	2.9498	0.3120	-0.1284	0.1268	0.3501

4.4.3 Piacenzian residual variation

To assess how well the best-fitting models predict the extinction rates of the marine megafaunal extinction in the Piacenzian, residuals were calculated for each stage for the top three BC metric models globally and within each ocean basin (Figure 4.6). For the global dataset and the North Pacific, South Pacific and Mediterranean basins, the Piacenzian exhibits the largest residuals, indicating that extinction rates during this stage were least well-explained by the regression models. This pattern is consistent across all three top models, with the Mediterranean showing the largest residuals. In contrast, the North Atlantic is the only basin where the Piacenzian does not display the largest residuals, instead, the Tortonian shows the largest residuals for the first and second models, and the Calabrian for the third.

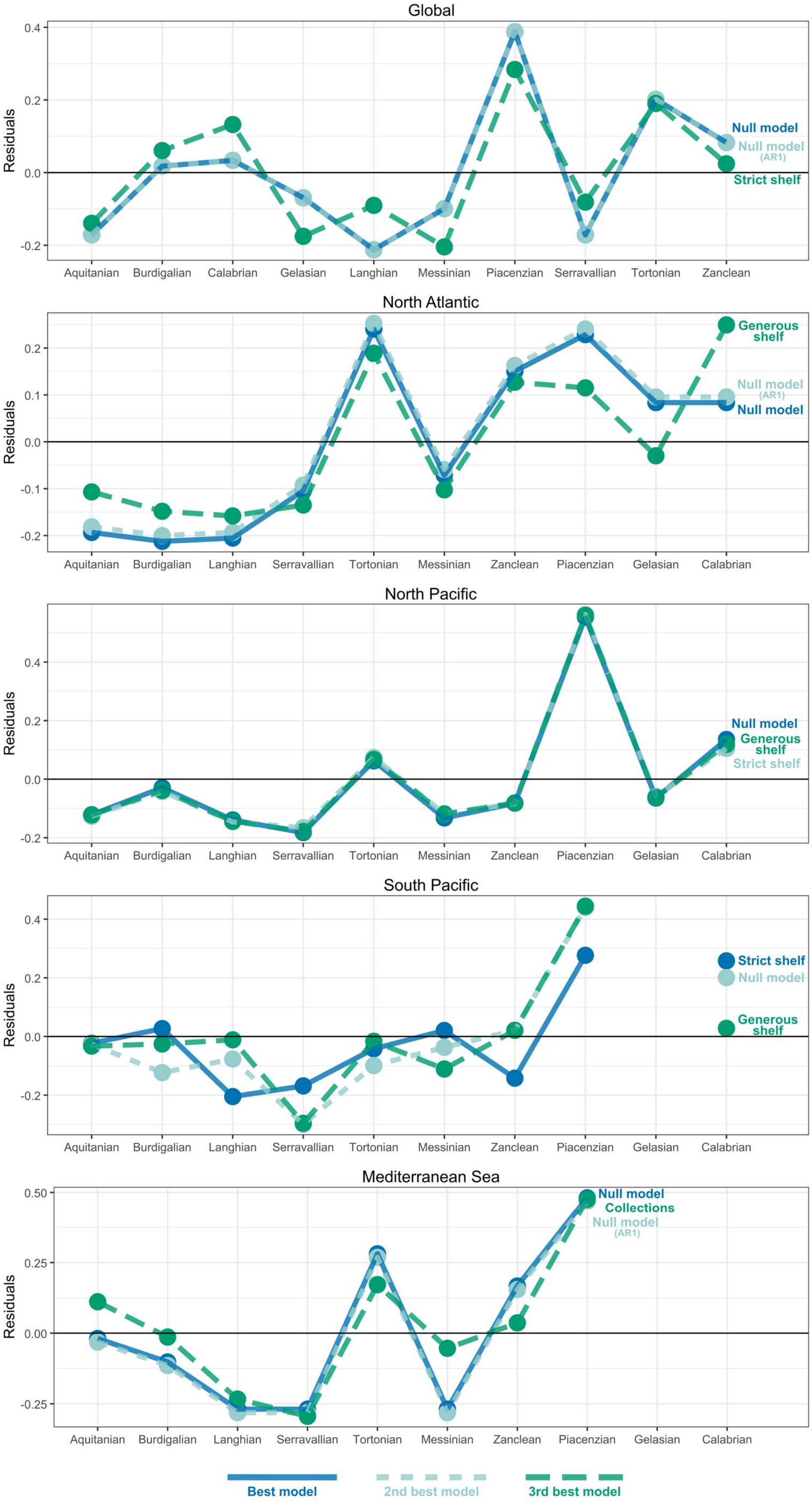

Figure 4.6 Residuals of the top three best-fitting BC metric models, globally and for each basin.

