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The Pliocene marine megafauna extinction and its impact on functional diversity

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Supplementary Methods

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Supplementary Methods

Cenozoic Dataset. We gathered all marine megafauna data from the Paleobiology Database (PBDB, <https://paleobiodb.org>). In our query we searched for the occurrence list (output data format) at the generic level (taxonomic level) as follows. Mammals: Sirenia, Cetacea and Pinnipedimorpha, *Ursus maritimus*, *Enhydra*, *Enhydritherium*, *Thalassocnus*. Seabirds: Alcidae, Fregatidae, Haematopodidae, Laridae, Pelagornithidae, Pelecaniformes, Phaethontes, Phalacrocoracidae, Procellariiformes, Sphenisciformes, Stercorariidae, Sulidae and Mancallinae. Sea turtles: Cheloniidae, Pancheloniidae and Dermochelyidae. Sharks: Chondrichthyes. We did not lump the occurrences of the same genus from the same collection (as we aimed to detect within-genus trait variations) and we excluded taxa with equivocal generic identifications (e.g. *cff* and *aff*). The PBDB follows the most recent age for the Pliocene-Pleistocene boundary, at 2.58 Ma (see manuscript). Accordingly, all Gelasian records were treated as Pleistocene occurrences (PBDB collections 45485, 48093, 58868, 66819, 69541, 45488, 77632, 77634, 77637, 77640, 77746, 77747, 98241). All the references supporting each record used in this study are available in the Supplementary Dataset 2.

Extinction Rates. We estimated origination and extinction rates using the software PyRate¹, which implements Bayesian algorithms to analyze fossil occurrences, while accounting for preservation and sampling biases²⁻³ (Supplementary Tables 2-3; Supplementary Figure 11). To account for dating uncertainties when calculating extinction rates, we resampled the age of fossil occurrences uniformly between the respective minimum and the maximum ages, typically the boundaries of stratigraphic ranges. We produced 10 randomly resampled data sets, performed all the analyses outlined below on each, and combined the results¹. In the first set of analyses we estimated the preservation rates and times of origination and extinction using the default time-variable birth-death prior (Supplementary Tables 2-3). We assumed a time-variable Poisson preservation model, in which rates are estimated as independent parameters within each geological Epochs (from the Paleocene to the Holocene). We obtained posterior estimates of preservation rates and times of origination and extinction after running 20,000,000 Markov Chain Monte Carlo (MCMC) iterations, sampling the parameters every 5,000 iterations. We then used the estimated times of origination and extinction for subsequent analyses², more specifically aimed to assess the dynamics of origination and extinction rates in marine megafauna. When estimating origination and extinction rates within epochs, we set a half-Cauchy prior on the origination and extinction rates, centered in 0 and with scale parameter estimated from the data in the MCMC, to reduce the risk of overparameterization³.

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 are not fixed, but estimated as time-continuous parameters². We used thermodynamic integration^{1,4} to determine the number of rate shifts best explaining the data, in a comparison among 25 birth-death models with different number of shifts in origination and extinction (ranging from 0, i.e. constant rates, to 4; Supplementary Table 1). To reduce the parameter space, and because we were mostly interested in the more recent part of the Cenozoic, we only allowed rate shifts to occur after the Paleogene/Neogene boundary i.e., between 23.03 Ma and the Present. Thermodynamic integration is an algorithm that computes the marginal likelihood of a model as a measure of model fit in a Bayesian framework. Marginal likelihoods can be used to compute Bayes factors

(BF) and relative probabilities to rank models based on their support⁵. We ran 2,000,000 MCMC iterations under PyRate default settings for thermodynamic integration under all 25 birth-death models. We found the highest support for a model with constant origination rates in the Neogene and Quaternary and 3 rate shifts in extinction rates. The second-best model, which also assumed constant origination rates but had only two shifts in extinction rates, obtained a very similar support. The two models together accounted for a relative probability of 0.875 (0.511+0.364; Supplementary Table 3).

As stated above, fossil occurrences were not lumped by genus. Therefore, in some cases the PBDB returned multiple occurrences of the same genus from a single locality. We treated these occurrences the same way we treated occurrences from different localities. We justify this data treatment as follows: 1) multiple occurrences of the same genus are only returned where these occurrences represent different species (i.e. two occurrences of a given genus are equivalent to two species of this genus occurring in the same locality); therefore, they represent distinctive occurrences of a genus; 2) when estimating origination and extinction rates, PyRate models preservation as a stochastic process where the number of occurrences is a function of time (i.e. expected number of occurrences per lineage/Myr, as opposed to the number of occurrences per lineage per locality/Myr)³; and 3) removing multiple occurrences per genus/collection would result in discarding information, whereas PyRate was designed to analyze all observed occurrences³.

Nevertheless, we further assessed whether our results were sensitive to our data treatment by running the extinction rate analysis using a subsampled data set that included only single genus occurrence per locality. We found that extinction rates per epoch do not change with this data treatment, except for the Pliocene, where the estimated extinction rate is slightly higher using lumped occurrences (Supplementary Fig. 12). As expected, we found preservation rates to be slightly lower using the subsampled data (Supplementary Table 2, grey part; Supplementary Figure 11, all subsampled). Overall, the differences between analyses with lumped vs. not-lumped occurrences were small or negligible, indicating that our results are robust to different ways of compiling the data.

Plio-Pleistocene Dataset for Functional Diversity Analyses Purposes. To avoid mistakenly reporting taxa as extinct in the Plio-Pleistocene dataset, we added some records manually. This took place in three instances: 1) when there was an extant genus recorded in the Pliocene, but not in the Pleistocene, we added an artificial record with a Pleistocene age; 2) when there was a record from the Miocene and Pleistocene, but not from the Pliocene, we added an artificial record with a Pliocene age; and 3) when the dating included both the Pliocene and the Pleistocene (e.g. Blancan), we duplicated the records so that they had occurrences in both epochs. Furthermore, we fixed duplicated synonymic records.

After a systematic evaluation of all fossil occurrences in which we: 1) examined the references associated with each entry to assess specimen's morphology and age; 2) studied a number of supplementary references that further documented or refined the age; and 3) visited relevant museum collections where we analyzed specimen's morphology, labels, and explored the collection databases (details in reference 6); we found some erroneous entries. When possible, we corrected these directly in the PBDB. Nevertheless, we excluded the following records,

which did not meet our evaluation criteria, were dubious, or were not sufficient to assign functional traits:

1. All records from the Red Crag Formation, UK: known to have reworked fossil material⁶.
2. PBDB collections 51680, 52582, 57701, 67029, 88806: *Gryphoca*, species based on postcranial material, affinities uncertain, not possible to assess size.
3. PBDB collections 49404, 49895, 76977: *Heterocetus*, considered as *nomen dubium*⁷.
4. PBDB collection 47428: *Mesocetus*, considered as *nomen dubium*⁸.
5. PBDB collections 18535, 45474, 52582, 57701: *Phocanella*, taxon based on limb elements, affinities uncertain.
6. PBDB collections 52582, 57701, 67023: *Platyphoca*, taxon based on limb elements, affinities uncertain.
7. PBDB collections 47307: *Plesiocetopsis*, taxon is of uncertain affinities.

Whenever a genus had a species with different occurrences in the Pliocene and Pleistocene, they were treated independently. Accordingly, we made distinctions for the following genera:

1. *Orcinus*: *O. citonensis* from the Pliocene and *O. orca* from the Pleistocene.
2. *Herpetocetus*: *H. morrowi* from the Pliocene and Pleistocene and several taxa that occurred both in the Pliocene and Pleistocene.
3. *Balaenoptera*: *B. cortesii* from the Pliocene and several taxa that occurred both in the Pliocene and Pleistocene.

Trait Assignments. Traits were coded as follows. Guild (most frequent diet in adults): herbivores (feeding upon plants and/or algae), micropredators (suspension/filter feeders), mesopredators (feeding mainly upon fish and/or invertebrates) and macropredators (feeding mainly upon large vertebrates, e.g. mammals, birds, reptiles). Maximum body size (total length) reached: <1 m, 1-3 m, 3-6 m, 6-9 m, 9-12 m and >12m. Vertical position (most frequent vertical position where they feed): benthic, benthopelagic and pelagic. Habitat (typical zone where they occur): terrestrial/marine (marine animals that use terrestrial habitats), coastal (animals occurring in the neritic zone, <200 m of depth), coastal-oceanic (animals that occur both in coastal and oceanic habitats) and oceanic (animals exclusively occurring in oceanic zone, >200 m of depth). And finally, thermoregulation capability: Poikilotherms (internal temperature varies with environment: most fish and sea turtles), mesotherms (some ability to control internal temperature, also called regional endothermy: Laminid sharks and the leatherback turtle), and endotherms (animals able to maintain a constant body temperature: all placental mammals and seabirds). It is worth noting that we included organisms of <1m of length because they are part of the megafauna as defined based on taxonomic affiliation (see main text). In the absence of a size-based definition of what constitutes being part of the marine megafauna, we included all species within these groups in our analyses to avoid introducing an arbitrary size cut-off. However, we also ran the functional diversity analyses excluding animals of <1m and our results remained unchanged (i.e. we obtained the same number of Functional Entities (FEs) lost and gained after the extinction event studied here, and the same difference between FEs from the Pliocene vs. the Pleistocene).

We used the following references to assign functional traits:

1. Sharks and rays: References 9-23, Fishbase (<http://www.fishbase.org>) and the IUCN Red List of threatened species (<http://www.iucnredlist.org>).
2. Marine mammals: References 21, 24-39 and the IUCN Red List of threatened species (<http://www.iucnredlist.org>).
3. Sea turtles: References 21-22, 40-42.
4. Seabirds: Reference 43.

Whenever a genus had several species with different trait values, each record was treated independently to assign traits. This occurred for the following genera:

1. *Alopias*: We identified two Functional Taxonomic Units (FTUs, see main text, Methods section) reported in the literature, one with the traits of *A. vulpinus* and one with the traits of *A. superciliosus*.
2. *Carcharhinus*: We identified two FTUs, one with the traits of *C. perezi/plumbeus/limbatus* and one with the traits of *C. leucas/faciformis/obsucrus*.
3. *Carcharodon*: We identified two FTUs, one with the traits of the modern great white shark *C. carcharias* and one with the traits of the fossil great white shark (*Isurus hastalis* or *Cosmopolitodus*).
4. *Sphyrna*: We identified two FTUs, one larger *S. zygaena/mokarran* and one smaller *S. media/lweini*.
5. *Balaenoptera*: We identified two FTUs, one with the traits of *B. cortesi/iberate/davidsoni*) and one of *B. acutorostrata*.
6. *Orcinus*: We identified two FTUs, one with the traits of *O. citoniensis* and the other with the traits of the modern *O. orca*.
7. *Herpetocetus*: We identified two FTUs, one with the traits of *H. transatlanticus/bramblei*/sp., and one with those of *H. morrowi*.

