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1 **The Pliocene marine megafauna extinction and its impact on functional diversity**

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

37 In the Anthropocene, rapid environmental change and resultant loss of habitat pose a major
38 threat to marine fauna¹⁻². Throughout geological time, habitat loss caused by sea level changes
39 has been widely associated with extinction events³. After the last mass extinction at the
40 Cretaceous-Paleogene (K-Pg) boundary and throughout the last 66 million years, the largest
41 global sea level changes occurred mainly during the Pliocene and Pleistocene Epochs (herein, the
42 Plio-Pleistocene; from 5.33 to 0.01 Ma), with multiple large eustatic oscillations that were
43 amplified after the onset of the Northern Hemisphere Glaciation in the late Pliocene⁴⁻⁷.

44 Although global cooling and sea level fluctuations in the Plio-Pleistocene have been proposed to
45 be responsible for the regional extinction of marine invertebrates⁸, it has been assumed that
46 global marine biodiversity was generally resistant to these environmental changes^{3,9}. Individual
47 examples of faunal turnover and extinctions of large marine vertebrates (collectively known as
48 ‘marine megafauna’, which includes, but is not limited to marine mammals, seabirds, turtles,
49 sharks and rays¹⁰⁻¹¹) have been observed around this period. These include a substantial drop in
50 cetacean¹²⁻¹⁴ (but see¹⁵) and penguin diversity¹⁶⁻¹⁷, the extinction of dugongids in the Western
51 Atlantic and Mediterranean regions¹⁸⁻²⁰, the loss of the largest shark that ever lived
52 (*Carcharocles megalodon*)²¹⁻²², as well as extinctions of sea turtles (e.g. *Psephophorus*, a
53 leatherback turtle)²³. But it remains unclear whether these megafauna losses were simply
54 conspicuous background extinctions, or formed part of a global marine extinction event resulting
55 from the environmental changes of the Plio-Pleistocene^{8,24}. Evaluating the extent and
56 consequences of the marine megafauna extinctions is relevant because these organisms play
57 fundamental roles in ecosystems²⁵⁻²⁷ and because modern megafaunal assemblages were
58 established during the Pleistocene (e.g. ²⁸; Supplementary Fig. 1).

59 Historically, studies of marine extinctions have focused almost exclusively on taxonomic loss
60 (e.g. species, genera, family; but see²⁹). While this taxonomic perspective quantifies the loss of
61 diversity *sensu stricto* (e.g.³⁰), it ignores the ecological contributions of these species to
62 ecosystems. Linking taxonomic identity with ecological roles can be used to assess the
63 selectivity of extinctions^{24,31-35}, evaluate shifts in the structure of communities after an extinction
64 event³², and gauge the potential implications for ecosystem functioning³⁶. This ‘functional
65 diversity’ approach (reviewed by³²) consists of quantifying the distribution of species in a
66 multidimensional functional space defined by species’ traits (i.e. species’ intrinsic characteristics
67 that directly influence their ecological role³²). The few studies that have used this or similar
68 approaches have focused specifically on the ecological consequences of the extinction of
69 invertebrates^{24,33-35} (but see³⁷). These organisms have important ecological roles, but are usually
70 small-sized, occupy low trophic levels, and tend to be highly speciose. Conversely, marine
71 vertebrates include the largest organisms on Earth, occupy a variety of trophic roles, are
72 relatively species-poor, and are accordingly less likely to be ecologically redundant³⁸. Moreover,
73 they are often wide-ranging, and are known to structure modern food webs from the top down²⁵.
74 The goal of linking extinctions of large animals with consequences for ecosystem functioning is
75 particularly relevant today, as large-bodied marine species are the most vulnerable to current
76 human impacts².

77 Here we evaluate the severity of the extinction of marine megafauna during the Pliocene, and
78 examine the potential causes and consequences of this event. To do so, we first assess if the
79 Pliocene extinction rates were higher than those of the rest of the Cenozoic, and examine the
80 proportional loss of genera from the Pliocene to the Pleistocene. Then we quantify the

81 differences in functional diversity between the Pliocene and Pleistocene coastal megafaunal
82 assemblages, to assess the potential effects of extinctions on ecosystem functioning. Finally, we
83 evaluate the possible drivers of extinction by estimating the habitat loss due to eustatic
84 variations, and by modelling traits as predictors of extinction. The results of this research provide
85 a broader understanding of the state and vulnerability of the marine megafauna in the recent
86 geological past, and forewarn of the likely sensitivity of megafaunal biodiversity as
87 anthropogenic climate change accelerates and brings massive perturbations to coastal
88 ecosystems³⁹⁻⁴¹.

89 **Results and Discussion**

90 **The extinction event.** We estimated the expected number of extinction events per genus/Myr
91 during the Cenozoic, while accounting for preservation biases and dating uncertainties using a
92 Bayesian framework⁴² (Supplementary Tables 1-3; Supplementary Fig. 2). Marine megafauna
93 present significantly elevated extinction rates in the Pliocene (Fig 1a), with a 3-fold increase
94 relative to the rest of the Cenozoic, and with the highest rates occurring in the late Pliocene,
95 specifically between 3.8 and 2.4 Ma (Supplementary Fig. 3). Per-clade analyses reveal that all
96 groups of marine megafauna follow this trend, except that sea birds present higher extinction
97 rates in the Paleocene (Supplementary Fig. 4). Conversely, we did not find evidence of changes
98 in origination rates during the entire Cenozoic (Supplementary Fig. 3). Until now,
99 disappearances of Pliocene marine megafauna species were thought to represent isolated
100 examples within a broader assemblage that remained largely intact (e.g.³, but see⁴³). Our results

101 show that these extinctions, which peaked in the late Pliocene, are part of a hitherto
102 unrecognized global loss of marine megafaunal biodiversity.