4.5 Discussion

The environmental variables of continental shelf proportion and sea temperature exerted little control on marine megafaunal extinction rates throughout the Neogene. Generalised least squares (GLS) analyses showed that the null model provided the best fit for all extinction rate data for all metrics at the global scale and for nearly all ocean basins, indicating that extinction patterns were better explained by random variation than by the environmental variables tested. These results contrast with both proposed hypotheses, which predicted that neritic habitat loss or temperature decline would drive increased extinction. However, sampling effects are unlikely to explain these findings, as unique collection counts never ranked among the top explanatory models, suggesting that sampling bias had minimal influence on the observed patterns.

Although the null model consistently outperformed other models, continental shelf proportion frequently ranked within the top five and was the best-fitting model for the South Pacific. This suggests that shelf availability may have exerted some, albeit limited, influence on marine megafaunal extinction rates, certainly more than sea temperature. The relationship between shelf proportion and extinction rate, however, was not uniform across basins. In several regions, particularly the North Atlantic, a negative correlation was observed, providing some support for the neritic zone hypothesis (Pimiento *et al.*, 2017), which predicts that contraction of shallow continental shelf habitat reduces the spatial extent of productive coastal ecosystems that sustain large marine consumers. These findings align with previous studies where a correlation between shelf area loss and taxonomic extinction has been identified in other marine extinctions (for example Newell, 1967; Hallam & Wignall, 1999; Harnik *et al.*, 2012; Finnegan *et al.*, 2016; Tian *et al.*, 2021) reinforcing the importance of these productive zones for marine ecosystem stability.

In contrast, some regions, notably the South Pacific, exhibited a positive correlation between continental shelf proportion and extinction rates, implying that expansion of shelf area, and thus of neritic habitat, was associated with increased extinction. This could reflect ecological disruption caused by rapid sea level rise, which may have destabilised key coastal habitats. Such consequences have been documented in extant ecosystems, notably estuaries and seagrass meadows (Rullens *et al.*, 2022; Capistrant-Fossa & Dunton, 2024; Chen & Mai, 2024), which serve as important breeding and nursery grounds for marine megafauna (Sievers *et al.*, 2019). This turnover may have temporarily increased extinction risk despite an overall expansion in neritic habitat area and impacts would have likely been locally restricted, having greater extinction effects in some regions than others. While sea level rise has been associated with heightened extinction rate in the fossil record (for example Hallam & Wignall, 1999; Flannery-Sutherland *et al.*, 2024), and the relationship between sea level rise and shallow marine habitats is known to be complicated (Holland, 2012), there are no clear examples of marine extinctions directly linked to an increase in flooded continental shelf area. Thus, these contrasting relationships may represent regionally specific ecological responses to environmental instability rather than direct habitat effects.

Interpretations of basin-specific relationships are further complicated by discrepancies between the strict (≤200m) and generous (≤400m) shelf measures, which sometimes produced conflicting correlations. These inconsistencies may stem from model resolution limitations. Even with the high-resolution palaeogeographic reconstructions employed here, depth averaging across grid cells likely underestimates true shelf extent, particularly near continental margins. While defining both strict and generous thresholds of continental shelf aimed to mitigate this, finer-scale spatial datasets would be necessary to more accurately capture neritic habitat variability and its influence on extinction risk. Further, it should be noted that neither positive nor negative correlations with the shelf variables were found to be statistically predictors for most of the top models. While these non-significant results may be partially attributed to small sample sizes, interpreting these basin-specific relationships should be approached with caution.