Whenever the information to assign traits was not available, the fossil preservation of a published specimen was poor, or when a taxon known to have different functional units was not identified to the species level, we did not include it in our analyses. This occurred in the following instances:

1. PBDB# 87489: *Aprionodon* sp., lack of taxonomic information.
2. PBDB#20639, 46167, 50068, 51414, 52644, 59003, 73485, 77594, 96580, 96738, 100174, 136597, 151704, 151705, 151893, 154111, 154115, 159914, 161451, 161453, 161454, 161503: *Carcharhinus* sp., lack of taxonomic information.
3. PBDB# 96541, 96580: *Carcharodon arnoldi*, lack of information.
4. PBDB# 20639, 20645, 52218, 60940, 66819, 76844, 77479, 77596, 117470: *Carcharodon* sp. lack of taxonomic information.
5. PBDB#159914: *Carcharias* sp., lack of taxonomic information.
6. PBDB#136597: *Rhinobatos* sp., lack of taxonomic information.
7. PBDB# 50343, 66819, 96761, 117471, 136597: *Sphyrna* sp., lack of taxonomic information.
8. PBDB# 22221, 22222, 50068, 52582, 59003, 66819, 117471, 161453: *Squatina* sp., lack of taxonomic information.
9. PBDB#136597: *Taeniura* sp., lack of taxonomic information.
10. PBDB#56693: *Siphonocetus* sp. from France: specimen consists of a vertebra, therefore not enough information for body size estimations.

11. PBDB#51589: *Anoplassa* sp.: extinct species known from mandibles, body size could not be assessed.
12. PBDB#57058: *Arimidelphis* sp.: extinct species, skull fragmentary, body size could not be assessed.
13. PBDB#52062, 52063, 118104, 123588: *Astadelphis* sp.: extinct species, body size could not be assessed.
14. PBDB#52582: *Auroracetus*: extinct species, type is a juvenile, fragmentary skull, body size could not be assessed.
15. PBDB#45497, 47428, 49404, 57908, 67027, 86251, 96768: *Balaenotus*: extinct species, based on cervical vertebrae, body size could not be assessed; junior synonym of *Balaenula*³⁷.
16. PBDB#123227: *Belemnoziphius*: extinct species, based on rostrum, body size could not be assessed; synonym of *Ziphirostrum*³⁸.
17. PBDB#47462, 49404, 57701, 56942, 57783, 67023, 67028, 67029, 67030, 76006, 89534: *Burtinopsis*: extinct species, body size could not be assessed; taxon is of uncertain affinities⁴⁴.
18. PBDB#123227: *Eboroziphius*: extinct species, specimens fragmentary (e.g.⁴⁵), body size could not be assessed.
19. PBDB#18535, 154720: *Goniodelphis*: extinct species, based primarily on fragmentary skull, body size could not be assessed.
20. PBDB#47462, 49404, 56300, 56942, 56947, 56948, 57138, 57912, 67027, 76006, 77492, 77496, 77498: *Herpetocetus*: extinct species, body size could not be assessed based on available material.
21. PBDB#56693, 57138, 79950: *Hoplocetus*: extinct species, based on incomplete material, physeteroid of uncertain affinities, body size could not be assessed.
22. PBDB#52582: *Kogiopsis*: extinct species, species is based on incomplete mandible, regarded as physeteroid of uncertain affinities; body size could not be assessed.
23. PBDB#107396: *Platearostrum*: extinct species, known material too incomplete for proper estimation of body size.
24. PBDB#52582: *Gricetoides*: extinct species, taxon based on fragmentary skull, no measurements available for body size estimation.
25. PBDB#49404, 52582, 56692, 57138, 57701, 57978, 96774: *Plesiocetus*: extinct species; lacks a type species, identification uncertain³⁵.
26. PBDB#45474, 46167, 50068, 51335, 52219, 52223, 52582, 85022, 87376: *Scaldicetus*: extinct species; genus is based on non-diagnostic material and genus usually applied to isolated teeth or very fragmentary material; physeteroid of uncertain affinities, body size could not be assessed.
27. PBDB#28039, 46167, 47428, 50990, 51328, 51335, 51414, 55759, 56883, 56942, 57906, 57907, 60940, 71093, 71916, 74753, 75997, 76001, 77749, 77754, 104046, 117470, 153709: *Balaenoptera* sp.: species identified only to genus level, body size could not be assessed.
28. PBDB#75990, 75998: *Balaenoptera*: species identified as *B. borealis*, but stated without evidence.
29. PBDB#67023, 67028, 57701, 57783, 89535: *Balaenoptera*: specimens are of uncertain taxonomic identity and validity³⁵.

30. PBDB#67027, 67029, 67030, 89534: *Balaenoptera*: consists of material too fragmentary for proper assessment.
31. PBDB#13488: *Balaenoptera*: identified as *B. taiwanica*, but specimen based on periotic, body size could not be assessed.
32. PBDB#32052, 47428, 76013: *Kogia*: specimens of uncertain affinities.
33. PBDB#28039, 51304, 56358, 76019: *Orcinus* sp.: body size could not be assessed.
34. PBDB#47464: *Palaeocetus*: extinct species, based on a set of vertebrae, body size could not be assessed³⁶.

The records excluded because of equivocal identifications (e.g. *cff* and *aff*) include:

- 1.
2. PBDB#73697, 73692, 73693, 46167 and 76014: *Balaena*.
3. PBDB#77754, 104046, 47428, 51414, 74753, 117470: *Balaenoptera*.
4. PBDB#76014: *Balaenoptera borealis*.
5. PBDB#102985, 59062, 101859, 154092: *Callorhinus*.
6. PBDB#20643, 73693: *Delphinapterus*.
7. PBDB#52582: *Delphinus*.
8. PBDB#65160, 50343, 50343: *Dugong*.
9. PBDB#52217: *Dusignathus*.
10. PBDB#107397: *Globicephala*.
11. PBDB#65405: *Halichoerus*.
12. PBDB#52218: *Herpetocetus*.
13. PBDB#52582, 57779: *Kogia*.
14. PBDB#52582, 52580: *Lagenorhynchus*.
15. PBDB#84891, 84891: *Lissodelphis*.
16. PBDB#51414: *Megaptera*.
17. PBDB#51414, 77492, 28039, 51335: *Mesoplodon*.
18. PBDB#124818, 123588: *Metaxytherium*.
19. PBDB#52582: *Monodon*.
20. PBDB#65405: *Odobenus*.
21. PBDB#74757: *Orcinus*.
22. PBDB#52582: *Orycterocetus*.
23. PBDB#85511: *Pachyacanthus*.
24. PBDB#140365, 140364, 140360, 140366: *Phoca*.
25. PBDB#117471: *Phocoena*.
26. PBDB#51328, 51335, 52582: *Physeter*.
27. PBDB#52582: *Physeterula*.
28. PBDB#57779, 2582: *Pontoporia*.
29. PBDB#87896 74757: *Pseudorca*.
30. PBDB#20643: *Pusa*.
31. PBDB#57779: *Scaphokogia*.
32. PBDB#50343, 50343: *Steno*.
33. PBDB#102184: *Thalassoleon*.
34. PBDB#49690, 133432, 20624, 84896, 20636, 51328, 77492: *Tursiops*.
35. PBDB#59062, 58989: *Zalophus*.

References

1. Silvestro D, Schnitzler J, Liow LH, Antonelli A, & Salamin N (2014) Bayesian Estimation of Speciation and Extinction from Incomplete Fossil Occurrence Data. *Syst Biol* 63:349-367.
2. Silvestro D, Antonelli A, Salamin N, & Quental TB (2015) The role of clade competition in the diversification of North American canids. *Proc Natl Acad Sci USA* 112:8684-8689.
3. Silvestro D, Cascales-Miñana B, Bacon CD, & Antonelli A (2015) Revisiting the origin and diversification of vascular plants through a comprehensive Bayesian analysis of the fossil record. *New Phytol* 207: 425–436.
4. Lartillot N & Philippe H (2006) Computing Bayes factors using thermodynamic integration. *Syst Biol* 55:195-207.
5. Kass RE & Raftery AE (1995) Bayes Factors. *J Am Stat Assoc* 90:773-795.
6. Pimiento C & Clements CF (2014) When Did Carcharocles megalodon Become Extinct? A New Analysis of the Fossil Record. *Plos One* 9(10):e111086.
7. Steeman ME (2010) The extinct baleen whale fauna from the Miocene-Pliocene of Belgium and the diagnostic cetacean ear bones. *J Syst Palaeontol* 8(1):63-80.
8. Bouetel V & de Muizon C (2006) The anatomy and relationships of *Piscobalaena nana* (Cetacea, Mysticeti), a Cetotheriidae s.s. from the early Pliocene of Peru. *Geodiversitas* 28(2):319-395.
9. Musick JA, Harbin MM, & Compagno LJ (2004) Historical zoogeography of Selachii. *Biology of sharks and their relatives*, eds Carrier, J.C. et al. (CRC Marine Biology Series), pp. 33-78.
10. Cappetta H (2012) *Handbook of paleoichthyology. Volume 3B. Chondrichthyes. Mesozoic and Cenozoic Elasmobranchii: Teeth* (Gustav Fisher, Stuttgart, Germany).
11. Compagno LJ (1973) Interrelationships of living elasmobranchs. *Zoological J Linn Soc* 53(1):15-61.
12. Compagno LJ (1977) Phyletic relationships of living sharks and rays. *Am Zoo* 17:303-322.
13. Compagno LJ (1984) *FAO species catalogue. Vol. 4 sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 1. Hexanchiformes to Lamniformes* (FAO Fisheries Synopsis, Rome).
14. Compagno LJ (1984) *FAO species catalogue. Vol. 4. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 2. Carcharhiniformes* (FAO Fisheries Synopsis, Rome).
15. Compagno LJ (1988) *Sharks of the order Carcharhiniformes* (Princeton University Press, Princeton).
16. Compagno LJ & Cook SF (1995) The exploitation and conservation of freshwater elasmobranchs: Status of taxa and prospects for the future. *The Biology of Freshwater Elasmobranchs, a Symposium to Honor Thomas B. Thorson*, eds Oettinger MI & Zorzi GD (Journal of Aquaculture and Aquatic Sciences VII), pp 62-90.
17. Compagno LJ (2001) *Sharks of the world: an annotated and illustrated catalogue of shark species known to date. Volume 2: Bullhead, mackerel and carpet sharks (Heterodontiformes, Lamniformes and Orectolobiformes)* (FAO Fisheries Synopsis, Rome).
18. Compagno LJ, Dando VM, & Flower S (2005) *Sharks of the world* (Princeton University Press, Princeton).