103 Closer examination of the Pliocene megafauna fossil record reveals the proportional losses of
104 genera (see Supplementary Table 4 for numbers of genera and samples). We found that 36% of
105 Pliocene genera were extirpated (i.e. not present in the Pleistocene). In line with previous
106 studies^{3,44}, marine mammals present the highest proportional extinction, losing 55% of their
107 generic diversity (e.g., the aquatic sloth *Thalassocnus*, the beluga-like odontocete *Bohaskaia*).
108 Seabirds lost 35% of their generic diversity (e.g. the penguin *Inguza*), sea turtles 43% (e.g.
109 *Syllomus* and *Psephophorus*), and sharks 9% (e.g. *Carcharocles*) (Fig. 1b; Supplementary Table
110 4). New genera also evolved: 25% of the Pleistocene genera were new (not reported in the
111 Pliocene), including 38% of mammals (e.g. the polar bear *Ursus*) and 41% of the seabirds (e.g.,
112 the storm petrel *Oceanodroma* and the penguin *Megadyptes*) (Supplementary Table 4).

113 Nevertheless, in line with the elevated extinction relative to origination rates, generic diversity of
114 global megafauna suffered a net decline of 15% between the Pliocene and Pleistocene.

115 Furthermore, we found that most of the Plio-Pleistocene marine megafauna (86%;
116 Supplementary Table 4) were associated with coastal habitats (i.e. the neritic zone, <200 m of
117 depth), where the absolute loss of genera was greater (Fig. 1b; Supplementary Dataset 1).

118 However, since this finding could be biased by differential fossil preservation and/or sampling, it
119 should be interpreted with caution.

120 **Impacts on functional diversity.** To assess the potential effects of the Pliocene extinction on
121 ecosystem functioning, we performed trait-based analyses following the methods described in

122 Mouillot *et al.*³² for genera associated with coastal environments. Accordingly, we assigned traits
123 to the Plio-Pleistocene coastal megafauna (184 genera, Supplementary Table 4) to (i) determine
124 the Functional Entities (i.e. groups with unique trait combinations, herein FEs) and (ii) construct
125 a functional space³². The coastal megafauna dataset includes 146 Pliocene genera from 711
126 occurrences, and 129 Pleistocene genera from 858 occurrences (Supplementary Table 4).

127 We found that 55 (38%) coastal Pliocene genera went extinct (Fig. 2c), resulting in the loss of 7
128 (14%) FEs (Fig. 2a) along with 17% of functional richness (Fig. 2e; the volume of functional
129 space; after accounting for sample size differences [Supplementary Fig. 5; also see Methods]).
130 The post-extinction Pleistocene assemblage hosted 38 new genera (29%) reducing the net
131 taxonomic loss of coastal habitats to 12% (Fig. 2d). The evolution of these new genera resulted
132 in the addition of 4 FEs (9%; Fig. 2b) and net loss of 3 FEs. But these new FEs, which were
133 exclusively occupied by mammals, minimally compensated for the functional richness lost (by
134 1%), leaving a net functional richness loss of 16%. Further, the loss and gain of Plio-Pleistocene
135 FEs drove a functional shift (non-overlap of functional volume³²) of 21% (Fig. 2f).

136 We next investigated the interaction between extinction and the functional structure of the
137 megafauna assemblage. The functional structure of the Pliocene assemblage ultimately rendered
138 it sensitive in the face of taxonomic extinctions: although it had an average of 3 genera per FE
139 (functional redundancy *sensu*⁴⁵), they were concentrated within specific FEs (over-
140 redundancy⁴⁵), leaving over half with only a single genus (functional vulnerability⁴⁵)
141 (Supplementary Fig. 6; Supplementary Table 6). All lost and gained FEs (except one) contained
142 a single genus (Fig. 2a-b, see legend), suggesting that low-redundancy FEs largely drove the

143 changes in functional space. The net losses of functional richness and the functional shift were
144 greater than expected given the mean background extinction rate over the Cenozoic (22 genera,
145 see Methods) and the new Pleistocene FEs (Supplementary Figs. 7a-b.). However, these
146 functional changes were no different than would be expected given the 55 genera lost
147 (Supplementary Figs. 7c-d) and the functional structure of the assemblage, indicating that the
148 loss of genera *per se* from the functionally vulnerable Pliocene assemblage, rather than the
149 observed pattern of genera loss, determined the functional changes. Ultimately, the Pleistocene
150 assemblage was left with a greater proportion of single genus FEs (80%), i.e., a greater
151 functional vulnerability, than the pre-extinction Pliocene assemblage (59%) (Supplementary
152 Table 6). In light of the growing literature linking functional diversity to ecosystem
153 functioning⁴⁶⁻⁴⁹, it follows that the contributions of megafauna to marine ecosystems may have
154 been diminished (loss of functional richness), altered (functional shift), and rendered less
155 resistant to subsequent extinctions (increased functional vulnerability) after the Pliocene
156 extinction event.