In contrast to continental shelf proportion, sea temperature had minimal explanatory power in the regression models. All temperature depth variables were consistently outperformed by both the null and shelf proportion models. Where temperature did appear within the top models, it showed a negative relationship with extinction rate, consistent with the expectation that cooling could increase extinction risk through elevated metabolic demands and contraction of prey habitats (John *et al.*, 2021; Williams, 2022). However, the limited influence of temperature may reflect the physiological resilience of marine homeotherms to thermal fluctuations. Although their metabolism demands are high (Legendre & Davesne, 2020), homeothermic megafuna can maintain activity independent of ambient temperature, conferring an advantage over ectothermic taxa during cooling events (Rolland *et al.*, 2018; Grady *et al.*, 2019; Fusi *et al.*, 2024). Homeothermic megafauna represent a substantial proportion of this dataset and their thermoregulatory capacity may have buffered much of marine megafaunal community from direct temperature-driven extinction pressures.

Nevertheless, the role of temperature should also be interpreted cautiously due to the potential effects of time-averaging. Using mean sea temperature values averaged across entire geological stages likely obscures shorter-term climatic fluctuations, such as the mid-Piacenzian warming preceding the major global cooling (Zhang, K. *et al.*, 2024). This smoothing effect also likely explains why the autoregressive AR-1 model, designed to account for temporal autocorrelation, did not improve model performance. Although finer-scale palaeoclimate data is available, the temporal resolution of megafaunal fossil occurrences remains too coarse for sub-stage or finer analyses. As such, the influence of rapid climatic perturbations may be underestimated. Even so, temperature appears to have had a weaker influence on extinction risk than continental shelf dynamics overall, and similarly few models found this variable to be significant predictor.

While neither environmental variable adequately explains extinction trends across the Neogene, residual analyses reveal that the Piacenzian consistently exhibited the largest residuals, both globally and across most ocean basins, indicating that the high extinction rates during this interval were least well explained by the tested models. This pattern underscores that the marine megafaunal extinction event was a distinct and exceptional phenomenon, likely driven by processes that differed from those driving Neogene background extinction. The North Atlantic represents a notable exception, as its lower extinction rates during the Piacenzian correspond with minimal residuals, suggesting this basin was somewhat buffered from the drivers of the global extinction event with extinction risk patterns largely conforming to those of Neogene background extinction.

Taken together, these analyses indicate that continental shelf availability and sea temperature alone cannot account for the magnitude or selectivity of marine megafaunal extinctions throughout the Neogene and, moreover, the marine megafaunal extinction event in the Piacenzian was exceptional in that extinction rates were higher than would be expected if driven by Neogene background patterns alone. Although data limitations caution against dismissing the influence of the extent of neritic habitat and temperature entirely, the elevated extinction rates of the Piacenzian likely reflect the combined effects of broader tectonic, climatic, and ecological shifts rather than any single abiotic factor. Potential mechanisms include changes in ocean circulation and nutrient fluxes following the formation of the Isthmus of Panama (Schneider & Schmittner, 2006; O'Dea *et al.*, 2016), which could have reduced primary productivity in upwelling systems and reorganised marine food webs; reduced energy transfer to high trophic levels could have disproportionately affected large consumers. This would support findings from reconstructions of marine food webs before and after the marine megafaunal extinction, where a decrease in vertical food web complexity was observed (Chapter 2).

Overall, this study examined whether Neogene marine megafaunal extinctions were driven by habitat loss linked to continental shelf contraction or by long-term ocean cooling and found little evidence that either factor exerted a dominant influence on extinction dynamics. Instead, patterns of extinction appear to have been shaped by more complex and regionally variable processes. Continental shelf availability may have played a minor role, with some evidence suggesting that the loss of productive neritic habitats increased extinction risk in certain regions. However, this relationship was not consistent, implying that the effects of sea-level and habitat change were highly localised. Temperature, meanwhile, had minimal explanatory power, indicating that most marine megafauna were relatively resilient to long-term cooling trends, possibly due to physiological adaptations that buffered them from thermal stress. However, the marked increase in extinction rates during the Piacenzian stands out as a distinctive global event not explained by gradual Neogene environmental trends. This suggests that broader ecological and oceanographic reorganisations may have driven the Pliocene marine megafaunal extinction event, and the large-scale marine vertebrate extinctions likely resulted from the interplay of multiple abiotic and biotic factors rather than any single environmental pressure. Understanding these complex mechanisms provides valuable context for assessing the vulnerability of modern marine megafauna facing similarly rapid climatic and ecological shifts.

Chapter 5.

