

# The Pliocene marine megafauna extinction and its impact on functional diversity

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**The end of the Pliocene marked the beginning of a period of great climatic variability and sea-level oscillations. Here, based on a new analysis of the fossil record, we identify a previously unrecognized extinction event among marine megafauna (mammals, seabirds, turtles and sharks) during this time, with extinction rates three times higher than in the rest of the Cenozoic, and with 36% of Pliocene genera failing to survive into the Pleistocene. To gauge the potential consequences of this event for ecosystem functioning, we evaluate its impacts on functional diversity, focusing on the 86% of the megafauna genera that are associated with coastal habitats. Seven (14%) coastal functional entities (unique trait combinations) disappeared, along with 17% of functional richness (volume of the functional space). The origination of new genera during the Pleistocene created new functional entities and contributed to a functional shift of 21%, but minimally compensated for the functional space lost. Reconstructions show that from the late Pliocene onwards, the global area of the neritic zone significantly diminished and exhibited amplified fluctuations. We hypothesize that the abrupt loss of productive coastal habitats, potentially acting alongside oceanographic alterations, was a key extinction driver. The importance of area loss is supported by model analyses showing that animals with high energy requirements (homeotherms) were more susceptible to extinction. The extinction event we uncover here demonstrates that marine megafauna were more vulnerable to global environmental changes in the recent geological past than previously thought.**

In the Anthropocene, rapid environmental change and the resultant loss of habitat pose a major threat to marine fauna<sup>1,2</sup>. Throughout geological time, habitat loss caused by sea-level changes has been widely associated with extinction events<sup>3</sup>. After the last mass extinction at the Cretaceous/Palaeogene boundary and throughout the past 66 million years, the largest global sea-level changes occurred mainly during the Pliocene and Pleistocene epochs (herein, the Plio–Pleistocene; from 5.33 to 0.01 million years ago (Ma)), with multiple large eustatic oscillations that were amplified after the onset of the Northern Hemisphere glaciation in the late Pliocene<sup>4–7</sup>.

Although it has been proposed that global cooling and sea-level fluctuations in the Plio–Pleistocene were responsible for the regional extinction of marine invertebrates<sup>8</sup>, it has been assumed that global marine biodiversity was generally resistant to these environmental changes<sup>3,9</sup>. Individual examples of faunal turnover and extinctions of large marine vertebrates (collectively known as ‘marine megafauna’, which includes, but is not limited to marine mammals, seabirds, turtles, sharks and rays<sup>10,11</sup>) have been observed around this period. These include a substantial drop in cetacean<sup>12–14</sup> (but see ref. <sup>15</sup>) and penguin diversity<sup>16,17</sup>, the extinction of dugongids in the Western Atlantic and Mediterranean regions<sup>18–20</sup>, the loss of the largest shark that ever lived (*Carcharocles megalodon*)<sup>21,22</sup> and extinctions of sea turtles (for example, *Psephophorus*, a leatherback turtle)<sup>23</sup>. However, it remains unclear whether these megafauna losses were simply conspicuous background extinctions or formed part of a global marine extinction event resulting from the environmental changes of the Plio–Pleistocene<sup>8,24</sup>. Evaluating the extent

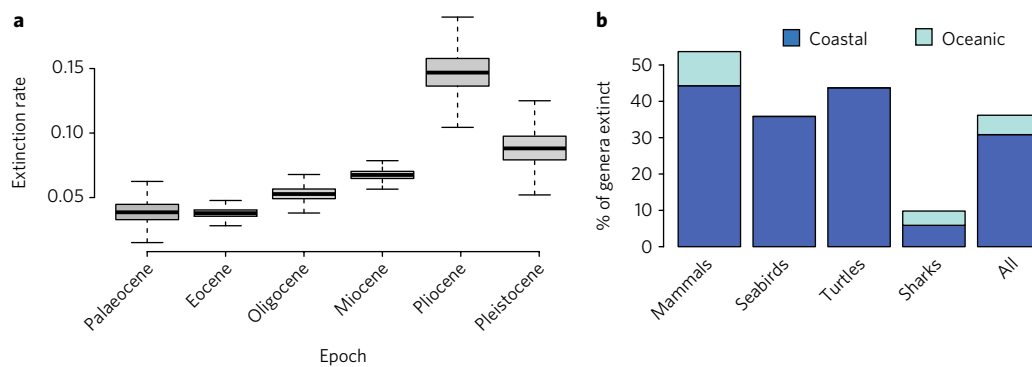
and consequences of the marine megafauna extinctions is relevant because these organisms play fundamental roles in ecosystems<sup>25–27</sup> and because modern megafauna assemblages were established during the Pleistocene (for example, ref. <sup>28</sup>; Supplementary Fig. 1).