157 A common finding among the handful of previous studies that have used a multi-trait-based
158 approach in this context is that losses in global functional diversity are negligible after an
159 extinction event, even in the face of *mass* extinctions, when >70% of genera were lost³³⁻³⁵. Our
160 detection of a larger, though still modest (16-21%), functional diversity change, despite lower
161 taxonomic loss (38%), is probably because most previous studies have focused on benthic,
162 smaller-bodied, more speciose invertebrate assemblages, while ours focuses on large vertebrates.
163 Ecosystems hold fewer large than small species⁵⁰, thus among large-bodied species there is likely
164 to be less scope for functional insurance provided by redundant species, making functional

165 diversity among large animals more sensitive in the face of extinction⁵¹⁻⁵². This conclusion is
166 supported by the high levels of functional vulnerability among Plio-Pleistocene coastal
167 megafauna (Supplementary Table 6), the singular roles megafaunal taxa are thought to play in
168 modern systems²⁶, and the accumulating evidence of ecosystem consequences induced by their
169 declines²⁵.

170 **Extinction mechanisms.** It has been widely stated in the literature that the onset of the Northern
171 Hemisphere Glaciation at the end of the Pliocene resulted in an abrupt transition to a new
172 climatic state dominated by colder and more variable temperatures, and large sea level
173 oscillations^{4-7,12}. But to our knowledge there are no quantitative and global assessments of
174 consequent changes in the extent of coastal habitats during this time (but see⁵³ for specific
175 regions). We therefore reconstructed the global extent of neritic (i.e. <200m depth) areas based
176 on eustatic variations⁴⁻⁵ during the Plio-Pleistocene, and found that as sea level regressed, neritic
177 areas dropped precipitously during the late Pliocene. This abrupt change coincides in time with
178 the highest extinction rates found (Supplementary Fig. 3). After this sudden drop in coastal
179 habitat availability, large area oscillations took place: there was a 250% increase in coefficient of
180 variation from the Pliocene (0.07) to the Pleistocene (0.17). Additionally, the total neritic area
181 available was significantly reduced: from 79.1 million km² in the Pliocene to 57.9 million km² in
182 the Pleistocene, representing a 27% reduction in the mean area (t-test: $p < 0.001$; Fig. 3;
183 Supplementary Fig. 8).

184 Numerous studies have identified a regional invertebrate extinction during the Plio-Pleistocene
185 and attributed this to climatic changes (mainly temperature)^{8,54-56}, but only a single region-

186 specific study has implicated habitat loss associated with sea level changes in extinctions⁵⁷. Here,
187 we document a global-scale reduction of coastal habitat availability that abruptly started in the
188 late Pliocene, and hypothesize that this, probably acting alongside oceanographic alterations such
189 as changes in productivity and ocean circulation (e.g. ^{24,58-61}) were extinction drivers of the
190 Pliocene marine megafauna. Some genera may have only succumbed to repeated sea level
191 oscillations or when habitat loss coincided with other extinction drivers (e.g. prey availability
192 and/or competition)⁶²⁻⁶³ which may explain the continuation of elevated extinction rates in the
193 Pleistocene. Similar mechanisms might be responsible for the previously noted decline of some
194 megafaunal groups in the late Miocene^{16,43}, although such losses were not comparable in
195 magnitude to those Pliocene losses documented here (Fig. 1a).

196 To assess extinction selectivity, we modelled traits as predictors of survivorship using
197 generalized linear models (GLMs). Thermoregulation is the trait that best predicts extinctions in
198 the Pliocene (Fig. 4a), with endotherms and mesotherms (homeotherms; those able to regulate, at
199 least to some degree, their internal temperatures⁶⁴⁻⁶⁵) having significantly higher chances of
200 going extinct than their poikilothermic counterparts (Fig. 4b; Supplementary Tables 7-8). Large
201 body size, a trait associated with extinction risk in the Anthropocene^{3,66}, does not predict
202 extinction risk, nor affect the explanatory power of thermoregulation. Although we found a
203 taxonomic signal in extinction probabilities, with mammals and sharks presenting significant
204 differences (grey part of Supplementary Tables 7-8), the signal of thermoregulation was
205 independent and held when Class was controlled as a fixed or random factor in the GLMs
206 (Supplementary Table 9). Notably, homeotherms that became extinct were not exclusively

207 endothermic mammals or seabirds: three of five mesotherms (two shark genera and a turtle
208 genus) were also lost.

209 Unlike poikilotherms, homeotherms are buffered against external temperature changes, but
210 require greater resources to sustain higher metabolic demands^{64-65,67-68}. Homeotherms should
211 therefore show greater extinction susceptibility in the face of declining habitat and associated
212 resource availability⁶⁹, as our results indeed show. In contrast, if temperature fluctuations or
213 overall cooling had directly driven this extinction, the opposite result would have been expected
214 (i.e. greater susceptibility of poikilotherms compared to homeotherms). Feeding plasticity, as
215 grey whales seem to have exhibited during the late Pleistocene, and possibly even across the
216 Pliocene/Pleistocene boundary⁷⁰, may have aided the survival of some homeothermic genera in
217 the face of habitat loss. Overall, the greater susceptibility of energy-demanding homeotherms
218 supports our hypothesis that the abrupt reduction of neritic areas was a key driver of the marine
219 megafauna extinction. Whether thermoregulation covaries with other traits (e.g. those associated
220 with extinction risk)⁷¹, and the effects of such correlation in determining the selectivity of the
221 Pliocene marine megafauna extinction, are beyond the scope of this study but should be further
222 explored.

