



Geographical distribution patterns of *Carcharocles megalodon* over time reveal clues about extinction mechanisms

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ABSTRACT

Aim Given its catastrophic consequences, the extinction of apex predators has long been of interest to modern ecology. Despite major declines, no present-day species of marine apex predator has yet become extinct. Because of their vulnerability, understanding the mechanisms leading to their extinction in the past could provide insight into the natural factors that interact with human threats to drive their loss. We studied the geographical distribution patterns of the extinct macro-predatory shark *Carcharocles megalodon* in order to elucidate its pathway to extinction.

Location World-wide from the Miocene to the Pliocene (c. 23–2.6 Ma).

Methods A meta-analysis of *C. megalodon* occurrence records was performed using the Paleobiology Database as a platform. The data were binned into geological time slices, and the circular home range around each data point was mapped in reconstructions made in GPlates. We then quantitatively assessed the species' geographical range and global abundance over time, and the relationship between distribution and climate.

Results The pathway to extinction of *C. megalodon* probably started in the late Miocene with a decrease in its global abundance. This decrease was then followed by a decline in its geographical range during the Pliocene. Although the extinction of *C. megalodon* has been attributed to climate change, we found no evidence of direct effects of global temperature. Instead, we found that the collapse in geographical distribution coincided mainly with a drop in the diversity of filter-feeding whales and the appearance of new competitors (large predatory whales and the great white shark).

Main conclusions This research represents the first study of the distributional trends of an extinct, cosmopolitan apex predator in deep-time. Our results suggest that biotic factors, and not direct temperature limitations, were probably the primary drivers of the extinction of the largest marine apex predators that ever lived.

Keywords

apex predator, area coverage, extinction drivers, Miocene, Pliocene, sharks, species occupancy

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INTRODUCTION

Apex predators are ecologically important because they stabilize the populations of their prey (Estes *et al.*, 2011). Accordingly, their local elimination or global extinction can trigger large shifts in ecosystem structure and function

(Myers *et al.*, 2007; Estes *et al.*, 2011; DeLong *et al.*, 2015). For example, it has been shown that the removal of sharks considerably degrades marine ecosystems (Myers *et al.*, 2007; Ferretti *et al.*, 2010). This is a concern because large sharks are declining significantly throughout the world's oceans (Dulvy *et al.*, 2014).

Given their importance and vulnerability, understanding the extinction of apex predators is of interest to modern ecology. Despite major shifts in baseline abundances (Harnik *et al.*, 2012; McCauley *et al.*, 2015), so far no species of modern marine apex predator has become extinct. However, because apex predators are vulnerable to extinction today, understanding the mechanisms that led to their extinction in the past could provide insight into the natural factors that interact with human threats to drive their loss.

Carcharocles megalodon (megalodon) is the largest marine apex predator to have ever lived. It reached a maximum length of 18 m and ranged world-wide during the Miocene and Pliocene (Gottfried *et al.*, 1996; Purdy, 1996; Pimiento & Balk, 2015). Recent studies suggest that it became extinct c. 2.6 Ma, at the Pliocene/Pleistocene boundary (Pimiento & Clements, 2014). Bite marks on fossil bones and associated fauna suggest that this species preyed on marine mammals (Spizuco *et al.*, 1993; Morgan, 1994; Gottfried *et al.*, 1996; Purdy, 1996; Aguilera & De Aguilera, 2004; Aguilera *et al.*, 2008). Based on its trophic level, cosmopolitan distribution and the impact that modern sharks have on prey populations and ecosystem structure (Myers *et al.*, 2007; Estes *et al.*, 2011), it can be inferred that the extinction of *C. megalodon* had a major impact on ancient marine communities (Pimiento & Clements, 2014).

It has been hypothesized that the extinction of *C. megalodon* was caused by: (1) a decline in diversity of filter-feeding whales and pinnipeds; (2) competition with large predatory whales (e.g. odontocetes, killer whales); (3) climate change (mainly cooling); or (4) a shift in the distribution of large marine mammal prey species towards higher latitudes (Morgan, 1994; Allmon *et al.*, 1996; Gottfried *et al.*, 1996; Allmon, 2001; Lindberg & Pyenson, 2006). The first two hypotheses imply that biotic factors such as competition and prey availability were major extinction drivers, whereas the second two hypotheses imply that *C. megalodon* was physiologically constrained to warmer temperatures. These hypotheses remain untested because the extinction pathway of this apex predator has not been studied.

Geographical distribution correlates strongly with extinction susceptibility in a wide variety of modern and fossil taxa (Jablonski, 1986; Jablonski & Flessa, 1986; McKinney, 1997; Purvis *et al.*, 2000; Kiessling & Aberhan, 2007; Payne & Finnegan, 2007; Brook *et al.*, 2008; Davidson *et al.*, 2009, 2012). Geographical distribution consists of two closely related variables: geographical range and abundance (Kiessling & Aberhan, 2007; Lyons & Smith, 2010). Therefore, studying species' geographical range and abundance patterns over geological time could further our understanding of extinction pathways (e.g. Payne & Finnegan, 2007).

The fossil record of extinct terrestrial predators (e.g. dinosaurs) is particularly scarce (Wang & Dodson, 2006; Barrett *et al.*, 2009; O'Gorman & Hone, 2013), making it difficult to assess their distributional patterns, and hence pathways of extinction of a single species. Research into the geographical distribution of marine predators and extinction risk has been

carried out, but only for higher taxonomic levels (e.g. the generic level in Finnegan *et al.*, 2015). Because *C. megalodon* is a relatively long-lived species with a widely distributed fossil record, it provides the opportunity to study the geographical distribution patterns of a predator at the species level in deep-time.