Historically, studies of marine extinctions have focused almost exclusively on taxonomic loss (for example, species, genera and family; but see ref. <sup>29</sup>). While this taxonomic perspective quantifies the loss of diversity *sensu stricto* (for example, ref. <sup>30</sup>), it ignores the ecological contributions of these species to ecosystems. Linking taxonomic identity with ecological roles can be used to assess the selectivity of extinctions<sup>24,31–35</sup>, to evaluate shifts in the structure of communities after an extinction event<sup>32</sup> and to gauge the potential implications for ecosystem functioning<sup>36</sup>. This ‘functional diversity’ approach (reviewed in ref. <sup>32</sup>) consists of quantifying the distribution of species in a multidimensional functional space defined by species traits (that is, the intrinsic characteristics of species that directly influence their ecological role<sup>32</sup>). The few studies that have used this or similar approaches have focused specifically on the ecological consequences of the extinction of invertebrates<sup>24,33–35</sup> (but see ref. <sup>37</sup>). These organisms have important ecological roles, but are usually small in size, occupy low trophic levels and tend to be highly speciose. Conversely, marine vertebrates include the largest organisms on Earth, occupy a variety of trophic roles, are relatively species poor and are accordingly less likely to be ecologically redundant<sup>38</sup>. Moreover, they are often wide ranging and are known to structure modern food webs from the top down<sup>25</sup>. The goal of linking the extinctions of large animals with consequences for ecosystem

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**Figure 1 | Elevated extinction rates of marine megafauna in the late Pliocene.** **a**, Extinction rates within epochs. The extinction rates in the Pliocene are significantly higher than in any other epoch in the Cenozoic: they are 2.2-fold higher than in the Miocene, 60% higher than in the Pleistocene and threefold higher than the average Cenozoic rate ( $n = 11,241$  global occurrences). Boxes show the central 50% posterior credible intervals with error bars indicating the 95% credible intervals. **b**, Proportional extinction of the Pliocene megafauna. Species associated with coastal environments (strictly coastal, coastal-terrestrial or coastal-oceanic) represent 86% of the megafauna. Strictly oceanic species represent the remaining 14% of the megafauna.

functioning is particularly relevant today, as large-bodied marine species are the most vulnerable to current human impacts<sup>2</sup>.

Here, we evaluate the severity of the extinction of marine megafauna during the Pliocene, and examine the potential causes and consequences of this event. We first assess whether the Pliocene extinction rates were higher than those of the rest of the Cenozoic, and examine the proportional loss of genera from the Pliocene to the Pleistocene. Then, we quantify the differences in functional diversity between the Pliocene and Pleistocene coastal megafauna assemblages, to assess the potential effects of extinctions on ecosystem functioning. Finally, we evaluate the possible drivers of extinction by estimating the habitat loss due to eustatic variations, and by modelling traits as predictors of extinction. The results of this research provide a broader understanding of the state and vulnerability of the marine megafauna in the recent geological past, and forewarn of the likely sensitivity of megafauna biodiversity as anthropogenic climate change accelerates and brings massive perturbations to coastal ecosystems<sup>39–41</sup>.

## Results and discussion

**The extinction event.** We estimated the expected number of extinction events per genus per Myr during the Cenozoic, while accounting for preservation biases and dating uncertainties using a Bayesian framework<sup>42</sup> (Supplementary Tables 1–3 and Supplementary Fig. 2). Marine megafauna present significantly elevated extinction rates in the Pliocene (Fig. 1a), with a threefold increase relative to the rest of the Cenozoic, and with the highest rates occurring in the late Pliocene, specifically between 3.8 and 2.4 Ma (Supplementary Fig. 3). Per-clade analyses reveal that all groups of marine megafauna follow this trend except sea birds, which present higher extinction rates in the Paleocene (Supplementary Fig. 4). Conversely, we did not find evidence of changes in origination rates during the entire Cenozoic (Supplementary Fig. 3). Until now, disappearances of Pliocene marine megafauna species were thought to represent isolated examples within a broader assemblage that remained largely intact (for example, ref. <sup>3</sup>, but see ref. <sup>43</sup>). Our results show that these extinctions, which peaked in the late Pliocene, were part of a hitherto unrecognized global loss of marine megafauna biodiversity.

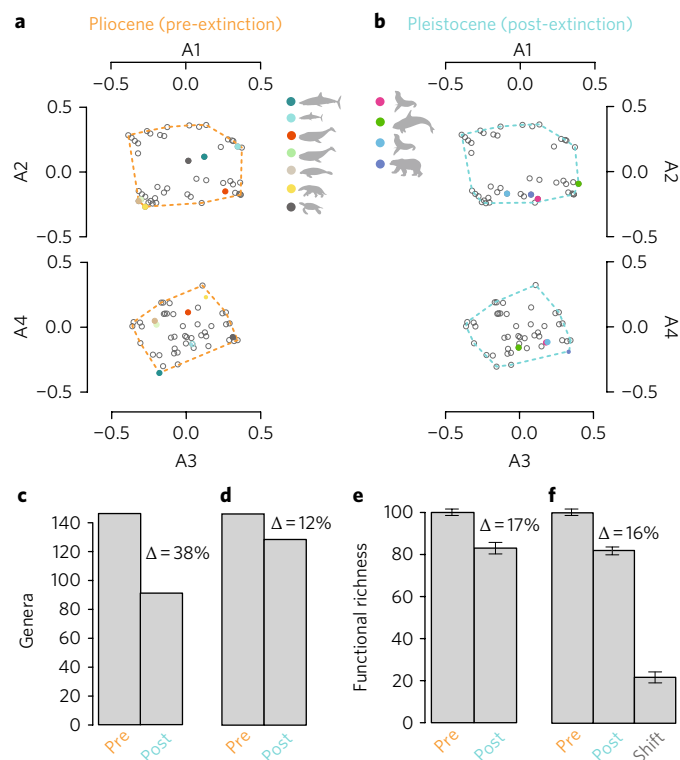
Closer examination of the Pliocene megafauna fossil record reveals the proportional losses of genera (see Supplementary Table 4 for numbers of genera and samples). We found that 36% of Pliocene genera were extirpated (that is, not present in the Pleistocene). In line with previous studies<sup>3,44</sup>, marine mammals present the highest proportional extinction, losing 55% of their generic diversity (for example, the aquatic sloth *Thalassocnus* and the beluga-