223 **Conclusions**

224 Here we report an extinction and consequent erosion of functional diversity of marine megafauna
225 during the Pliocene. We hypothesize that these extinctions were driven by habitat loss produced
226 by sea level oscillations, probably acting alongside other oceanographic alterations such as
227 changes in productivity and ocean circulation, in addition to biotic drivers such as prey

228 availability and/or competition. Since the modern marine megafauna became established in the
229 Pleistocene (Supplementary Fig. 1), this event shaped Earth's present-day assemblages of these
230 large ecosystem-structuring organisms (e.g. ^{25,27,32,72}). The discovery of this extinction event
231 reveals that the biodiversity and functional contributions of marine megafauna were more
232 sensitive to environmental changes in the recent geological past than hitherto assumed. Today,
233 and historically, over-exploitation has been considered the chief threat to marine megafauna²⁷.
234 Our study cautions that as anthropogenic climate change accelerates and triggers regime shifts in
235 coastal ecosystems³⁹⁻⁴¹ the potential consequences for marine megafauna should not be
236 underestimated.

237 **Methods**

238 **Cenozoic dataset.** We downloaded all the records of marine megafauna for the Cenozoic, (i.e.
239 last 66 Ma) from the Paleobiology Database (PBDB, <https://paleobiodb.org>, last search date:
240 November 2016). The PBDB follows the most recent geological timescale of Gradstein *et al.*⁷³.
241 In the absence of a formal, size-based definition of “marine megafauna” we included all the
242 genera of the groups of animals that contain the largest marine vertebrates (i.e. marine mammals,
243 seabirds, sea turtles, and sharks and rays¹⁰). We focused on the genus level because generic
244 assignments have a greater consistency across different research groups, and because it is more
245 robust to taxonomic error than the species level. All taxonomic identifications were evaluated
246 and corrected. Dubious and equivocal records were excluded from our analyses. Accordingly, we
247 used 11,241 occurrences (Supplementary Table 1). Details on the search criteria and data

248 assessment can be found in the Supplementary Information. Further, all references supporting the
249 occurrences can be found in the Supplementary Dataset 2.

250 **Extinction rates.** We estimated extinction and origination rates of marine megafauna for the
251 entire Cenozoic using PyRate⁷⁴. This program implements Bayesian algorithms to analyze all
252 available fossil occurrences (identified to genus level, in this case) while accounting for
253 preservation biases and dating uncertainties. Accordingly, three main sets of parameters were
254 simultaneously estimated: 1) the preservation rates quantifying the expected number of fossil
255 occurrences per sampled lineage per time unit (1 Myr); 2) the origination and extinction times
256 for each genus, which likely extend beyond the observed temporal range between first and last
257 appearances; and 3) the origination and extinction rates (expected number of
258 origination/extinction events per lineage/Myr) and their temporal variation⁴². We estimated
259 origination and extinction times assuming a time-variable Poisson preservation model, and used
260 them to infer origination and extinction rates within Epochs using a time-variable birth-death
261 model where the rates are estimated as independent parameters in each predefined time frame
262 (Supplementary Tables 1-3). To reduce the risk of over-parameterization we used half-Cauchy
263 priors on the origination and extinction rates with scale parameters estimated from the data using
264 hyper-priors⁷⁵. We ran 2,000,000 Markov Chain Monte Carlo (MCMC) iterations under this
265 model and summarized the posterior extinction rates in boxplots for each Epoch, except for the
266 Holocene, as the temporal and taxonomic resolution of our data was insufficient to reliably
267 estimate extinction in such a short time frame. We considered extinction rates as significantly
268 different between subsequent epochs when 0 fell outside the 95% credible interval of their
269 difference, based on all posterior samples. We ran these analyses on the full data set of all

270 megafauna groups first, and then repeated them for each group, namely marine mammals, sea
271 birds, sea turtles and sharks and rays. We ran additional analyses to assess more precisely the
272 timing of origination and extinction rate changes, using birth-death models in which the times of
273 shift are not fixed, but estimated as time-continuous parameters⁴². We tested models with
274 different number of rate shifts and combined the results from each model using Bayesian Model
275 Averaging (BMA), i.e., after resampling their posterior samples proportionally to the respective
276 relative probabilities⁷⁶. We then summarized the marginal extinction rates through time within
277 0.1 Myr time bins as mean and 95% credible intervals. More details can be found in the
278 Supplementary Methods.

279 **Plio-Pleistocene dataset.** We selected all marine megafauna genera occurring in the Pliocene
280 (5.3-2.6 Ma) and Pleistocene (2.6-0.01)⁷⁷. In total, we gathered 1,763 global occurrences. Most
281 of the data were not dated to the Stage level. Accordingly, we used geologic Epochs as our
282 interval unit, e.g., whenever a genus was reported in the Pliocene, the Zanclean, or the
283 Piacenzian, it was assigned to the Pliocene. Because the Plio-Pleistocene is our interval of
284 interest, we performed a second evaluation process for this subset of data in which the taxonomic
285 assignments and age of each record was assessed following a procedure described previously²²
286 (Supplementary Methods). We followed the most recent age for the Pliocene-Pleistocene
287 boundary, at 2.58 Ma⁷⁷. Accordingly, all Gelasian records were treated as Pleistocene
288 occurrences. More details can be found in the Supplementary Methods. It is worth noting that
289 even though it has been proposed that marine vertebrates from the Pleistocene are poorly known
290 (e.g.¹⁵), we were able to gather 906 occurrences from the Pleistocene, which is comparable with
291 the 857 records gathered from the Pliocene.