19. Jacobsen IP & Bennett MB (2013) A comparative analysis of feeding and trophic level ecology in stingrays (Rajiformes; Myliobatoidei) and electric rays (Rajiformes: Torpedinoidei). *PLoS ONE* 8(8):e71348.
20. Seret B & Guiol F (2006) *Identification Guide of the Main Shark and Ray Species of the Eastern Tropical Atlantic: For the Purpose of the Fishery Observers and Biologists* (FIBA, Paris).
21. McClain CR, *et al.* (2015) Sizing ocean giants: patterns of intraspecific size variation in marine megafauna. *PeerJ* 3:e715.
22. Grady JM, Enquist BJ, Dettweiler-Robinson E, Wright NA, & Smith FA (2014) Evidence for mesothermy in dinosaurs. *Science* 344(6189):1268-1272.
23. Heupel MR, Knip DM, Simpfendorfer CA, & Dulvy NK (2013) Sizing up the ecological role of sharks as predators. *Mar Ecol Prog Ser* 495:291-298.
24. Kelley NP & Motani R (2015) Trophic convergence drives morphological convergence in marine tetrapods. *Biol Lett* 11(1):20140709.
25. Pauly D, Trites AW, Capuli E, & Christensen V (1998) Diet composition and trophic levels of marine mammals. *Ices Journal of Marine Science* 55(6):1153-1153.
26. Jefferson TA, Webber MA, & Pitman RL (2008) *Marine mammals of the world: A comprehensive guide to their identification* (Academic Press, Cambridge).
27. Goodman-Lowe GD (1998) Diet of the Hawaiian monk seal (*Monachus schauinslandi*) from the Northwestern Hawaiian islands during 1991 to 1994. *Mar Biol* 132(3):535-546.
28. Sarko DK, Domning DP, Marino L, & Reep RL (2010) Estimating body size of fossil sirenians. *Marine Mammal Science* 26(4):937-959.
29. Churchill M, Clementz MT, & Kohno N (2015) Cope's rule and the evolution of body size in Pinnipedimorpha (Mammalia: Carnivora). *Evolution* 69(1):201-215.
30. Pyenson ND & Sponberg SN (2011) Reconstructing body size in extinct crown Cetacea (Neoceti) using allometry, phylogenetic methods and tests from the fossil record. *J Mamm Evol* 18(4):269-288.
31. Boessenecker RW (2013) Pleistocene survival of an archaic dwarf baleen whale (Mysticeti: Cetotheriidae). *Naturwissenschaften* 1;100(4):365-71.
32. El Adli JJ, Deméré TA, Boessenecker RW (2014) *Herpetocetus morrowi* (Cetacea: Mysticeti), a new species of diminutive baleen whale from the Upper Pliocene (Piacenzian) of California, USA, with observations on the evolution and relationships of the Cetotheriidae. *Zoological Journal of the Linnean Society* 170(2):400-66.
33. Lambert O *et al.* (2010) The giant bite of a new raptorial sperm whale from the Miocene epoch of Peru. *Nature* 466(7302):105-8.
34. Fordyce RE, Quilty PG, Daniels J (2002) *Australodelphis mirus*, a bizarre new toothless ziphiid-like fossil dolphin (Cetacea: Delphinidae) from the Pliocene of Vestfold Hills, East Antarctica. *Antarctic Science* 14(1):37-54.
35. Deméré TA, Berta A, McGowen MR (2005) The taxonomic and evolutionary history of fossil and modern balaenopteroid mysticetes. *Journal of Mammalian Evolution* 12(1-2):99-143.
36. Deméré TA (1986) The fossil whale, *Balaenoptera davidsonii* (Cope 1872), with a review of other Neogene species of Balaenoptera (Cetacea: Mysticeti). *Marine Mammal Science* 2(4):277-98.

37. Gol'din P, Startsev D, Krakhmalnaya T (2013) The anatomy of the Late Miocene baleen whale *Cetotherium riabinini* from Ukraine. *Acta Palaeontologica Polonica* 59(4):795-814.
38. Bisconti M (2010) A new balaenopterid whale from the Late Miocene of the Stirone River, northern Italy (Mammalia, Cetacea, Mysticeti). *Journal of Vertebrate Paleontology* 30(3):943-58.
39. Pyenson ND, Goldbogen JA, Shadwick RE (2013) Mandible allometry in extant and fossil Balaenopteridae (Cetacea: Mammalia): the largest vertebrate skeletal element and its role in rorqual lunge feeding. *Biological Journal of the Linnean Society* 108(3):586-99.
40. Wyneken J, Lohmann KJ, & Musick JA (2013) *The biology of sea turtles: volume III. Marine Turtle Newsletter* 141(2014):18-19.
41. Weems RE (1980) *Syllomus aegyptiacus*, a Miocene Pseudodont sea turtle. *Copeia* 1980(4):621-625.
42. Weems RE (1974) Middle Miocene sea turtles (*Syllomus*, *Procolpochelys*, *Psephophorus*) From Calvert Formation. *J Paleontol* 48(2):278-303.
43. Schreiber EA & Burger J (2001) *Biology of marine birds* (CRC Press, Boca Raton).
44. Whitmore FC, Jr. & Kaltenbach JA (2008) Neogene Cetacea of the Lee Creek Phosphate Mine, North Carolina. *Virginia Museum of Natural History Special Publication* 14:181-269.
45. Lambert O (2005) Systematics and phylogeny of the fossil beaked whales *Ziphirostrum* du Bus, 1868 and *Choneziphius* Duvernoy, 1851 (Mammalia, Cetacea, Odontoceti), from the Neogene of Antwerp (North of Belgium). *Geodiversitas* 27(3):443-497.

Supplementary Tables

Supplementary Table 1 | Summary of all Cenozoic fossil occurrences analyzed in this study.

	n. genera	extant genera	n. occurrences
All megafauna	880	209	11241
Birds	126	48	1275
Mammals	535	73	4740
Reptiles	30	4	129
Sharks	188	85	5108

Supplementary Table 2 | Preservation rates estimated using PyRate across epochs. The rates indicate the expected number of fossil occurrences per sampled lineage/Myr. We report the posterior mean and 95% highest posterior densities (HPDs) as estimated through Bayesian analyses. Estimates are given for marine megafauna as a whole and for the four individual clades. Grey part shows the results from a subsample in which occurrences of the same genus from the same collection were lumped.

		Time (Ma)					
		66.0 - 56.0	56.0 - 33.9	33.9 - 23.03	23.03 - 5.33	5.33 - 2.58	2.58 - 0.012
All	mean	0.541	0.771	0.256	0.953	1.916	2.581
	95% HPD lower	0.448	0.737	0.230	0.915	1.800	2.440
	95% HPD upper	0.615	0.805	0.281	0.986	2.029	2.720
Birds	mean	0.422	0.521	0.198	0.491	1.981	3.337
	95% HPD lower	0.093	0.392	0.118	0.421	1.703	2.989
	95% HPD upper	0.829	0.657	0.286	0.565	2.255	3.708

Mammals	mean	0.345	1.147	0.540	0.784	2.342	4.799
	95% HPD lower	0.037	1.028	0.451	0.744	2.151	4.469
	95% HPD upper	0.756	1.284	0.630	0.831	2.539	5.153
Reptiles	mean	0.178	0.306	0.214	0.329	0.806	0.362
	95% HPD lower	0.068	0.197	0.115	0.219	0.391	0.077
	95% HPD upper	0.303	0.416	0.317	0.449	1.251	0.695
Sharks	mean	0.599	0.772	0.217	1.278	1.472	0.589
	95% HPD lower	0.515	0.730	0.191	1.224	1.320	0.491
	95% HPD upper	0.689	0.813	0.245	1.333	1.623	0.691
All subsampled	mean	0.4571	0.6664	0.2192	0.8187	1.6482	2.3122
	95% HPD lower	0.3935	0.6359	0.1959	0.7894	1.5464	2.1762
	95% HPD upper	0.5217	0.6972	0.2413	0.8461	1.7503	2.4523

Supplementary Table 3 | Relative fit for birth-death models with different number of rate shifts. The models are sorted by their relative fit (marginal likelihoods). Log Bayes Factors (BF) are computed with respect to the best fitting model.

Number of shifts (23.03-0 Ma)		Log marginal Likelihood	Log BF	Relative probability
Origination	Extinction			
0	3	-5587.711	0	0.511
0	2	-5588.051	0.68	0.364
2	3	-5589.67	3.918	0.072
0	4	-5590.706	5.99	0.026
0	1	-5591.693	7.964	0.01
1	2	-5592.415	9.408	0.005
3	2	-5592.928	10.434	0.003
3	3	-5593.234	11.046	0.002
1	3	-5593.242	11.062	0.002
1	1	-5593.713	12.004	0.001
4	2	-5593.827	12.232	0.001
2	1	-5593.924	12.426	0.001
4	3	-5594.021	12.62	0.001
2	2	-5594.136	12.85	0.001
1	4	-5594.222	13.022	0
2	4	-5594.31	13.198	0
3	4	-5595.983	16.544	0
4	4	-5596.146	16.87	0
4	1	-5596.423	17.424	0
3	1	-5597.568	19.714	0
0	0	-5612.911	50.4	0
1	0	-5616.9	58.378	0
3	0	-5618.054	60.686	0
2	0	-5618.174	60.926	0
4	0	-5619.549	63.676	0

Table 4 | Plio-Pleistocene global marine megafauna taxonomic diversity (number of genera). Sample sizes (i.e., occurrences) are in parenthesis. *Coastal* denotes genera associated with coastal habitats (i.e. strictly coastal, coastal-terrestrial, coastal-oceanic); *extinct* indicates the number of Pliocene genera absent from the Pleistocene; *originated* indicates the number of genera first recorded in the Pleistocene. Note that combined, the Plio-Pleistocene number of genera is not the same as the sum of the Pliocene and the Pleistocene genera, as they can co-occur in both Epochs.