like odontocete *Bohaskaia*). Seabirds lost 35% of their generic diversity (for example, the penguin *Inguza*), sea turtles 43% (for example, *Syllomus* and *Psephophorus*) and sharks 9% (for example, *Carcharocles*) (see Fig. 1b and Supplementary Table 4). New genera also evolved: 25% of the Pleistocene genera were new (that is, they were not reported in the Pliocene), including 38% of mammals (for example, the polar bear *Ursus*) and 41% of seabirds (for example, the storm petrel *Oceanodroma* and the penguin *Megadyptes*) (Supplementary Table 4). Nevertheless, in line with the elevated extinction relative to origination rates, generic diversity of global megafauna suffered a net decline of 15% between the Pliocene and Pleistocene. Furthermore, we found that most of the Plio–Pleistocene marine megafauna (86%; Supplementary Table 4) were associated with coastal habitats (that is, the neritic zone at a depth of less than 200 m), where the absolute loss of genera was greater (see Fig. 1b and Supplementary Dataset 1). However, since this finding could be biased by differential fossil preservation and/or sampling, it should be interpreted with caution.

**Impacts on functional diversity.** To assess the potential effects of the Pliocene extinction on ecosystem functioning, we performed trait-based analyses following the methods described by Mouillot *et al.*<sup>32</sup> for genera associated with coastal environments. Accordingly, we assigned traits to the Plio–Pleistocene coastal megafauna (184 genera; Supplementary Table 4) to (1) determine the functional entities (groups with unique trait combinations, herein FEs) and (2) construct a functional space<sup>32</sup>. The coastal megafauna dataset includes 146 Pliocene genera from 711 occurrences and 129 Pleistocene genera from 858 occurrences (Supplementary Table 4).

We found that 55 (38%) coastal Pliocene genera went extinct (Fig. 2c), resulting in the loss of seven (14%) FEs (Fig. 2a) along with 17% of functional richness (Fig. 2e; the volume of functional space after accounting for sample size differences (see Supplementary Fig. 5 and the Methods)). The post-extinction Pleistocene assemblage hosted 38 new genera (29%), reducing the net taxonomic loss of coastal habitats to 12% (Fig. 2d). The evolution of these new genera resulted in the addition of four FEs (9%; Fig. 2b) and the net loss of three FEs. However, these new FEs, which were exclusively occupied by mammals, minimally compensated for the functional richness lost (by 1%), leaving a net functional richness loss of 16%. Furthermore, the loss and gain of Plio–Pleistocene FEs drove a functional shift (non-overlap of functional volume<sup>32</sup>) of 21% (Fig. 2f).

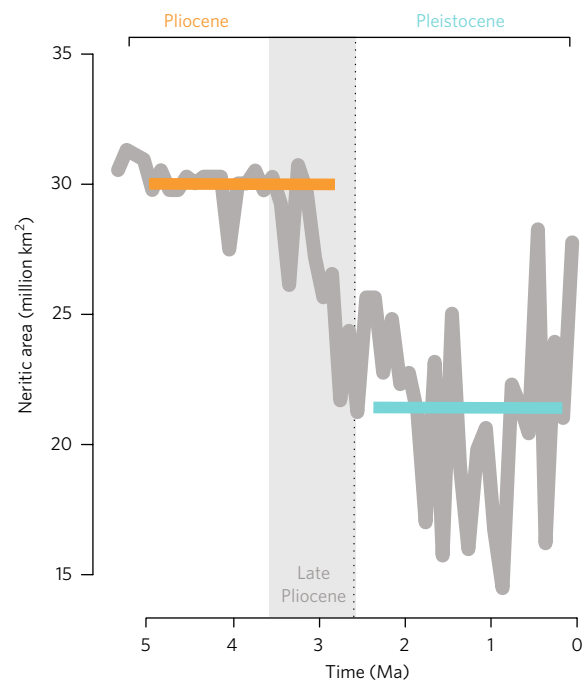
We next investigated the interaction between extinction and the functional structure of the megafauna assemblage. The functional structure of the Pliocene assemblage ultimately rendered it sensitive



**Figure 2 | Changes in coastal marine megafauna functional diversity from the Pliocene (pre-extinction) to the Pleistocene (post-extinction).**