292 **Proportional extinction.** In total, we compiled data for 215 Plio-Pleistocene genera. Of these,
293 177 occurred in the Pliocene and 151 in the Pleistocene (Supplementary Table 4). Sixty-one
294 genera occurred only in the Pliocene and 37 only in the Pleistocene. Based on these numbers, we
295 calculated the proportion (%) of genera extirpated from the Pliocene, and originated in the
296 Pleistocene. We did this for all megafauna, and for each individual group. Finally, we calculated
297 the net loss of genera (%) as the % of Pliocene genera that were lost passing into the Pleistocene.

298 **Functional traits and Functional Taxonomic Units (FTUs).** We used five ordered categorical
299 functional traits to assign to the Pliocene and Pleistocene marine megafauna: Guild (most
300 frequent diet in adults); body size (maximum total length); vertical position (most frequent
301 vertical position where they feed); habitat (typical zone where they occur); and thermoregulation
302 capability (endotherms, mesotherms or poikilotherms). Traits are inferred properties of
303 individual organisms known to directly influence their ecological role^{32,45}. More details on how
304 traits were coded can be found in the Supplementary Methods. Our Plio-Pleistocene occurrences
305 dataset had a generic taxonomic resolution (see above), which facilitated the assignment of traits
306 given that most genera have modern analogues on which we could base our assessments. Traits
307 were assigned using authoritative taxon-specific texts, online databases, and expert assessments
308 based on both extant relatives and the fossil record (references provided in Supplementary
309 Methods). Whenever we found a genus consisting of multiple known species with different trait
310 values, we treated them independently to assign traits (see specific cases in Supplementary
311 Methods). As a result, our traits were assigned mostly (95%) to genera, and sub-divisions of
312 certain genera according to shared traits. These ‘Functional Taxonomic Units’ (FTUs) are in our
313 opinion, the lowest taxonomic resolution to systematically assign functional traits to fossil

314 marine vertebrates. Given that FTUs correspond to genera in 95% of cases, we still refer to them
315 as “genera” in the main text and figures for consistency and simplicity. Traits were assigned to
316 each occurrence of each FTU. Whenever there was not enough information to assign traits, we
317 disregarded such an occurrence in our analyses (see specific cases in Supplementary Methods,
318 which represent ~12% of the total number of occurrences gathered from the PBDB).

319 **Functional Entities (FEs), redundancy, over-redundancy and vulnerability.** For our trait-
320 based analyses we focused on genera that are associated with coastal habitats (i.e. strictly coastal,
321 coastal-terrestrial, coastal-oceanic). These genera represent 86% of the megafauna
322 (Supplementary Table 4) and had 1,569 global occurrences in our dataset. Based on the trait
323 assignments, we calculated the number of possible unique trait combinations, or Functional
324 Entities (FEs)^{32,45}. Pliocene and Pleistocene marine megafauna fill the 8% of the total number of
325 FEs (i.e. 53 out of 648 FEs). Genera were assigned to FEs independent of taxonomy. Based on
326 the number of FEs and their corresponding genera, we then calculated the functional redundancy
327 (FR: genera per FE), over-redundancy (FOR: overrepresentation of some FEs) and vulnerably
328 (FV: potential decrease of functional diversity following species loss) as follows: FR = mean
329 genera:FEs; FOV = % genera that fill FEs above the mean level of FR; and FV = % genera with
330 one genus⁴⁵.

331 **Functional space.** We used the methods of Mouillot *et al*³² to create the functional space based
332 on the FEs calculated above. We used the R package FD⁷⁸ to create the distance matrix (using
333 the function “gowdis”), and to retrieve axes of the principal coordinate analysis (PCoA; using the
334 function “dbFD”). Using the “quality_funct_space” R function⁷⁹ we determined that our data is

335 best represented using four dimensions, or PCoA axes (Supplementary Fig. 9). We then used the
336 “FDChange” function to calculate the functional richness (FRic, % of the total volume occupied
337 in the functional space) and shift (non-overlap of functional volume)³². Given the
338 multidimensional nature of the functional diversity analyses, the four axes used to represent the
339 functional space of Plio-Pleistocene marine megafauna are correlated with multiple trait
340 combinations (Supplementary Fig. 10) and therefore, it is not possible to associate portions of the
341 functional space to single traits, nor to pinpoint changing segments of the space.

342 **Resampling simulations.** We tested the effects of sample size in the calculation of functional
343 diversity indices by randomly resampling each community (Pliocene and Pleistocene) without
344 replacement, bootstrapping the data 1,000 times over 20 evenly spaced bins from 10 to 711 (711
345 = the lowest sample size for coastal habitats, which is found in the Pliocene) using the R function
346 “sample”. Indeed, we found variation in functional indices due to sample size. We standardized
347 the Pleistocene communities to 711 occurrences and recalculated the functional diversity indices
348 based on this resampled community running 1,000 permutations (with replacement)⁸⁰. Finally,
349 we tested for significant differences between the Pliocene and the Pleistocene using a Wilcox
350 test.

351 **Comparative simulations.** We investigated whether the changes in functional diversity during
352 the Pliocene were significantly higher than those expected under background extinction rates
353 among genera associated with coastal habitats. To do so, we calculated the mean extinction rate
354 for the Cenozoic (except for the Pliocene) as described in the Extinction Rates section above.