Discussion

5.1 New Insights in the Pliocene Marine Megafaunal Extinction

This thesis examines the largely understudied Pliocene marine megafaunal extinction event, focussing on the ecological consequences for community structure and function, and the temporal and spatial environmental drivers underlying the selective loss of large-bodied taxa. The findings presented in Chapter 2 show that changes in North Atlantic food web structure and function across the extinction interval were minimal, despite substantial megafaunal losses of approximately 25% of genera in this basin. The stability of trophic network metrics across this event are striking, given that marine megafauna typically occupy key ecological roles (Tavares *et al.*, 2019; Moleón *et al.*, 2020; Pimiento *et al.*, 2020). Such losses might intuitively be expected to trigger cascading effects through marine ecosystems, potentially impacting food web topology (Estes *et al.*, 2011; Hammerschlag *et al.*, 2019; Wilting *et al.*, 2025).

The apparent robustness of these ecosystems may reflect high functional redundancy in feeding niches. The feeding-trait combinations exhibited by the taxa that went extinct were mostly maintained among surviving taxa, ensuring that these trophic roles persisted into the Pleistocene. Complete losses of feeding trait combinations were rare and included only a few cases, notably the very large, trophic level 6 apex predator role of *Otodus megalodon*. At first glance, this seems in contrast to the findings of Pimiento *et al.* (2017), who reported substantial losses of unique functional entities and a 16% decline in functional richness. However, functional richness estimates of Pimiento et al. (2017) were derived from a different trait framework that was not designed to predict feeding interactions. Thus, although functional diversity may indeed have declined, food-web composition, specifically its structure, function, and trophic organisation, appears to have remained largely intact, with most functional feeding niches still occupied (albeit by fewer genera). This distinction highlights that vulnerability inferred from functional diversity metrics does not necessarily equate to diminished ecological functioning at the metacommunity level.

The minor structural shifts observed across the event, such as increased generality and increased vulnerability, are consistent with patterns expected following mass or regional extinctions (for example Dunhill *et al.*, 2024). These expectations suggest specialist taxa are more likely to go extinct during times of perturbation, increasing the predation pressure within ecosystems, and have been documented in both extant and extinct communities (Clavel *et al.*, 2011). Therefore, these results align with established ecological theory and with current understanding of how past communities responded to taxonomic losses.

The food web reconstructions across the Pliocene marine megafaunal extinction event (Chapter 2) also provide additional insight into the extinction of *Otodus megalodon*. Despite the loss of this apex predator, the trophic positions of other top predators remained largely stable with no evidence of trophic release or the restructuring typically associated with competitive displacement which has been suggested by some studies (McCormack *et al.*, 2022; Shimada *et al.*, 2025). Although direct interspecific competition, particularly with *Carcharodon carcharias*, cannot be fully excluded, the results from Chapter 2 indicate relatively limited niche overlap, with *O. megalodon* consistently occupying higher trophic levels. This trophic disparity between *O. megalodon* and *C. carcharias* is also supported by isotopic analyses (Martin *et al.*, 2015; Kast *et al.*, 2022). Collectively, these findings suggest that *O. megalodon* most likely succumbed to the same environmental pressures driving broader megafaunal declines, or to prey depletion associated with these losses, rather than to the pressures of direct competition with other sharks. While the precise extinction mechanism remains unresolved, this study contributes a community-level perspective to ongoing research on the demise of one of the largest apex predators to ever exist.

These insights into Pliocene and Pleistocene food web structure also contribute to a broader understanding of how marine ecosystems respond to the loss of large-bodied taxa. While previous studies have documented the cascading ecological effects associated with modern megafaunal decline (for example Estes *et al.*, 2011; Estes *et al.*, 2016; Doughty *et al.*, 2016; Malhi *et al.*, 2016; Sherman *et al.*, 2020), the reconstructions of pre- and post-extinction communities presented here allow assessment of multiple, concurrent megafaunal extinctions and their influence on network topology across deeper timescales. The results show that, from a structural standpoint, marine ecosystems can remain functionally cohesive even after substantial loss of large taxa, especially predatory species, provided that trophic redundancy buffers most key trophic roles. The extinction of *O. megalodon* further informs discussion on the impacts of the loss of marine apex predators. Despite being one of the largest apex predators to ever exist, its disappearance did not disrupt trophic organisation, suggesting that top-down regulatory effects, while influential at population or biomass scales (Estes *et al.*, 2011; Hammerschlag *et al.*, 2019; Hammerschlag *et al.*, 2022; Jordaan *et al.*, 2023), may exert limited control over the overarching trophic structure of marine food webs.