**a, b**, Functional space plotted using the first four axes (A1–A4) from a principal coordinate analysis and the empirical data (not accounting for differences in sample size). The coloured dashed line denotes the convex hull and the dots represent the Functional Entities (FEs): Pliocene = 49 FEs; Pleistocene = 46 FEs. The filled dots denote FEs that changed (those that were either extirpated or originated), whereas the open dots denote unchanged FEs (winners). Note that since multiple genera can occupy a single FE, the loss or gain of genera does not necessarily result in the loss or gain of a FE. FE codes can be found in Supplementary Table 5. Refer to the Methods section ‘Functional traits and functional taxonomic units’ for details on the differences between taxonomic levels. **a**, Pliocene space showing FEs that went extinct and their taxonomic affiliations. Dark blue = FE 25, one genus (*Carcharocles*, Lamniformes); light blue = FE 36, one genus (*Parotodus*, Lamniformes); red = FE 27, two genera (*Cetotherium* and *Nannocetus*, Mysticeti); green = FE 49, one species (*Herpetocetus morrow*, Mysticeti); light grey = FE 50, one genus (*Nanosiren*, Sirenia); yellow = FE 52, one genus (*Thalassocnus*, Xenarthra); and dark grey = FE 46, one genus (*Psephophorus*, Testudines). **b**, Pleistocene space showing the new FEs and their taxonomic affiliations. Pink = FE 47, one genus (*Mirounga*, Pinnipedia); green = FE 13, one species (*Orcinus orca*, Odontoceti); blue = FE 31, one genus (*Proterozetes*, Pinnipedia); and red = FE 3, one genus (*Ursus*, Carnivora). **c, d**, Taxonomic richness (number of genera) loss after the extinction event. **c**, Raw genus loss (not including the new genera that originated in the Pleistocene). **d**, Net genus loss (including the new genera that originated in the Pleistocene). **e, f**, Functional richness (functional space volume<sup>32</sup>) loss and shift. The vertical lines are error bars resulting from the 1,000 permutations of the resampled data (see the Methods). **e**, Raw functional richness. **f**, Net functional richness.

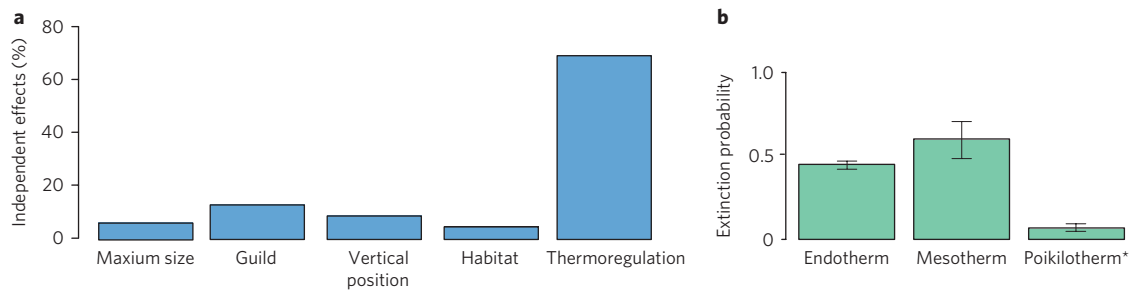
in the face of taxonomic extinctions: although it had an average of three genera per FE (functional redundancy *sensu*<sup>45</sup>), they were concentrated within specific FEs (over-redundancy<sup>45</sup>), leaving over half with only a single genus (functional vulnerability<sup>45</sup>) (Supplementary Fig. 6 and Supplementary Table 6). All lost and gained FEs (except one) contained a single genus (Fig. 2a,b, see legend), suggesting that



**Figure 3 | Reduction of neritic areas as a putative extinction driver.** Global extent of neritic areas based on eustatic levels reported by deBoer *et al.*<sup>5</sup>. The horizontal lines represent mean values for the Pliocene and Pleistocene.

low-redundancy FEs largely drove the changes in functional space. The net losses of functional richness and the functional shift were greater than expected given the mean background extinction rate over the Cenozoic (22 genera; see the Methods) and the new Pleistocene FEs (Supplementary Fig. 7a,b). However, these functional changes were no different than would be expected given the 55 genera lost (Supplementary Fig. 7c,d) and the functional structure of the assemblage, indicating that the loss of genera *per se* from the functionally vulnerable Pliocene assemblage, rather than the observed pattern of genera loss, determined the functional changes. Ultimately, the Pleistocene assemblage was left with a greater proportion of single genus FEs (80%)—that is, a greater functional vulnerability—than the pre-extinction Pliocene assemblage (59%) (Supplementary Table 6). In light of the increasing volume of literature linking functional diversity to ecosystem functioning<sup>46–49</sup>, it follows that the contributions of megafauna to marine ecosystems may have been diminished (loss of functional richness), altered (functional shift) and rendered less resistant to subsequent extinctions (increased functional vulnerability) after the Pliocene extinction event.

A common finding among the handful of previous studies that have used a multi-trait-based approach in this context is that losses in global functional diversity are negligible after an extinction event, even in the face of mass extinctions, when greater than 70% of genera were lost<sup>33–35</sup>. Our detection of a larger, although still modest (16–21%), functional diversity change, despite lower taxonomic loss (38%), is probably because most previous studies have focused on benthic, smaller-bodied, more speciose invertebrate assemblages, while ours focuses on large vertebrates. Ecosystems hold fewer large than small species<sup>50</sup>, thus among large-bodied species there is likely to be less scope for functional insurance provided by redundant species, making functional diversity among large animals more sensitive in the face of extinction<sup>51,52</sup>. This conclusion is supported by the high levels of functional vulnerability among Plio–Pleistocene coastal megafauna (Supplementary Table 6), the singular roles megafauna taxa are thought to play in modern systems<sup>26</sup> and the accumulating evidence of ecosystem consequences induced by their declines<sup>25</sup>.