355 Then we estimated the number of genera that would have been lost under background rates using
356 Foote's boundary crossing method⁸¹ as in Equation 1:

357
$$ER = -\ln(N_{bt} / [N_{bt} + N_b]) / \Delta t$$

358 where N_{bt} is the genera that crossed the bottom and the top of the interval (i.e. sampled in both
359 the Pliocene and the Pleistocene); N_b is the genera that only crossed the bottom of the interval
360 (i.e. sampled only in the Pliocene); and Δt is the length of the interval in million of years (i.e.
361 2.75 myr following the timescale Gradstein *et al.*)⁷³. We then solved for N_b in Equation 1,
362 replacing the extinction rate (ER) with 0.05 (= mean extinction rate during the Cenozoic). Based
363 on this, 22 genera would have been lost in the Pliocene under mean background conditions
364 (whereas 55 were actually lost in coastal habitats). Accordingly, running 1,000 permutations, we
365 simulated a Pleistocene subset in our Plio-Pleistocene dataset by randomly removing 22 Pliocene
366 genera, and calculating the delta (Pliocene FRIC – Pleistocene FRIC), and the functional shift (see
367 Functional Space section of the Methods). We then compared the observed delta and shift with
368 the distributions of these metrics under background conditions. Additionally, we investigated if
369 the loss of functional diversity was greater than expected given the number of taxa lost. This was
370 achieved by randomly removing 55 (i.e. the number of coastal genera lost) Pliocene genera and
371 calculating the delta and shift. We tested the significance of these comparisons by running 1,000
372 permutations. Although the above simulations did not account for the modest sample size
373 differences between the Pliocene and Pleistocene, the post-extinction (Pleistocene) assemblage
374 had more samples and thus the tests are conservative.

375 **Environmental reconstructions.** We calculated the global extent of the neritic areas available
376 during the Pliocene and Pleistocene, given the sea level changes of these time periods. We
377 regarded as neritic area the section of the ocean with a water depth of a maximum of 200 meters.
378 To estimate the global extent of these areas, we used the current land topography and ocean
379 bathymetry model Etopo 1 Global Relief Model⁸². We selected the ocean cells within the neritic
380 zone and quantified their area using the function “area” from the R package raster⁸³, which takes
381 into account the latitudinal decrease of the projected map cells as a consequence of the globe
382 curvature. In order to calculate changes in the global extent of the neritic areas across time, we
383 used two independent measures of the sea level change during the last 5.3 myrs^{4,5} applying a
384 temporal resolution of 100,000 years; the choice of measure had no bearing on the qualitative
385 patterns of sea level change. The model based on deBoer *et al.*⁵ is presented in the main text.
386 Global sea level changes were calculated using oxygen isotopes variation⁴ and an ice-sheet
387 model forced by benthic delta $\delta^{18}O$ ⁵. Based on these data, we assessed the temporal changes in
388 the global extent of neritic areas available, and in temperature, in the Pliocene (N = 27) vs.
389 Pleistocene (N = 26), calculated the coefficient of variation for each Epoch, and tested for
390 significant differences in mean values using a t-test. Both time bins (Pliocene and Pleistocene)
391 have similar temporal extents (2.7 and 2.6 myrs respectively), allowing direct comparisons.

392 **Generalized linear models.** We evaluated the effects of traits on extinction probabilities by
393 modelling survivorship (i.e. status: extinct or not extinct) in response to genus traits. We initially
394 used a Generalized Linear Model (GLM) with binomial error and a logit link to simultaneously
395 assess the effects of all traits (i.e. $\text{glm}(\text{status} \sim \text{trait1} + \text{trait2} \dots)$). Further, we used a metric of
396 pseudo R^2 ($1 - (\text{residual deviance} / \text{null deviance})$) to assess its explanatory power. This model

397 was then re-run, first by adding taxonomic identity (i.e. Class: Mammalia, Aves, etc.) as a fixed
398 effect (i.e. `glm (status ~ trait1 + trait2... + Class)`) to account for its influence on extinction
399 probabilities; and second, by adding Class as a random effect using a Generalized Linear Mixed
400 Model (GLMM) in the R package `lme4`⁸⁴ (i.e. `glmer (status ~ trait1 + trait2... (1|Class))`) to
401 control for the potential non-independence of species' extinction probabilities within each Class.
402 Furthermore, in case the explanatory power of a trait was contingent on the inclusion/exclusion
403 of other traits in the model, we used a hierarchical partitioning approach to run all possible single
404 and multiple traits as additive extinction predictors and partition the proportional independent
405 effects of each trait using the R package `hier.part`⁸⁵. Finally, we modelled extinction probability
406 as a function of thermoregulation (the most explanatory trait) and elucidated differences among
407 categories using Tukey tests.

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610 D.S., M.U. and C.J. improved final manuscript; C.P. and J.N.G. wrote the paper.

611 **Additional Information**

612 **Supplementary information** is available for this paper.

613 **Code** utilized to infer origination, extinction, and preservation rates is available here:

614 <https://github.com/dsilvestro/PyRate>.