These findings provide a valuable comparative framework for evaluating the vulnerability and future trajectories of modern marine ecosystem health, many of which contain megafaunal taxa currently facing heightened extinction risk (Estes *et al.*, 2016; Pimiento *et al.*, 2020; Grose *et al.*, 2020; Pacoureau *et al.*, 2021). Although the results from Chapter 2 might suggest that modern communities could exhibit similar structural robustness, modern biodiversity loss is unfolding under intense, multifactorial anthropogenic pressures (Dulvy *et al.*, 2014; Grose *et al.*, 2020; Pacoureau *et al.*, 2021; van Weelden *et al.*, 2021), at an unprecedented scale (Hatfield *et al.*, 2025). Consequently, the structural and functional consistency observed in past ecosystems cannot be fully assumed to predict future resilience. Instead, the ecological consequences of ongoing megafaunal decline are likely to be more severe, complex and less predictable than those implied from Pliocene analogues.

Chapter 3 provides the first evidence for spatial variation in the Pliocene marine megafaunal extinction event. Regional heterogeneity in extinction rates is consistent with other marine extinction events (for example Krug & Patzkowsky, 2007; Danise *et al.*, 2019; He *et al.*, 2025). However, the pattern of high extinction rates across all ocean basins except the North Atlantic is unusual, with this regional variation having not been linked to any other marine extinctions. Moreover, the comparatively low extinction rates in the North Atlantic, contrasted with the high rates in the Mediterranean, run counter to predictions that losses should scale with continental shelf availability, as proposed by the neritic zone hypothesis (Pimiento *et al.*, 2017).

The neritic zone hypothesis is further challenged by the analyses presented in Chapter 4. When modelling marine megafauna extinction drivers across the Neogene, neither continental shelf proportion nor sea temperature adequately accounted for the observed extinction trends. Although the influence of these environmental variables cannot be entirely ruled out, the results suggest that other factors were likely more important in shaping marine megafaunal extinction selectivity. Notably, the Piacenzian, the interval corresponding to the Pliocene marine megafaunal extinction, shows anomalously high extinction residuals relative to the model predictions, indicating that this was an exceptional event and not readily explained by long-term abiotic trends. It is, therefore, plausible that the drivers of the Pliocene marine megafaunal extinction were distinct from those underlying extinction selectivity in other Neogene intervals. Such distinctions have been documented in other extinction events, where certain periods of perturbation do not just intensify background extinction rates, but result in a notable shift in extinction selectivity (for example Dunhill *et al.*, 2018).

The results of Chapter 4 provide insight into the environmental sensitivities of marine megafauna, suggesting that they were largely resilient to changes in both neritic zone area and sea temperature over Neogene timescales. The apparent resilience to shifts in temperature may seem surprising, given the negative impacts of contemporary climate change on marine megafauna (Albouy *et al.*, 2020; Grose *et al.*, 2020). However, this discrepancy likely reflects differences in the rate and magnitude of current warming (Glikson, 2016). While the specific drivers of the Pliocene marine megafaunal extinction remain unresolved, these results provide a foundation for exploring alternative hypotheses beyond those previously proposed.

5.2 Methodological Innovations and Limitations

The research presented in this thesis provides novel insights into the Pliocene marine megafaunal extinction by applying established methodologies in new and targeted ways. Chapter 2 employed the Paleo Food web Inference Model (PFIM) but adapted the framework to accommodate a predominantly pelagic vertebrate dataset. Although PFIM has been successfully applied to other extinction events (Dunhill *et al.*, 2024), it is optimised for mixed benthic and pelagic faunal assemblages with abundant invertebrate taxa, designating feeding interactions using Bambach's ecospace rules (Bambach *et al.*, 2007). In vertebrate-dominated datasets, several of these functional traits, such as motility, offer little discriminatory power and provide limited resolution of feeding-niche separation. Through iterative testing, this research proposes a modified set of trait combinations better suited for defining feeding niches in pelagic marine vertebrates. These traits and their associated rules remain grounded in optimal foraging theory (Beckerman *et al.*, 2006; Pyke & Starr, 2021), accounting for encounter likelihood, feeding preferences and energetic feasibility. This adaptation strengthens the ecological basis for inferred feeding interactions in pelagic vertebrate-dominated food webs and offers a useful framework for future reconstructions of similarly structured communities.