**Figure 4 | Thermoregulation explains the susceptibility of genera to the Pliocene megafauna extinction.** **a**, Hierarchical partitioning output based on generalized linear models showing the proportion of explained deviance in extinction probabilities that can be attributed to each trait. In the full model, traits collectively explained 20% of deviance in extinction probabilities. **b**, Extinction probabilities among the thermoregulation categories (see Supplementary Table 8). The vertical lines denote error bars and the asterisk denotes statistical significance compared with both of the other categories according to Tukey tests.

**Extinction mechanisms.** It has been widely stated in the literature that the onset of the Northern Hemisphere glaciation at the end of the Pliocene resulted in an abrupt transition to a new climatic state dominated by colder and more variable temperatures, and large sea-level oscillations<sup>4–7,12</sup>. However, to our knowledge, there have been no quantitative and global assessments of consequent changes in the extent of coastal habitats during this time (but see ref. <sup>53</sup> for specific regions). We therefore reconstructed the global extent of neritic areas based on eustatic variations<sup>4,5</sup> during the Plio–Pleistocene and found that as the sea level regressed, neritic areas dropped precipitously during the late Pliocene. This abrupt change coincides in time with the highest extinction rates found (Supplementary Fig. 3). After this sudden drop in coastal habitat availability, large-area oscillations took place: there was a 250% increase in the coefficient of variation from the Pliocene (0.07) to the Pleistocene (0.17). Additionally, the total neritic area available was significantly reduced from 79.1 million km<sup>2</sup> in the Pliocene to 57.9 million km<sup>2</sup> in the Pleistocene, representing a 27% reduction in the mean area (*t*-test: *P* < 0.001; Fig. 3 and Supplementary Fig. 8).

Numerous studies have identified a regional invertebrate extinction during the Plio–Pleistocene and attributed this to climatic changes (mainly temperature)<sup>8,54–56</sup>, but only one region-specific study has implicated habitat loss associated with sea-level changes in extinctions<sup>57</sup>. Here, we document a global-scale reduction in coastal habitat availability that abruptly started in the late Pliocene and hypothesize that this, probably acting alongside oceanographic alterations such as changes in productivity and ocean circulation (for example, refs <sup>24,58–61</sup>) was the extinction driver for the Pliocene marine megafauna. Some genera may have only succumbed to repeated sea-level oscillations or when habitat loss coincided with other extinction drivers (for example, prey availability and/or competition)<sup>62,63</sup>, which may explain the continuation of elevated extinction rates in the Pleistocene. Similar mechanisms might be responsible for the previously noted decline of some megafauna groups in the late Miocene<sup>16,43</sup>, although such losses were not comparable in magnitude to the Pliocene losses documented here (Fig. 1a).

To assess extinction selectivity, we modelled traits as predictors of survivorship using generalized linear models. Thermoregulation is the trait that best predicts extinctions in the Pliocene (Fig. 4a), with endotherms and mesotherms (homeotherms; that is, those able to regulate, at least to some degree, their internal temperatures<sup>64,65</sup>) having significantly higher chances of going extinct than their poikilothermic counterparts (Fig. 4b and Supplementary Tables 7 and 8). Large body size—a trait associated with extinction risk in the Anthropocene<sup>3,66</sup>—does not predict extinction risk, nor affect the explanatory power of thermoregulation. Although we found a taxonomic signal in extinction probabilities, with mammals and sharks presenting significant differences (the grey part of Supplementary Tables 7 and 8), the signal of thermoregulation was independent and

held when ‘class’ (Aves, Chondrichthyes, Mammalia and Reptilia) was controlled as a fixed or random factor in the generalized linear models (Supplementary Table 9). Notably, the homeotherms that became extinct were not exclusively endothermic mammals or seabirds: three of the five mesotherms (two shark genera and a turtle genus) were also lost.

Unlike poikilotherms, homeotherms are buffered against external temperature changes, but require greater resources to sustain higher metabolic demands<sup>64,65,67,68</sup>. Homeotherms should therefore show greater extinction susceptibility in the face of declining habitat and associated resource availability<sup>69</sup>, as our results show. In contrast, if temperature fluctuations or overall cooling had directly driven this extinction, the opposite result would have been expected (that is, a greater susceptibility of poikilotherms compared with homeotherms). Feeding plasticity, as grey whales seem to have exhibited during the late Pleistocene, and possibly even across the Pliocene–Pleistocene boundary<sup>70</sup>, may have aided the survival of some homeothermic genera in the face of habitat loss. Overall, the greater susceptibility of energy-demanding homeotherms supports our hypothesis that the abrupt reduction of neritic areas was a key driver of the marine megafauna extinction. Whether thermoregulation covaries with other traits (for example, those associated with extinction risk)<sup>71</sup>, and the effects of such correlations in determining the selectivity of the Pliocene marine megafauna extinction, are beyond the scope of this study but should be further explored.