615 **Figure Legends**

616 **Figure 1 | Elevated extinction rates of marine megafauna in the late Pliocene. a,** Extinction
617 rates (grey) within Epochs. The extinction rates in the Pliocene are significantly higher than in
618 any other Epoch in the Cenozoic: they are 2.2 times higher than in the Miocene, 60% higher than
619 in the Pleistocene and three times higher than the average Cenozoic rate (N = 11,241 global
620 occurrences). **b,** Proportional extinction of the Pliocene megafauna (blue). Dark blue bars denote
621 species associated with coastal environments (i.e. strictly coastal, coastal-terrestrial, coastal-
622 oceanic), which represent 86% of the megafauna. Light blue bars denote strictly oceanic species,
623 which represent the remaining 14% of the megafauna.

624 **Figure 2 | Changes in coastal marine megafauna functional diversity from the Pliocene**
625 **(pre-extinction) to the Pleistocene (post-extinction). a-b,** Functional space plotted using the
626 first four axes (A1-A4) and the empirical data (i.e. not accounting for differences in sample size).
627 Pliocene = 49 Functional Entities (FEs); Pleistocene = 46 FEs. Filled dots denote FEs that

628 changed (i.e. that were either extirpated or originated) whereas open dots denote unchanged FEs
629 (i.e. winners). Note that, since multiple genera can occupy a single FE, the loss or gain of genera
630 does not necessarily result in the lost or gain of a FE. FE codes can be found in Supplementary
631 Table 5. Refer to the methods (Functional Traits and FTUs) for details on the differences
632 between taxonomic levels. **a**, Pliocene space showing FEs that went extinct and their taxonomic
633 affiliations. Dark blue = FE 25, one genus (*Carcharocles*, Lamniformes); light blue = FE 36, one
634 genus (*Paratodus*, Lamniformes; red = FE 27, two genera (*Cetotherium* and *Nannocetus*,
635 Mysticeti); green = FE 49, one species (*Herpetocetus morrow*, Mysticeti); light grey = FE 50,
636 one genus (*Nanosiren*, Sirenia); yellow = FE 52 one genus (*Thalassocnus*, Xenarthra); dark grey
637 = FE 46, one genus (*Psephophorus*, Testudines). **b**, Pleistocene space showing the new FEs and
638 their taxonomic affiliations. Pink = FE 47, one genus (*Mirounga*, Pinnipedia); green = FE 13 one
639 species (*Orcinus orca*, Odontoceti); blue = FE 31, one genus (*Proterozetes*, Pinnipedia); red =
640 FE 3, one genus (*Ursus*, Carnivora). **c-d**. Taxonomic Richness (# genera) loss after the extinction
641 event. **c**, Raw genus loss (not including the new genera that originated in the Pleistocene). **d**, Net
642 genus loss (including the new genera that originated in the Pleistocene). **e-f**, Functional Richness
643 (functional space volume, FRic³²) loss and shift. Vertical lines are error bars resulting from the
644 1,000 permutations of the resampled data (see Methods). **e**, Raw FRic. **f**, Net FRic.

645 **Figure 3 | Reduction of neritic areas as a putative extinction driver.** Global extent of neritic
646 areas based on eustatic levels reported in deBoer *et al.*⁵. Horizontal lines represent mean values
647 for the Pliocene and Pleistocene.