	Pliocene genera		Extinct genera		Pleistocene genera		Originated genera		Combined (Plio-Pleistocene)	
	total	coastal	total	coastal	total	coastal	total	coastal	total	coastal
Mammals	78 (381)	64 (323)	43	36	56 (448)	49 (428)	21	21	99 (829)	85 (751)
Birds	37 (148)	37 (148)	13	13	41 (311)	41 (311)	17	17	54 (459)	54 (459)
Turtles	7 (12)	7 (12)	3	3	4 (5)	4 (5)	0	0	7 (17)	7 (17)
Sharks	55 (316)	38 (228)	5	3	50 (142)	35 (114)	0	0	55 (458)	38 (342)
All	177 (857)	146 (711)	64	55	151 (906)	129 (858)	38	38	215 (1763)	184 (1569)

Supplementary Table 5 | Plio-Pleistocene marine megafauna's Functional Entities (FEs) and their corresponding status after the extinction event studied here. Data produced using the FDChange function (see methods).

No.	Functional Entities (FEs)	Status
1	1.0-3.0+mesopredator+benthic+terrestrial/marine+endotherm	winner
2	3.0-6.0+mesopredator+benthic+terrestrial/marine+endotherm	winner
3	1.0-3.0+macropredator+pelagic+terrestrial/marine+endotherm	originated
4	>12.0+micropredator+pelagic+coastal/oceanic+endotherm	winner
5	1.0-3.0+mesopredator+pelagic+terrestrial/marine+endotherm	winner
6	1.0-3.0+mesopredator+benthopelagic+terrestrial/marine+endotherm	winner
7	3.0-6.0+mesopredator+benthopelagic+coastal/oceanic+endotherm	winner
8	>12.0+micropredator+benthic+coastal+endotherm	winner
9	>12.0+micropredator+pelagic+coastal+endotherm	winner
10	6.0-9.0+micropredator+pelagic+coastal/oceanic+endotherm	winner
11	6.0-9.0+herbivore+benthic+coastal+endotherm	winner
12	1.0-3.0+mesopredator+benthic+coastal+poikilotherm	winner
13	9.0-12.0+macropredator+pelagic+coastal/oceanic+endotherm	originated
14	3.0-6.0+macropredator+benthopelagic+coastal/oceanic+poikilotherm	winner
15	3.0-6.0+mesopredator+benthopelagic+coastal+endotherm	winner
16	1.0-3.0+mesopredator+benthopelagic+coastal/oceanic+endotherm	winner
17	3.0-6.0+macropredator+pelagic+coastal/oceanic+endotherm	winner
18	1.0-3.0+macropredator+pelagic+coastal/oceanic+endotherm	winner
19	<1.0+mesopredator+benthic+terrestrial/marine+endotherm	winner
20	3.0-6.0+mesopredator+benthopelagic+coastal+poikilotherm	winner
21	9.0-12.0+micropredator+pelagic+coastal/oceanic+poikilotherm	winner
22	3.0-6.0+mesopredator+pelagic+coastal/oceanic+endotherm	winner
23	3.0-6.0+micropredator+pelagic+coastal/oceanic+endotherm	winner
24	3.0-6.0+herbivore+benthic+coastal+endotherm	winner
25	>12.0+macropredator+pelagic+coastal+mesotherm	extirpated
26	1.0-3.0+mesopredator+benthopelagic+coastal+endotherm	winner
27	1.0-3.0+micropredator+pelagic+coastal/oceanic+endotherm	extirpated
28	1.0-3.0+mesopredator+benthopelagic+coastal/oceanic+poikilotherm	winner
29	6.0-9.0+macropredator+pelagic+coastal/oceanic+mesotherm	winner
30	1.0-3.0+mesopredator+pelagic+coastal/oceanic+endotherm	winner
31	3.0-6.0+mesopredator+benthopelagic+terrestrial/marine+endotherm	originated
32	1.0-3.0+mesopredator+benthopelagic+coastal+poikilotherm	winner
33	1.0-3.0+mesopredator+pelagic+coastal/oceanic+mesotherm	winner
34	3.0-6.0+micropredator+benthic+coastal+endotherm	winner
35	1.0-3.0+mesopredator+benthic+coastal+endotherm	winner
36	3.0-6.0+macropredator+pelagic+coastal/oceanic+mesotherm	extirpated
37	<1.0+mesopredator+benthic+coastal/oceanic+poikilotherm	winner
38	3.0-6.0+mesopredator+benthopelagic+coastal/oceanic+poikilotherm	winner
39	6.0-9.0+micropredator+pelagic+coastal/oceanic+poikilotherm	winner
40	3.0-6.0+micropredator+pelagic+coastal/oceanic+poikilotherm	winner
41	6.0-9.0+mesopredator+benthopelagic+coastal+poikilotherm	winner
42	9.0-12.0+micropredator+pelagic+coastal/oceanic+endotherm	winner
43	1.0-3.0+mesopredator+benthic+terrestrial/marine+poikilotherm	winner
44	1.0-3.0+herbivore+benthic+terrestrial/marine+poikilotherm	winner
45	<1.0+mesopredator+benthic+terrestrial/marine+poikilotherm	winner

46	1.0-3.0+mesopredator+pelagic+terrestrial/marine+mesotherm	extirpated
47	6.0-9.0+mesopredator+pelagic+terrestrial/marine+endotherm	originated
48	<1.0+mesopredator+benthic+coastal+poikilotherm	winner
49	1.0-3.0+micropredator+benthic+coastal+endotherm	extirpated
50	1.0-3.0+herbivore+benthic+coastal+endotherm	extirpated
51	<1.0+mesopredator+benthopelagic+coastal+poikilotherm	winner
52	1.0-3.0+herbivore+benthic+terrestrial/marine+endotherm	extirpated
53	<1.0+mesopredator+pelagic+terrestrial/marine+endotherm	winner

Supplementary Table 6 | Pliocene and Pleistocene functional entity (FE) richness, functional redundancy (FR), functional over-redundancy and functional vulnerability. FR = genera:FES; FOV = % genera that fill FEs above the mean level of FR); and FV = % FEs with one genera (see Methods in the main text).

	Pliocene	Pleistocene
FES	49	46
Functional redundancy (FR)	3	3
Functional over-redundancy (FOR)	41%	45%
Functional Vulnerability (FR)	59%	80%

Supplementary Table 7 | Comparison of Generalized Linear Models (GLMs) with binomial error examining FTU's survivorship (i.e. status: extinct or not extinct) in response to their traits. Contribution of factors to the complete model was established by dropping each individually (drop1 in R). Hierarchical Partitioning analyses with all possible trait combinations as predictors of extinction probability show the proportional independent effects of each trait. Grey part denotes the inclusion of Class as an additional fixed factor alongside respective traits. Bold denotes significance. The traits-only model (i.e. excluding Class) explained 20% of the deviance (pseudo R^2) in survivorship.

glm(status~traits)					Hierarchical Partitioning			glm(status~all traits+class)				Hierarchical Partitioning		
Traits	Df	Deviance	AIC	Pr(>Chi)	Obs	Z.score	sig95	Df	Deviance	AIC	Pr(>Chi)	Obs	Z.score	sig95
Max size	1	159.02	179.02	0.07	0.81	0.23		1	154.54	178.54	0.05	1.10	1.05	
Guild	3	159.00	175.00	0.33	2.53	0.59		3	152.40	172.40	0.65	1.89	0.16	
Vertical	2	161.21	179.21	0.06	1.65	0.62		2	151.24	173.24	0.78	0.78	-0.29	
Zone	2	156.34	174.34	0.69	0.85	-0.16		2	151.10	173.10	0.84	0.56	-0.51	
Thermoregulation	2	182.09	200.09	< 0.001*	13.07	10.39	*	1	160.73	184.73	< 0.001*	8.88	5.66	*
Class								2	155.62	177.62	0.08	8.12	4.56	*

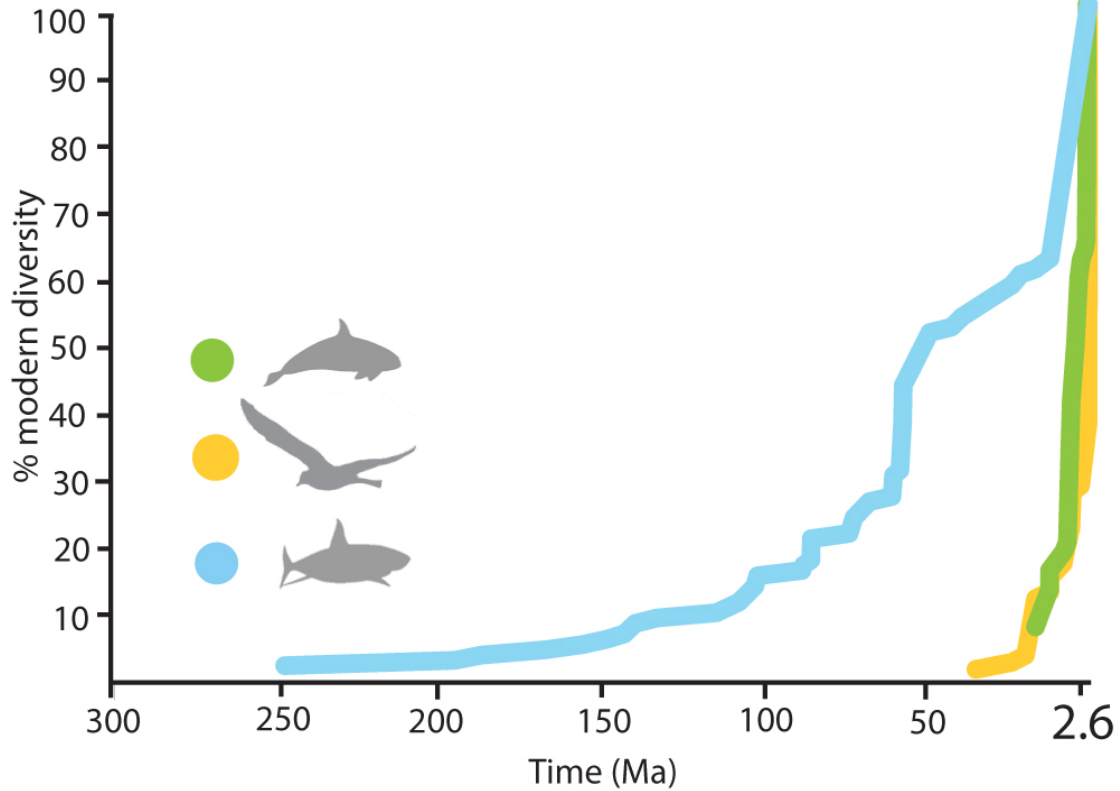
Supplementary Table 8 | Tukey tests comparing thermoregulation (trait that best explained extinction probability (Supplementary Table 6)). Grey part denotes the inclusion of Class as an additional fixed effect.