## Conclusions

Here, we report an extinction and consequent erosion of functional diversity of marine megafauna during the Pliocene. We propose that these extinctions were driven by habitat loss produced by sea-level oscillations, probably acting alongside other oceanographic alterations such as changes in productivity and ocean circulation, in addition to biotic drivers such as prey availability and/or competition. Since the modern marine megafauna became established in the Pleistocene (Supplementary Fig. 1), this event shaped the Earth’s present-day assemblages of these large ecosystem-structuring organisms (for example, refs <sup>25,27,32,72</sup>). The discovery of this extinction event reveals that the biodiversity and functional contributions of marine megafauna were more sensitive to environmental changes in the recent geological past than hitherto assumed. Today, and historically, over-exploitation has been considered the chief threat to marine megafauna<sup>27</sup>. Our study cautions that as anthropogenic climate change accelerates and triggers regime shifts in coastal ecosystems<sup>39–41</sup> the potential consequences for marine megafauna should not be underestimated.

## Methods

**Cenozoic dataset.** We downloaded all the records of marine megafauna for the Cenozoic (that is, the past 66 Ma) from the Paleobiology Database (<https://paleobiodb.org>; last search: November 2016). The Paleobiology Database follows



the most recent geological timescale of Gradstein *et al.*<sup>73</sup>. In the absence of a formal, size-based definition of ‘marine megafauna’, we included all the genera of the groups of animals that contain the largest marine vertebrates (that is, marine mammals, seabirds, sea turtles, and sharks and rays<sup>10</sup>). We focused on the genus level because generic assignments have greater consistency across different research groups, and because it is more robust to taxonomic error than the species level. All taxonomic identifications were evaluated and corrected. Dubious and equivocal records were excluded from our analyses. Accordingly, we used 11,241 occurrences (Supplementary Table 1). Details on the search criteria and data assessment can be found in the Supplementary Information. Furthermore, all references supporting the occurrences can be found in Supplementary Dataset 2.

**Extinction rates.** We estimated the extinction and origination rates of marine megafauna for the entire Cenozoic using PyRate<sup>74</sup>. This program implements Bayesian algorithms to analyse all available fossil occurrences (identified to genus level in this case) while accounting for preservation biases and dating uncertainties. Accordingly, three main sets of parameters were simultaneously estimated: (1) the preservation rates quantifying the expected number of fossil occurrences per sampled lineage per time unit (1 Myr); (2) the origination and extinction times for each genus, which probably extend beyond the observed temporal range between first and last appearances; and (3) the origination and extinction rates (expected number of origination and extinction events per lineage per Myr) and their temporal variation<sup>42</sup>. We estimated origination and extinction times assuming a time-variable Poisson preservation model, and used them to infer origination and extinction rates within epochs using a time-variable birth–death model where the rates are estimated as independent parameters in each predefined time frame (Supplementary Tables 1–3). To reduce the risk of over-parameterization, we used half-Cauchy priors on the origination and extinction rates with scale parameters estimated from the data using hyper-priors<sup>75</sup>. We ran 2,000,000 Markov chain Monte Carlo iterations under this model and summarized the posterior extinction rates in box plots for each epoch, except for the Holocene, as the temporal and taxonomic resolution of our data was insufficient to reliably estimate extinction in such a short time frame. We considered extinction rates as significantly different between subsequent epochs when 0 fell outside the 95% credible interval of their difference, based on all posterior samples. We ran these analyses on the full dataset of all megafauna groups first, and then repeated them for each group, namely marine mammals, sea birds, sea turtles, and sharks and rays. We ran additional analyses to assess more precisely the timing of origination and extinction rate changes, using birth–death models in which the times of shift were not fixed, but estimated as time-continuous parameters<sup>42</sup>. We tested models with a different number of rate shifts and combined the results from each model using Bayesian model averaging; that is, after resampling their posterior samples proportionally to the respective relative probabilities<sup>76</sup>. We then summarized the marginal extinction rates through time within 0.1 Myr time bins as mean and 95% credible intervals. More details can be found in the Supplementary Methods.

**Plio–Pleistocene dataset.** We selected all marine megafauna genera occurring in the Pliocene (5.3–2.6 Ma) and Pleistocene (2.6–0.01)<sup>77</sup>. In total, we gathered 1,763 global occurrences. Most of the data were not dated to the ‘stage’ level. Accordingly, we used geological epochs as our interval unit; for example, whenever a genus was reported in the Pliocene, the Zanclean or the Piacenzian, it was assigned to the Pliocene. Since the Plio–Pleistocene is our interval of interest, we performed a second evaluation process for this subset of data in which the taxonomic assignments and age of each record were assessed following a procedure described previously<sup>22</sup> (Supplementary Methods). We followed the most recent age for the Pliocene–Pleistocene boundary, at 2.58 Ma (ref. <sup>77</sup>). Accordingly, all Gelasian records were treated as Pleistocene occurrences. More details can be found in the Supplementary Methods. It is worth noting that even though it has been proposed that marine vertebrates from the Pleistocene are poorly known (for example, ref. <sup>15</sup>), we were able to gather 906 occurrences from the Pleistocene, which is comparable with the 857 records gathered from the Pliocene.