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

Fig. 1

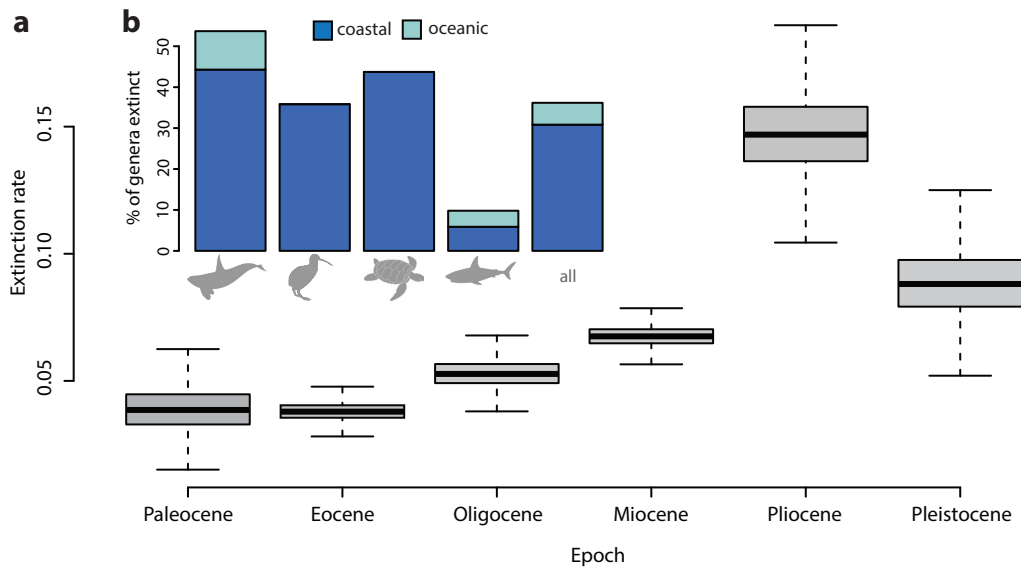


Fig. 4

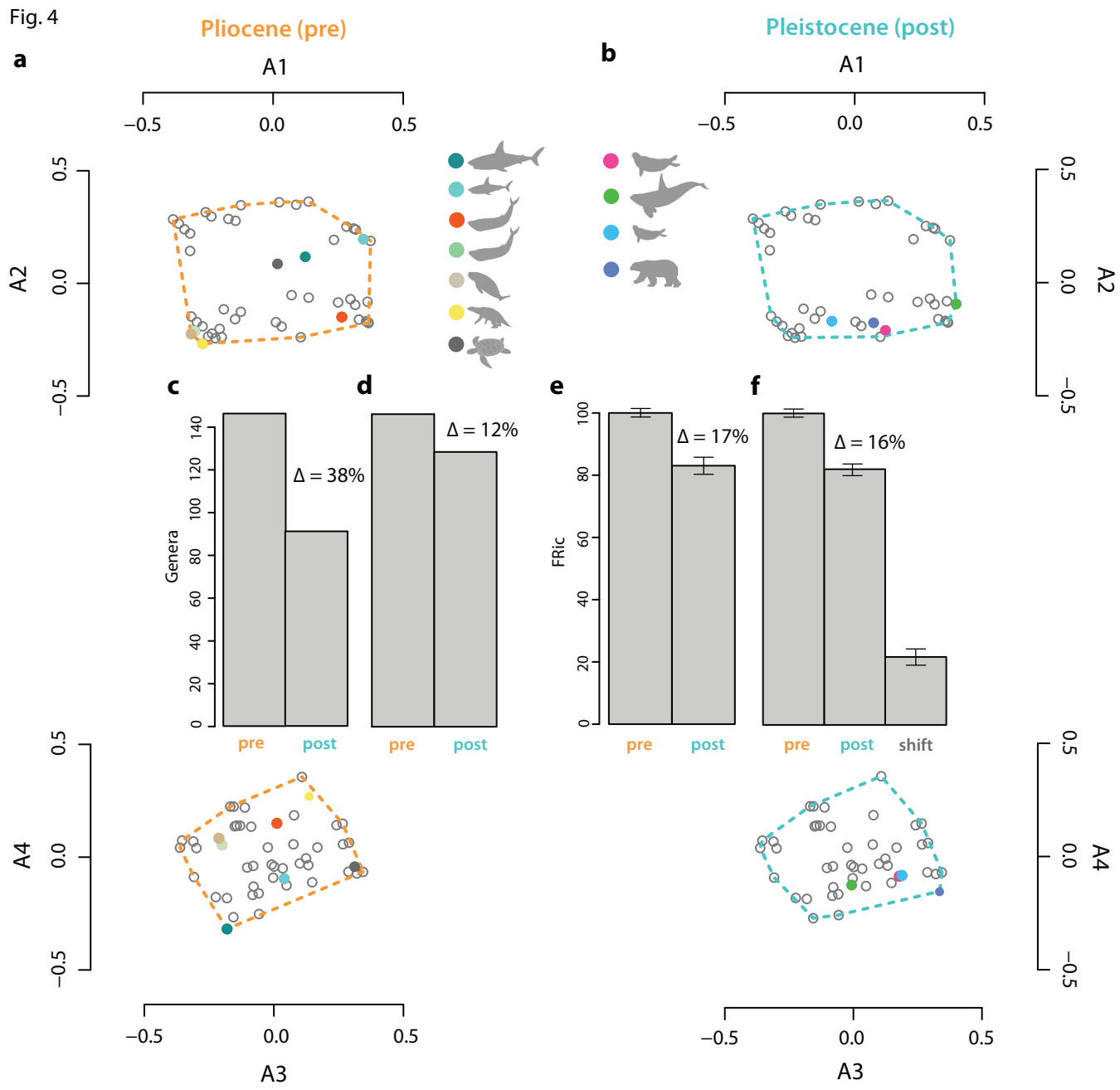


Fig. 3

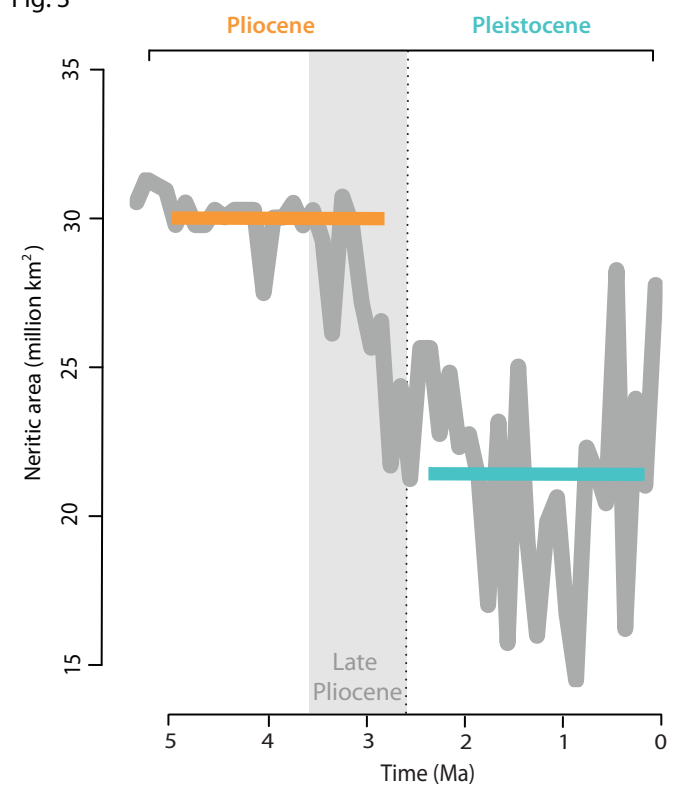


Fig. 4