Thermoregulation	Estimate	Std. Error	z value	Pr(> z)
mesotherm - endotherm	0.46	0.93	0.50	0.86
poikilotherm - endotherm	-2.45	0.63	-3.87	< 0.001*
poikilotherm - mesotherm	-2.91	1.09	-2.67	0.01*
Class				
Chondrichthyes - Aves	-1.84	0.69	-2.66	0.03
Mammalia - Aves	0.86	0.42	2.02	0.16
Reptilia - Aves	0.32	0.84	0.38	0.97
Mammalia - Chondrichthyes	2.70	0.65	4.15	< 0.001*
Reptilia - Chondrichthyes	2.16	0.97	2.23	0.11
Reptilia - Mammalia	-0.54	0.80	-0.67	0.90

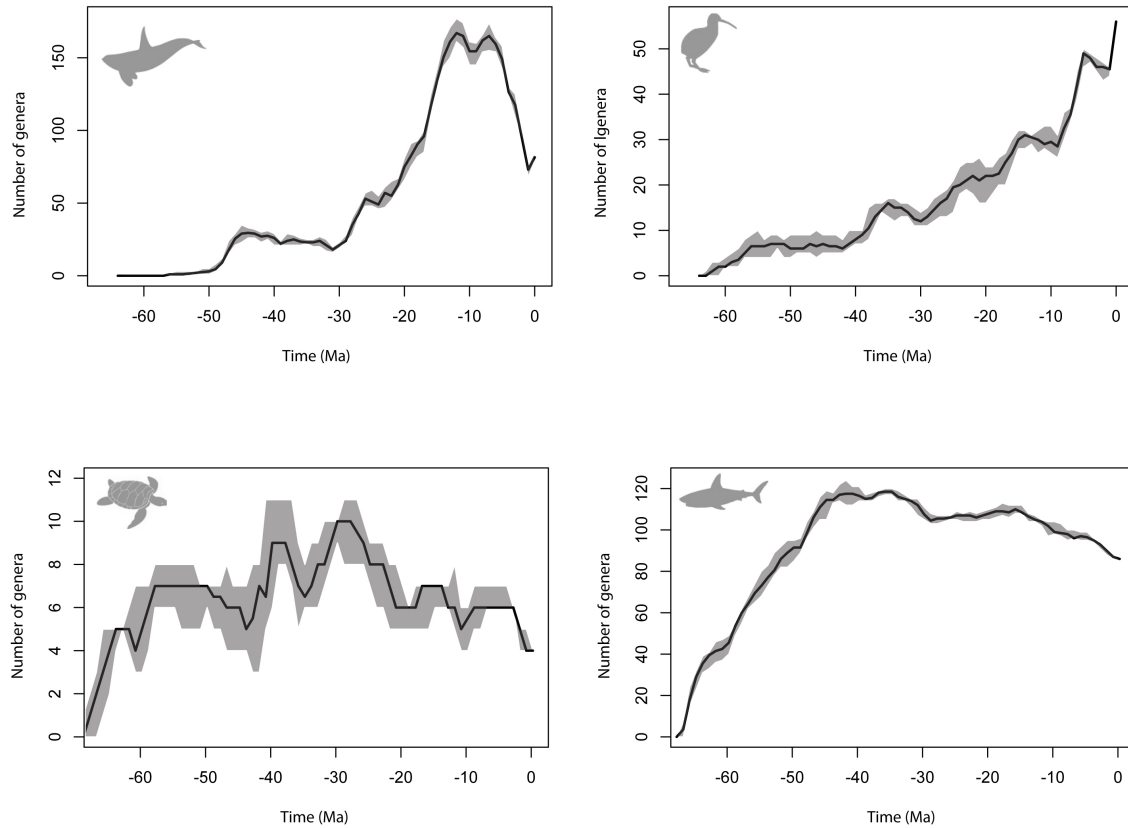
Supplementary Table 9 | Comparison of Generalized Linear Mixed-Effects Models (GLMMs; coded with the glmer function in the lme4 R package) with binomial error examining FTU's survivorship (i.e. status: extinct or not extinct) in response to their traits and including taxonomic identity (Class) as a random effect.

Traits	glmer(status~traits+(1 Class))			
	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-0.51	0.56	-0.91	0.36
Max Body Size	-0.10	0.07	-1.31	0.78
(Intercept) Guild-Herbivore	0.27	0.99	0.27	0.27
Guild-Macropredator	-0.44	1.23	-0.36	0.72
Guild-Mesopredator	-1.10	0.88	-1.24	0.21
Guild-Micropredator	-1.38	0.96	-1.43	0.15
(Intercept) Zone-Coastal	-0.85	0.65	-1.31	0.18
Zone-Coastal/Oceanic	0.04	0.53	0.08	0.93
Zone-Terrestrial/Marine	0.16	0.61	0.27	0.78
(Intercept) Vertical-Benthic	-0.64	0.59	-1.07	0.28
Vertical-Benthopelagic	-0.27	0.53	-0.51	0.61
Vertical-Pelagic	-0.12	0.52	-0.23	0.81
(Intercept) Thermoregulation-Endotherm	-0.14	0.37	-0.37	0.70
Thermoregulation-Mesotherm	0.75	1.13	0.66	0.51
Thermoregulation-Poikilotherm	-2.23	0.83	-2.69	0.01*