**Proportional extinction.** In total, we compiled data for 215 Plio–Pleistocene genera. Of these, 177 occurred in the Pliocene and 151 in the Pleistocene (Supplementary Table 4). Sixty-one genera occurred only in the Pliocene and 37 only in the Pleistocene. Based on these numbers, we calculated the proportion of genera that were extirpated from the Pliocene, and the proportion that originated in the Pleistocene. We did this for all megafauna, and for each individual group. Finally, we calculated the net loss of genera as the percentage of Pliocene genera that were lost passing into the Pleistocene.

**Functional traits and functional taxonomic units.** We assigned five ordered categorical functional traits to the Pliocene and Pleistocene marine megafauna: guild (most frequent diet in adults); body size (maximum total length); vertical position (most frequent vertical position when they fed); habitat (typical zone where they occurred); and thermoregulation capability (whether they were endotherms, mesotherms or poikilotherms). Traits are inferred properties of individual organisms known to directly influence their ecological role<sup>32,45</sup>. More details on how traits were coded can be found in the Supplementary Methods. Our Plio–Pleistocene occurrences dataset had a generic taxonomic resolution

(see above), which facilitated the assignment of traits given that most genera have modern analogues on which we can base our assessments. Traits were assigned using authoritative taxon-specific texts, online databases and expert assessments based on both extant relatives and fossil records (references are provided in the Supplementary Methods). Whenever we found a genus consisting of multiple known species with different trait values, we treated them independently to assign traits (see specific cases in the Supplementary Methods). As a result, our traits were assigned mostly (95%) to genera, and sub-divisions of certain genera according to shared traits. These functional taxonomic units are, in our opinion, the lowest taxonomic resolution for systematically assigning functional traits to fossil marine vertebrates. Given that functional taxonomic units correspond to genera in 95% of cases, we still refer to them as ‘genera’ in the main text and figures for consistency and simplicity. Traits were assigned to each occurrence of each functional taxonomic unit. Whenever there was not enough information to assign traits, we disregarded such an occurrence in our analyses (see specific cases in the Supplementary Methods, which represent around 12% of the total number of occurrences gathered from the Paleobiology Database).

**Functional entities, redundancy, over-redundancy and vulnerability.** For our trait-based analyses we focused on genera that are associated with coastal habitats (that is, strictly coastal, coastal–terrestrial and coastal–oceanic genera). These genera represent 86% of the megafauna (Supplementary Table 4) and had 1,569 global occurrences in our dataset. Based on the trait assignments, we calculated the number of possible unique trait combinations, or FEs<sup>32,45</sup>. Pliocene and Pleistocene marine megafauna fill 8% of the total number of FEs (that is, 53 out of 648 FEs). Genera were assigned to FEs independent of taxonomy. Based on the number of FEs and their corresponding genera, we then calculated the functional redundancy (FR: the mean genera per FE), over-redundancy (FOR: the percentage of genera that filled FEs above the mean level of functional redundancy, that is, the overrepresentation of some FEs) and vulnerability (FV: the percentage of FEs with only one genus<sup>45</sup>, representing a potential decrease in functional diversity following taxonomic loss).

**Functional space.** We used the methods of Mouillot *et al.*<sup>32</sup> to create the functional space based on the FEs calculated above. We used the R package FD<sup>78</sup> to create the distance matrix (using the function ‘gowdis’) and to retrieve axes of the principal coordinate analysis (using the function ‘dbFD’). Using the ‘quality\_function\_space’ R function<sup>79</sup>, we determined that our data are best represented using four dimensions, or principal coordinate analysis axes (Supplementary Fig. 9). We then used the ‘FDChange’ function to calculate the functional richness (the percentage of the total volume occupied in the functional space) and shift (non-overlap of functional volume)<sup>32</sup>. Given the multidimensional nature of the functional diversity analyses, the four axes used to represent the functional space of Plio–Pleistocene marine megafauna are correlated with multiple trait combinations (Supplementary Fig. 10) and, therefore, it is not possible to associate portions of the functional space to single traits, nor to pinpoint changing segments of the space.

**Resampling simulations.** We tested the effects of sample size in the calculation of functional diversity indices by randomly resampling each community (Pliocene and Pleistocene) without replacement, bootstrapping the data 1,000 times over 20 evenly spaced bins from 10 to 711 (711 being the lowest sample size for coastal habitats found in the Pliocene) using the R function ‘sample’. We found variation in functional indices due to sample size. We standardized the Pleistocene communities to 711 occurrences and recalculated the functional diversity indices based on this resampled community running 1,000 permutations (with replacement)<sup>80</sup>. Finally, we tested for significant differences between the Pliocene and the Pleistocene using a Wilcoxon test.