Chapter 2 also demonstrates that the inclusion of singular macroinvertebrate and microinvertebrate nodes can serve as effective substitutes for more detailed fossil data, which is particularly valuable when such data are unavailable. Where specific invertebrate prey were ecologically important, individual nodes could be incorporated selectively, as demonstrated by the addition of 19 squid nodes in this study, which produced meaningful and ecologically realistic changes to the food web. In addition, Chapter 2 also introduced a streamlined workflow for assessing changes in metrics and motifs in realised food webs. By calculating Cohen's *d* (Cohen, 2013) across large samples of realised webs, the approach quantifies effect sizes rather than relying solely on differences in means, thereby providing a more robust assessment of structural change and associated uncertainty. This workflow offers a simple and replicable method which can be used for comparing food web dynamics in other studies.

Finally, Chapter 3 applied and further validated the spatial extinction rate analysis framework originally developed by Allen *et al.*, (2023). By successfully implementing the three rate metrics (raw, boundary-crossover and 3-timer) at the regional scale of discrete ocean basins rather than latitudinal bands, this study demonstrates the flexibility of the framework and its suitability for analysing extinction dynamics across a wide range of spatially defined regions.

Despite these methodological advances, the impact of data limitations is apparent across all research chapters. The structural food web modelling approach taken in this thesis, is well established and can provide great insight into broad ecosystem structural and functional changes (for example Roopnarine *et al.*, 2007; Dunne *et al.*, 2014). However, structural food webs have some limitations; by only considering the presence/absence of taxa and interactions, topological changes will be more conservative than in food web models which account for population sizes, biomass or interaction strengths between nodes (Berlow *et al.*, 2004; O'Gorman *et al.*, 2019). As such, some of the structural and functional changes exhibited in Chapter 2 may be somewhat underestimated.

Other constraints primarily arise from the availability of occurrence data and from sampling biases in the marine megafauna fossil record. The vertebrate fossil record is generally more sparsely sampled, rarer, and more spatially restricted than the invertebrate record due to taphonomic, ecological and collection-related biases. When occurrences are further limited to genera exceeding 1m in length (consistent with the definition of megafauna used here; Pimiento *et al.*, 2024), sample sizes become even more restricted. This issue was less pronounced in Chapter 2, where the analysis focused on the best-sampled ocean basin (the North Atlantic), drew from entire epochs and included both megafaunal and non-megafaunal vertebrates, providing sufficiently rich data for food web reconstruction. In contrast, the analyses in Chapter 3 relied exclusively on megafaunal occurrences, making data limitations far more apparent. Estimating extinction rates for each temporal stage across multiple ocean basins resulted in patchy data coverage, particularly in under sampled regions, leading to the South Atlantic basin to be disregarded from the final results. The inconsistency in the ability to calculate extinction rates is especially apparent when compared to other similar studies underpinned by much larger datasets (Alroy, 2008; Benson *et al.*, 2021; Allen *et al.*, 2023).

Data scarcity further constrained the ability to test environmental drivers in Chapter 4. Although the palaeoclimate simulations and digital elevation models provide high-resolution reconstructions capable of generating modelled variables at finer temporal intervals, the coarse temporal resolution of the taxonomic occurrence data prevented comparable partitioning. Consequently environmental variables had to be time-averaged across stages, likely dampening the signals of within-stage variation. In addition, limitations in the climate and elevation data, most notably in the spatial averaging of ocean depth within the grid cells, systematically underestimate continental shelf area. Enhancing the spatial resolution of these models would substantially improve analyses of the kind presented here.

5.3 Avenues for Further Research

This thesis has contributed meaningfully to the current understanding of the ecological consequences of the Pliocene marine megafaunal extinction event by examining changes in ecosystem structure and function rather than solely on taxonomic patterns. However, as demonstrated in modern ecosystems, taxonomic losses impact far more than food-web topology, often triggering cascading effects on population dynamics, energy flow and biomass distribution (for example Estes *et al.*, 2016; Malhi *et al.*, 2022; Pereira *et al.*, 2023). Such impacts are especially pronounced following the removal of top predators (Heithaus *et al.*, 2008; Estes *et al.*, 2011; Sherman *et al.*, 2020). Therefore, although the analyses presented here identified only minimal topological changes, more substantial ecological shifts may emerge through the reconstructions of dynamic, rather than purely structural, food webs.