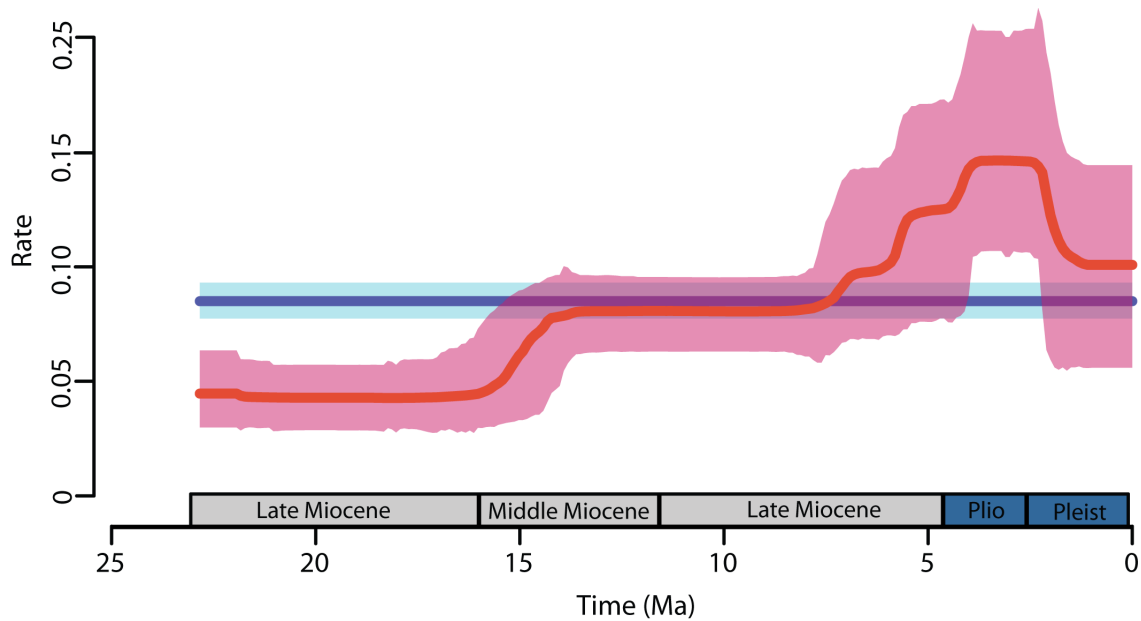
Supplementary Figures



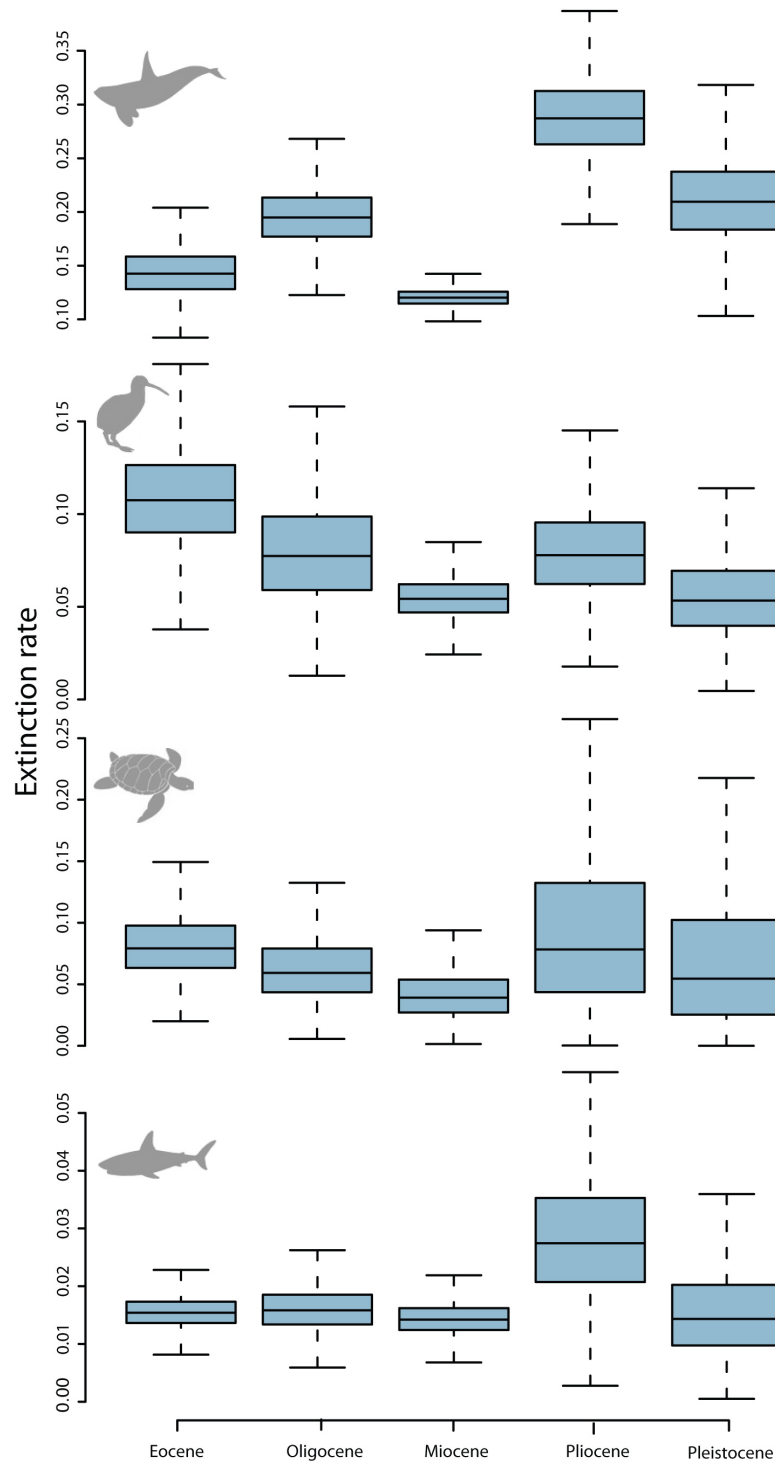
Supplementary Figure 1 | Most modern marine megafaunal genera were represented in Pleistocene assemblages. Survivorship curves showing the proportion of modern genera present into the past. Green curve represents mammalian data, which are composed by Cetacea, Pinnipedia and Sirenia. Yellow curve represents sea birds. Blue curve represents sharks. Turtles were not included given their low diversity.



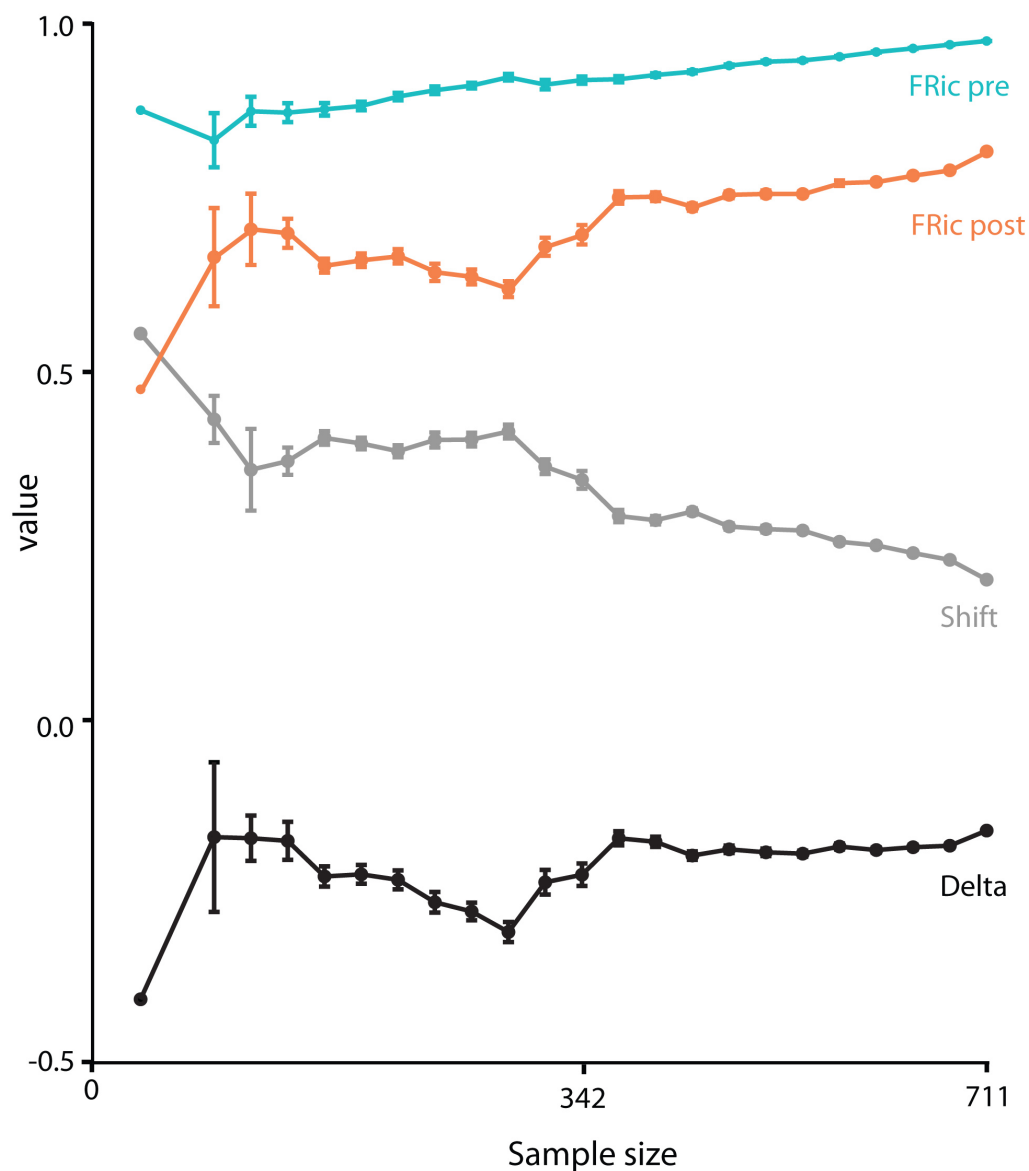
Supplementary Figure 2 | Diversity trajectories of marine megafauna groups. The curves show the number of genera plotted against time based on the temporal ranges estimated for each genus by the PyRate analyses. The gray shaded areas show the range of diversity trajectories from 10 replicated analyses incorporating uncertainties around the age of the fossil occurrences (more details in Supporting Methods). The black line shows the mean diversity trajectory across replicates.



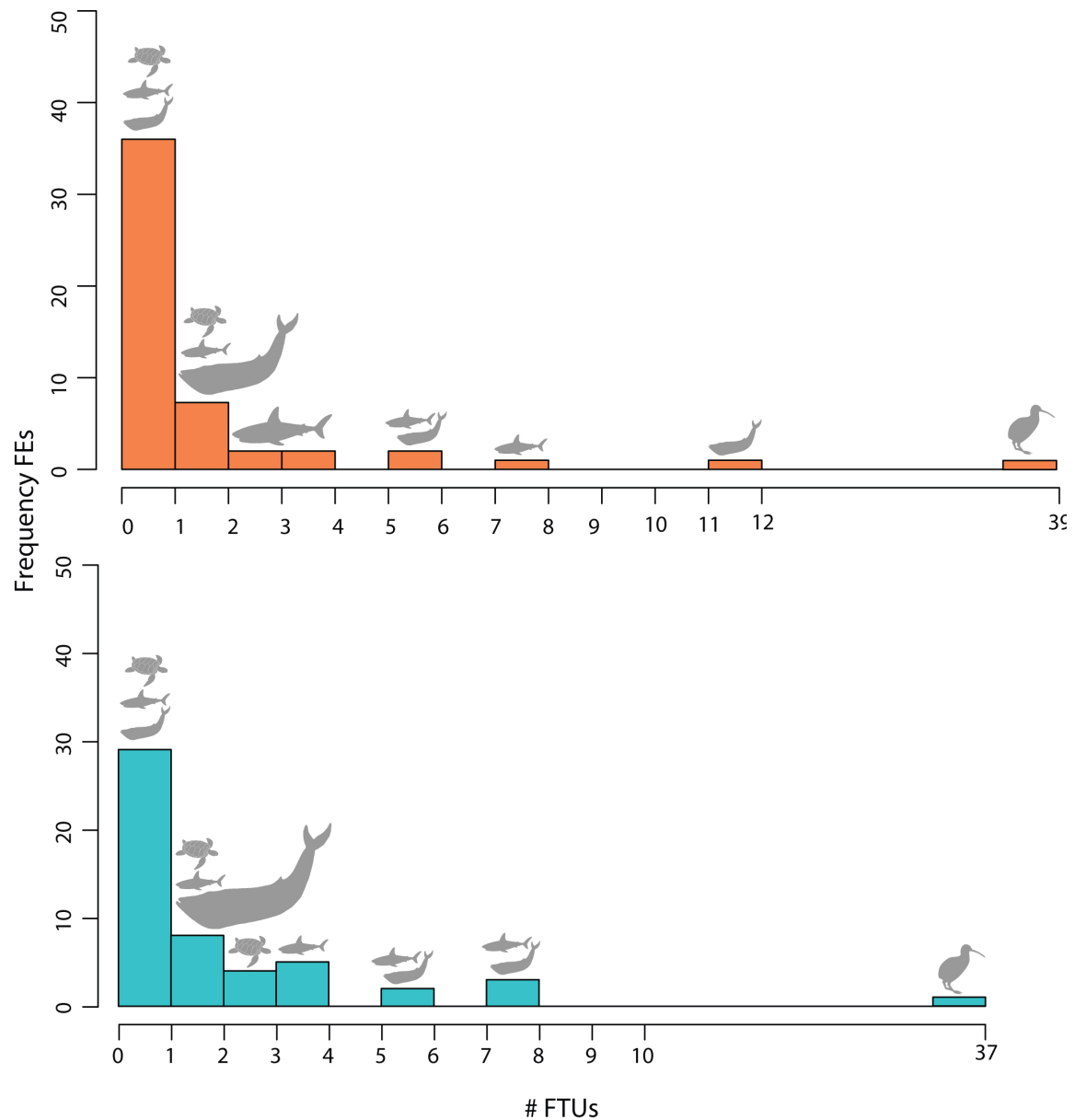
Supplementary Figure 3 | Marine megafauna origination (blue) and extinction rates (red) through time in a continuous time series using Bayesian Model Averaging (BMA). Graph shows only Neogene and Quaternary rates for simplicity. Summarized marginal origination rates are constant, whereas extinction rates increase since the middle Miocene, reaching maximum levels between 3.8 and 2.4 Ma. See main text for detailed methods. Shaded areas show 95% credible intervals around rate estimates.