**Comparative simulations.** We investigated whether the changes in functional diversity during the Pliocene were significantly higher than those expected under background extinction rates among genera associated with coastal habitats. To do so, we calculated the mean extinction rate for the Cenozoic (except for the Pliocene), as described in the ‘Extinction rates’ section above. Then, we estimated the number of genera that would have been lost under background rates using Foote’s boundary-crossing method<sup>81</sup> as in equation (1).

$$ER = -\ln(N_{bt}/(N_{bt} + N_b))/\Delta t \quad (1)$$

where  $N_{bt}$  is the genera that crossed the bottom and the top of the interval (that is, they were sampled in both the Pliocene and the Pleistocene);  $N_b$  is the genera that only crossed the bottom of the interval (that is, they were sampled only in the Pliocene); and  $\Delta t$  is the length of the interval in millions of years (that is, 2.75 Myr following the timescale of Gradstein *et al.*<sup>73</sup>). We then solved for  $N_b$  in equation (1), replacing the extinction rate (ER) with 0.05 (the mean extinction rate during the Cenozoic). Based on this, 22 genera would have been lost in the Pliocene under mean background conditions (whereas 55 were actually lost in coastal habitats). Accordingly, running 1,000 permutations, we simulated a Pleistocene subset in our Plio–Pleistocene dataset by randomly removing 22 Pliocene genera and calculating the delta (Pliocene functional richness – Pleistocene functional richness) and the functional shift (see ‘Functional space’ section of the Methods).

We then compared the observed delta and shift with the distributions of these metrics under background conditions. Additionally, we investigated whether the loss of functional diversity was greater than expected given the number of taxa lost. This was achieved by randomly removing 55 Pliocene genera (the number of coastal genera lost) and calculating the delta and shift. We tested the significance of these comparisons by running 1,000 permutations. Although the above simulations did not account for the modest sample size differences between the Pliocene and Pleistocene, the post-extinction (Pleistocene) assemblage had more samples and thus the tests are conservative.

**Environmental reconstructions.** We calculated the global extent of the neritic areas available during the Pliocene and Pleistocene, given the sea-level changes of these time periods. We regarded as the neritic area the section of the ocean with a water depth of a maximum of 200 m. To estimate the global extent of these areas, we used the current land topography and ocean bathymetry ETOPO1 Global Relief Model<sup>82</sup>. We selected the ocean cells within the neritic zone and quantified their area using the function 'area' from the R package raster<sup>83</sup>, which takes into account the latitudinal decrease of the projected map cells as a consequence of the globe curvature. To calculate changes in the global extent of the neritic areas across time, we used two independent measures of sea-level change during the past 5.3 Myr (refs <sup>4,5</sup>), applying a temporal resolution of 100,000 years; the choice of measure had no bearing on the qualitative patterns of sea-level change. The model based on deBoer *et al.*<sup>5</sup> is presented in the main text. Global sea-level changes were calculated using oxygen isotope variation<sup>4</sup> and an ice-sheet model forced by benthic  $\delta^{18}\text{O}$  (ref. <sup>5</sup>). Based on these data, we assessed the temporal changes in the global extent of neritic areas available, and in temperature, in the Pliocene ( $n=27$ ) versus Pleistocene ( $n=26$ ), calculated the coefficient of variation for each epoch, and tested for significant differences in the mean values using a *t*-test. Both time bins (Pliocene and Pleistocene) have similar temporal extents (2.7 and 2.6 Myr, respectively), allowing direct comparisons.

**Generalized linear models.** We evaluated the effects of traits on extinction probabilities by modelling survivorship (status: extinct or not extinct) in response to genus traits. We initially used a generalized linear model with binomial error and a logit link to simultaneously assess the effects of all traits (that is,  $\text{glm}(\text{status} \approx \text{trait1} + \text{trait2} \dots)$ ). Furthermore, we used a metric of pseudo  $R^2$  ( $1 - (\text{residual deviance}/\text{null deviance})$ ) to assess its explanatory power. This model was then re-run, first by adding taxonomic identity (for instance, 'class': Mammalia, Aves, and so on) as a fixed effect (for instance,  $\text{glm}(\text{status} \approx \text{trait1} + \text{trait2} \dots + \text{class})$ ) to account for its influence on extinction probabilities; and second, by adding class as a random effect using a generalized linear mixed model in the R package lme4 (ref. <sup>84</sup>) (for instance,  $\text{glmer}(\text{status} \approx \text{trait1} + \text{trait2} \dots | (\text{class}))$ ) to control for the potential non-independence of the extinction probabilities of species within each class. Furthermore, in case the explanatory power of a trait was contingent on the inclusion or exclusion of other traits in the model, we used a hierarchical partitioning approach to run all possible single and multiple traits as additive extinction predictors and to partition the proportional independent effects of each trait using the R package hier.part<sup>85</sup>. Finally, we modelled extinction probability as a function of thermoregulation (the most explanatory trait) and elucidated differences among categories using Tukey tests.

**Code availability.** The code used to infer the origination, extinction and preservation rates is available at <https://github.com/dsilvestro/PyRate>.

**Data availability.** The authors declare that all data supporting the findings of this study are available within the paper and its Supplementary Information files.

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## Author contributions

C.P., J.N.G. and C.J. designed the research, C.P., J.N.G. and M.D.U. performed the research, C.P., J.N.G., C.F.C., D.S., S.V. and M.D.U. analysed the data, C.P. and J.N.G. wrote the paper, and C.F.C., S.V., D.S., M.D.U. and C.J. improved the final manuscript.

## Competing interests

The authors declare no competing financial interests.

## Additional information

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