Dynamic food web models incorporate energy flow, simulate population dynamics, and allow for changes in productivity distribution to be quantified throughout the network (Curtsdotter *et al.*, 2011). These models require estimates of primary productivity at the base of the web, which can be obtained through modelling approaches, such as by using the coupled Earth-ecosystem model (EcoGEnIE) which simulates biomass for phytoplankton and zooplankton across the Phanerozoic (Wilson *et al.*, 2018; Ward *et al.*, 2018), providing realistic baseline conditions for dynamic simulations. Community dynamics can then be modelled using metabolic rate equations that describe population growth as a function of body size. Applying this framework to the Pliocene and Pleistocene marine communities examined in this thesis would enable a more mechanistic understanding of the ecological consequences of marine megafaunal extinction and represents the intuitive next step for advancing this research. These methods would also provide a means to test hypotheses concerning the population-level impacts of losing apex predators such as *Otodus megalodon*, potentially yielding further insight into the extinction dynamics of this shark.

The extinction rate analysis in Chapter 3 demonstrate that extinction impacts varied spatially, suggesting that reconstructing food webs, whether structural or dynamic, across multiple ocean basins would be highly informative. Such reconstructions would enable direct comparisons of trophic structure and network resilience among regions that experienced differing extinction rates and magnitudes. These comparisons would be particularly valuable in light of the findings from Chapter 2. In Chapter 2, the North Atlantic was selected for food web reconstruction because it is the best-sampled basin for the Pliocene and Pleistocene (albeit only marginally better sampled than the North Pacific). Chapter 3, however, identified the North Atlantic as experiencing the lowest extinction impacts. Although the extinction rates and the reconstructed marine communities are not directly comparable, given differences in temporal resolution and sampling-standardisation methods, this contrast raises the possibility that food webs from other basins may exhibit more pronounced structural shifts.

Finally, understanding the causes of the Pliocene marine megafaunal extinction remains an important and unresolved research challenge. Chapter 4 evaluated the neritic zone hypothesis (Pimiento *et al.*, 2017) alongside a new hypothesis proposing sea temperature decline as a potential extinction driver. However, neither mechanism adequately accounted for the observed extinction rate patterns across the Neogene. These findings underscore the need to explore additional environmental and ecological factors that may have influenced marine megafaunal extinction risk during the late Pliocene. Future research should incorporate a broader suite of abiotic variables, such as ocean circulation patterns and nutrient fluxes, both of which were likely perturbed by major tectonic and climatic shifts during this time (O'Dea *et al.*, 2016; Hill *et al.*, 2017). Biotic factors also warrant further attention. Results from Chapter 2 suggest that Pleistocene ecosystems were less productive than those of the Pliocene, raising the possibility that reduced energy flow from the base of the food web contributed to extinction selectivity. Testing primary productivity proxies as a potential drivers would help determine whether energy limitation underpinned these extinctions. Incorporating these additional variables may ultimately clarify the drivers of the extinction event and provide deeper insight into long-term relationships between environmental change and marine megafaunal extinction dynamics.

5.4 Concluding Remarks

In summary, this thesis advances understanding of the Pliocene marine megafaunal extinction, a significant yet understudied event that holds clear relevance for interpreting ongoing declines in marine megafauna. By integrating trait-based food web reconstructions, spatial extinction rate analyses and environmental modelling, this work provides a comprehensive evaluation of both the ecological consequences and potential drivers of this extinction event. The findings demonstrate that, despite substantial losses of large-bodied taxa, ecosystem structure and trophic organisation remained broadly resilient, suggesting that key aspects of ecological functioning persisted even under substantial taxonomic turnover. Additionally, this thesis challenges existing hypotheses concerning the primary drivers of the extinction event, offering limited support for both neritic zone reduction and sea temperature change. Collectively, this thesis contributes important new perspectives to the limited body of research on the Pliocene marine megafaunal extinction, highlighting both the resilience of past marine ecosystems and the implications this may hold for the future stability of modern marine communities under increasing anthropogenic pressures.

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