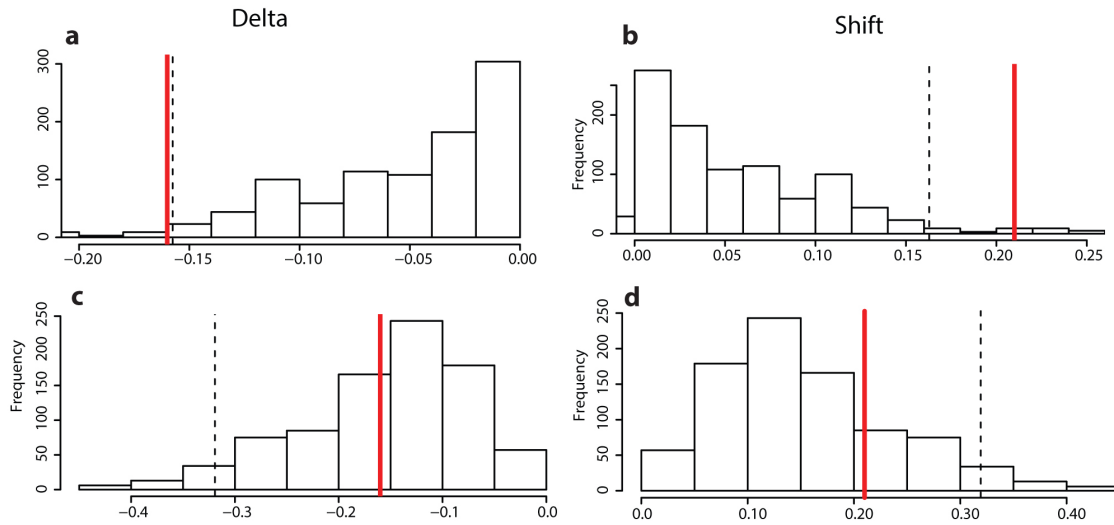
Supplementary Figure 4 | All groups of marine megafauna show elevated extinction rates in the Pliocene. Animals' shapes denote clades. Note that sea birds present higher rates in the Eocene. Extinction rates were estimated in a Bayesian framework within each geological epoch from the Eocene to the Pleistocene. Boxes show the central 50% posterior credible intervals with error bars indicating the 95% credible intervals.



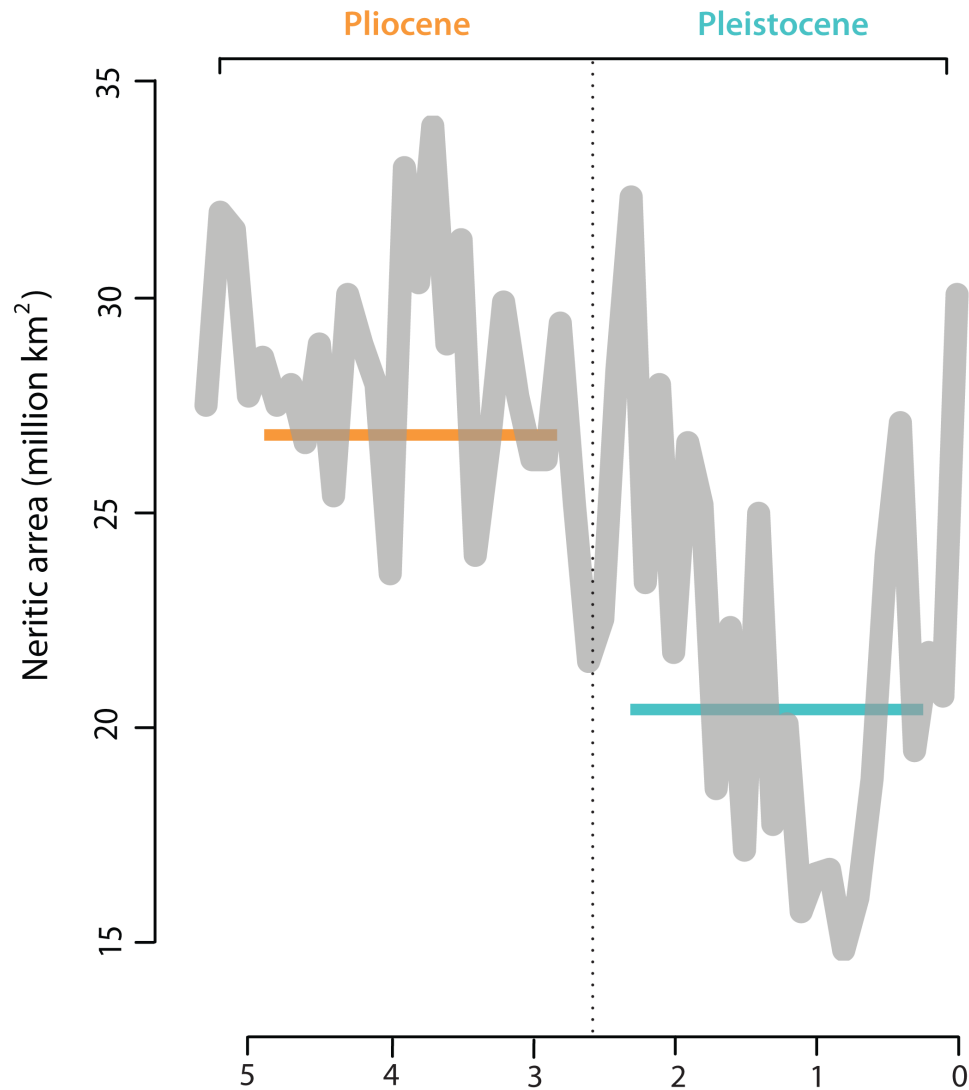
Supplementary Figure 5 | Functional Diversity measures vary with sample size. Simulations showing functional diversity values: Functional richness (FRic = % of the total volume occupied in the functional space) pre (blue) and post (orange) extinction event studied here; shift (non-overlap of functional space) and delta (FRic post - FRic pre). Vertical lines represent 95% confidence intervals of the mean. See methods for more details.



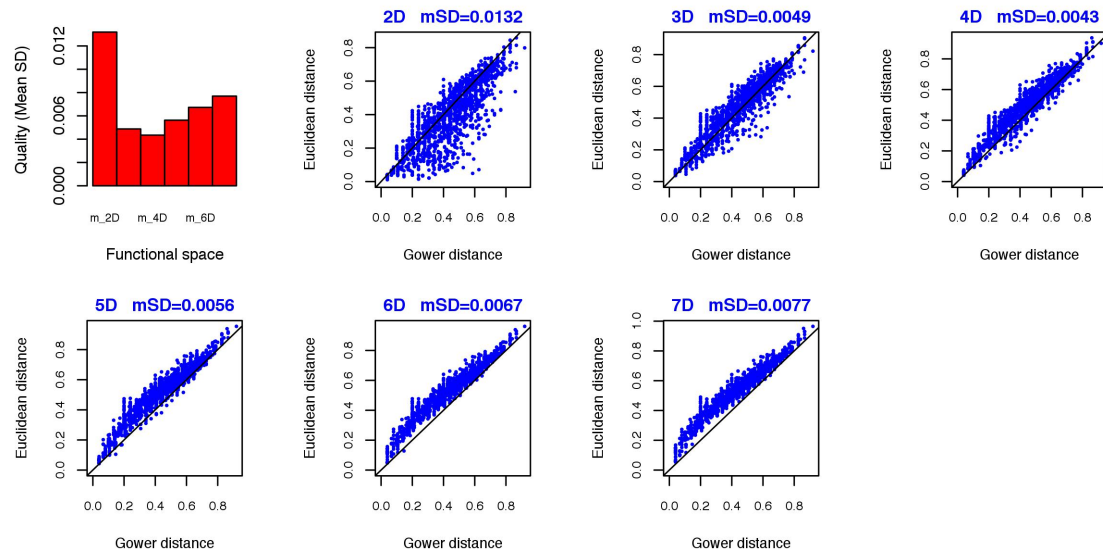
Supplementary Figure 6 | Distribution of species in FEs showing that most FEs are represented by one species in the Pliocene (blue) and Pleistocene (orange) communities. Animals' shapes show the taxonomic affiliations (i.e. Class: Mammalia, Reptilia, Chondrichthyes and Aves).



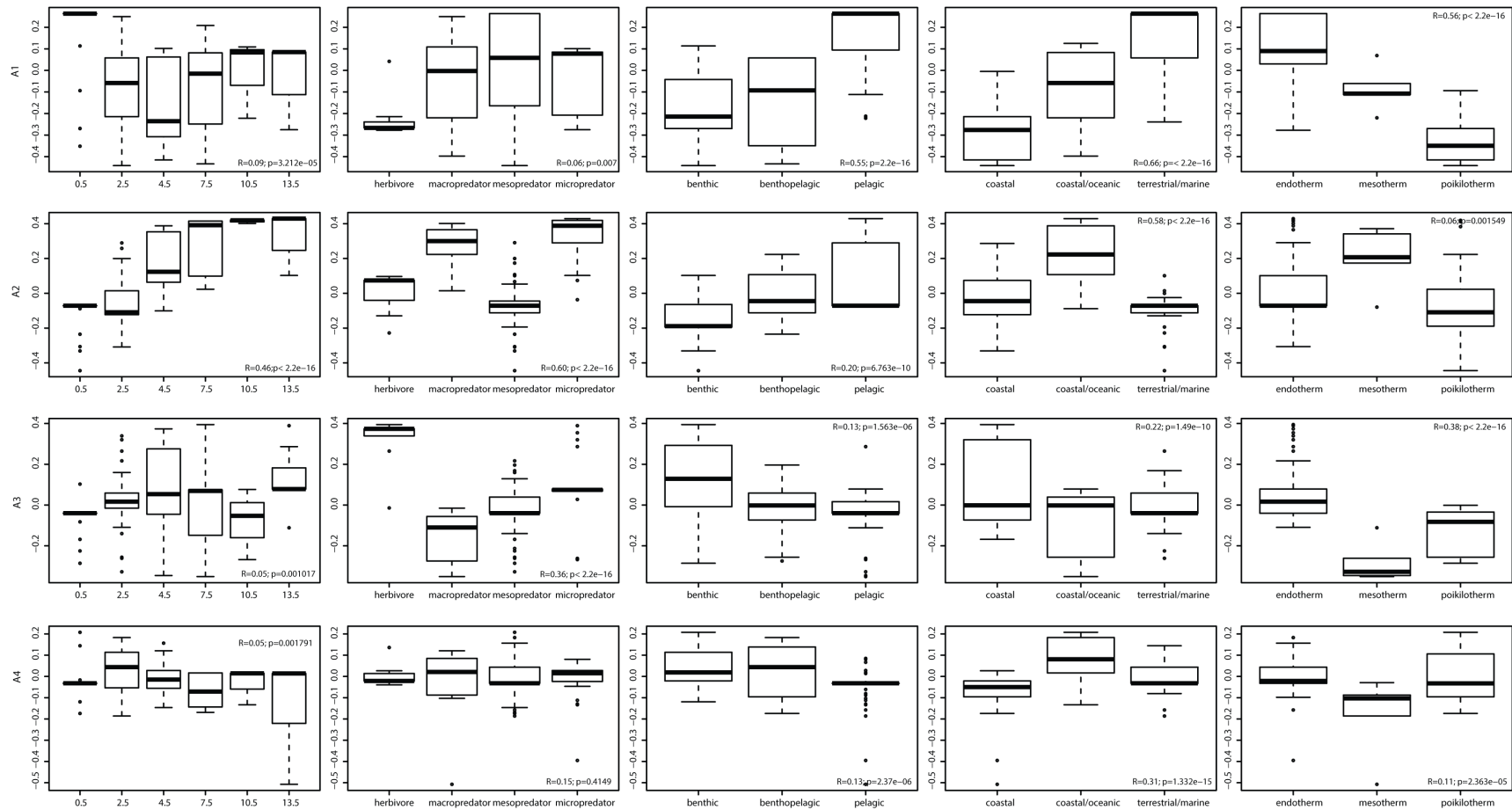
Supplementary Figure 7. Changes in functional diversity were significantly higher than expected given the mean extinction rates over the Cenozoic, but not higher than expected by chance. Histograms showing the distribution of the 1,000 permutation trails, simulating the results as if 22 random Pliocene genera were lost (a-b) and as if 55 random Pliocene genera were lost (c-d). The functional space used for the simulations also included the new taxa which originated in the Pleistocene. Red lines show our empirical values using the resampled data, and dashed lines show the start of the 95% confidence interval. Delta is the difference between the functional richness (FRic) of the Pliocene and Pleistocene coastal communities. Shift is the non-overlap of functional volume. In all cases the Pleistocene assemblage is inclusive of new genera.



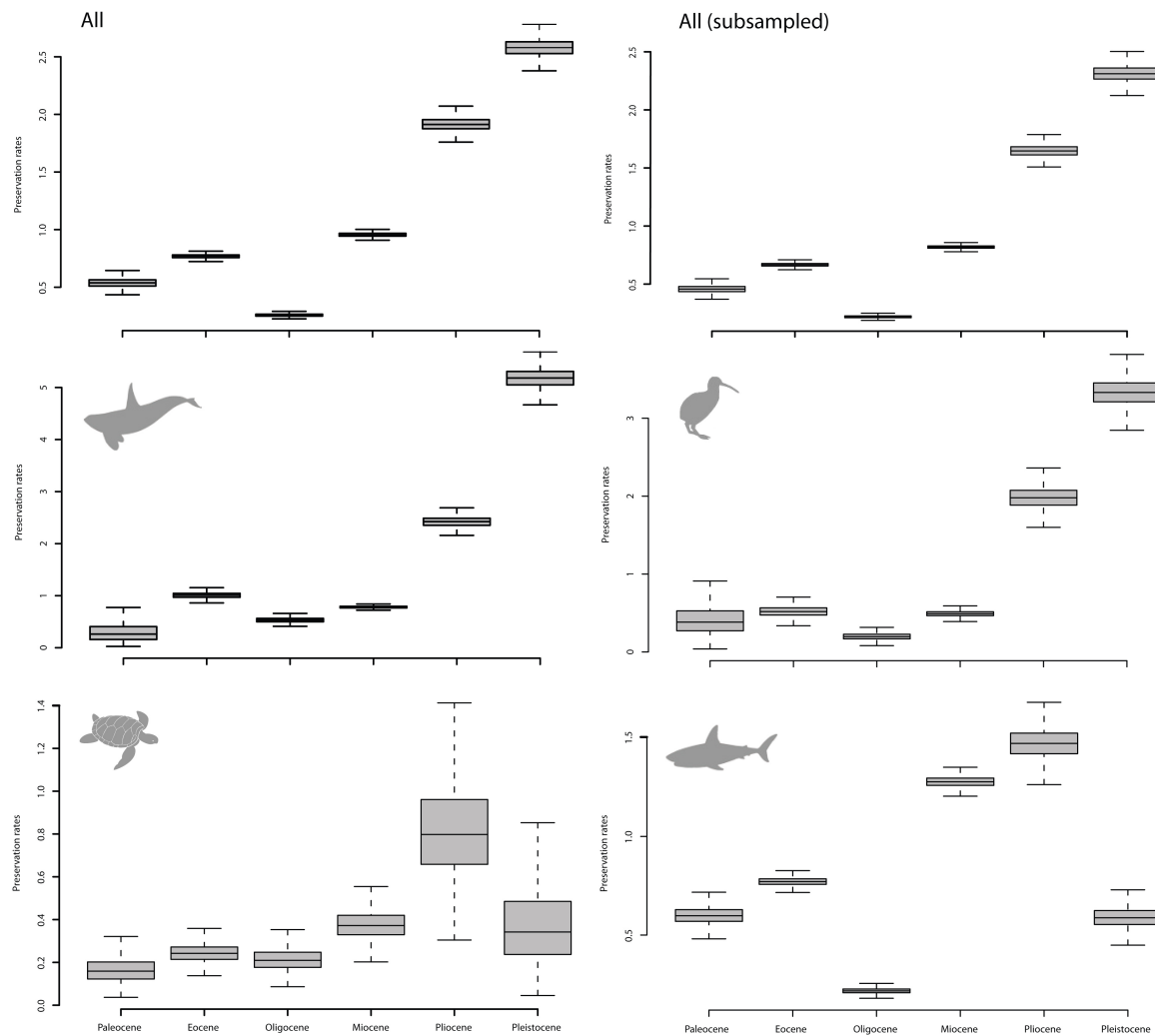
Supplementary Figure 8 | Area reconstruction of the neritic zone based on the eustatic levels reported in Miller *et al.* (see reference 4 in main text). Colored curve shows area changes over time (upper X-axis), whereas horizontal lines show the mean values of Pliocene and Pleistocene. Significant (t-test: $p < 0.001$). Coefficient of variation: Pleistocene = 0.23; Pliocene = 0.09.



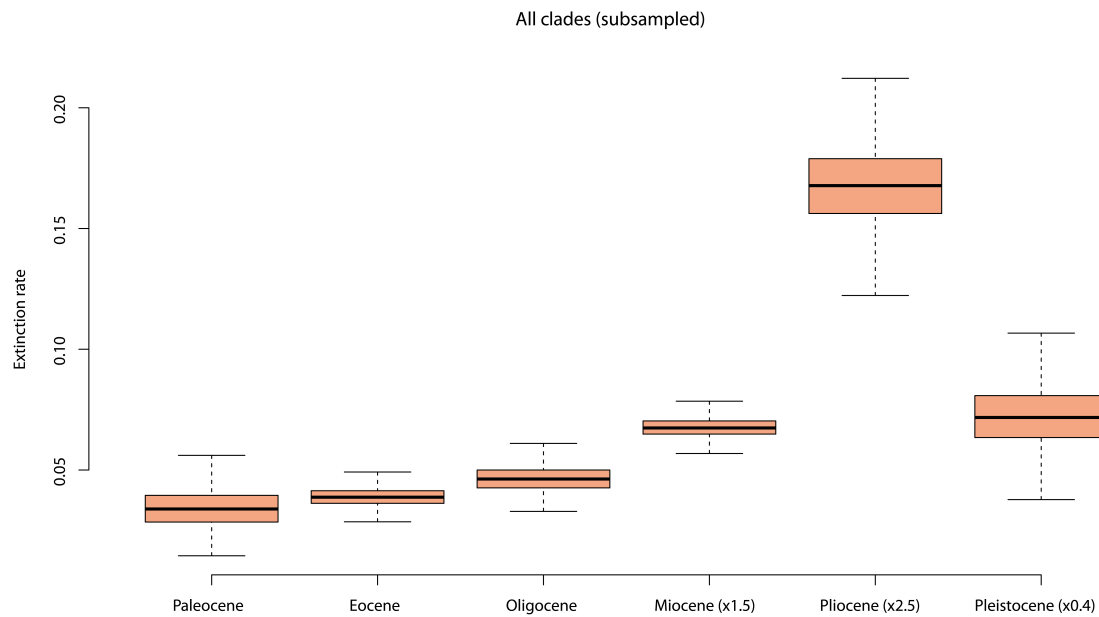
Extended Data Figure 9 | Quality of the functional space showing that our data is better represented in four dimensions (4 PCoA axes). Output from the “quality_funcn_space” R function.



Supplementary Figure 10 | The four axes used to represent of Plio-Pleistocene marine megafauna correlate with multiple trait combinations. Correlation between PCoA axes and functional traits estimated using linear mode.



Supplementary Figure 11 | Marine megafauna preservation rates during the Cenozoic. “All” denotes all megafauna groups using occurrences not lumped by genus. “All (subsampled)” denotes all groups but using only lumped occurrences. Animal shapes denote megafaunal clades. Boxes show the central 50% posterior credible intervals with error bars indicating the 95% credible interval



Supplementary Figure 12 | Extinction rate estimates are robust to different ways of compiling the data. The Pliocene presents higher extinction rates than the rest of the Cenozoic, even when using only occurrences lumped by genus. Boxes show the central 50% posterior credible intervals with error bars indicating the 95% credible interval.