We assessed the pathway to extinction of *C. megalodon* by studying its geographical distribution over geological time. Analysis of the results provided with insights into the mechanisms of extinction in light of the hypotheses that have been proposed (see above), which we categorized into two groups, i.e. biotic and climatic. Accordingly, we assessed *C. megalodon's* geographical distribution trends over time and how they related to biotic and climatic events. The distributional patterns of a cosmopolitan apex predator species have never been studied before over a geological time-scale. Hence, this research provides a deep-time perspective on the extinction of apex predators. In a broader context, our study has the potential to inform conservation efforts to address the current global extinction crisis of many species of large sharks.

MATERIALS AND METHODS

Data collection

All published records of *C. megalodon* were collected using the Paleobiology Database (PaleoBioDB, <https://paleobiodb.org>; parameters: species name = *Carcharocles megalodon*, last search date June 2013). The PaleoBioDB takes all synonyms into consideration when searching for a taxon. For a discussion of our taxonomic assignment of the species *megalodon* to the genus *Carcharocles*, see Pimiento *et al.* (2010), Ehret *et al.* (2012), Pimiento *et al.* (2013a,b) and Pimiento & Balk (2015).

We searched for additional *C. megalodon* reports using the ISI Web of Science (<http://webofknowledge.com>), GeoRef (<http://geoscienceworld.org>), Google Scholar (<http://scholar.google.com>) and Shark-References (<http://shark-references.com>) with the search terms: Megalodon OR *Carcharodon* AND *megalodon* OR *Carcharocles* AND *megalodon*. Any new data were catalogued as occurrences in PaleoBioDB (Archive #20: <http://goo.gl/PpIh0G>). In total, the data archive comprised 284 records consisting of 82 pre-existing records and 124 new records.

Each of our data points represented a fossil collection (i.e. a set of fossil occurrences that were co-located geographically and temporally) and were mostly represented by isolated teeth. Each collection was treated as an occurrence and was linked to one or more supporting references. Although *C. megalodon* teeth are typically large and easily recovered from their respective faunas, we also collected records of *C. megalodon* absences (i.e. all other records from the Miocene and Pliocene that reported shark assemblages but not *C. megalodon*). We used the absences in our analysis of occupancy (see below).

Data filtering

We performed a standardized evaluation following the stratigraphic assessment process described in Pimiento & Clements (2014) to determine which occurrence records to include in our analyses. When necessary, and taking into consideration the diagnostic characteristics of the dentition of the species (e.g. Pimiento *et al.*, 2013a), we performed a taxonomic assessment to verify that the specimens reported were indeed *C. megalodon*. This was done by examining the morphology of the fossil specimens. To do so, we either visited the museum collections housing the specimens, or we examined available published images. This was particularly useful when assessing records from the early Miocene, a period in which *Carcharocles chubutensis*, an ancestor of *C. megalodon*, occurs (Applegate & Espinosa-Arrubarrena, 1996; Ward & Bonavia, 2001; Pimiento *et al.*, 2013b; Pimiento & Balk, 2015). We distinguished the two species by the absence of lateral cusplets in the teeth of adults of *C. megalodon* (Pimiento *et al.*, 2013b). As it is not possible to assess ontogeny based merely on specimen examination, we referred those specimens showing a clear absence of lateral cusplets to *C. megalodon*, which were therefore only adults. This had the potential to reduce our sample size, but in turn it provided a robust taxonomic assessment for this time period (see Discussion). We did not include any Pleistocene records in our analyses because: (1) Pleistocene records of *C. megalodon* have been regarded as unconfirmed or unreliable (Applegate & Espinosa-Arrubarrena, 1996), and (2) a recent analyses concluded that *C. megalodon* was probably extinct by this time period (Pimiento & Clements, 2014).

As a result of our age evaluation process, we selected the 206 records that were deemed to be reliable (see Table S1 in Appendix S1 in the Supporting Information) and disregarded the records that did not meet the evaluation criteria (28 records; see Table S2). Additional information can be found in Appendix S2, where we describe the rationale behind the evaluation of each record. More detailed information and supporting references can be accessed by searching for the PaleoBioDB number for each record on the PaleoBioDB website: <https://paleobiodb.org>.

Analyses

All analyses were performed in R (R Core Team, 2015). To visualize all global occurrences of *C. megalodon*, a map with the fossil records was constructed following the methods described in Jaramillo *et al.* (2013). We included all known records, distinguishing between those with adequate stratigraphic and taxonomic information, and those without such information (see Appendix S2).

Using only the reliable records (see Table S1), we resampled the age of each occurrence 1000 times, bootstrapping the timing of each record from a uniform distribution between its upper and lower age. We then binned the resampled data into geological periods, from the early

Miocene to the Pliocene (23.03–2.57 Ma), following the geological time-scale of Gradstein *et al.* (2012). We did not subdivide Pliocene into early and late in order to maintain a relatively equal time span for each bin (i.e. early Miocene, middle Miocene, late Miocene and Pliocene). We then constructed *C. megalodon* occurrence maps for each time bin following the methods of Jaramillo *et al.* (2013) and the tectonic reconstructions provided by GPlates (Boyden *et al.*, 2011).

We placed the occurrences on the maps by creating a circular home range area around each point using 'gBuffer' in the R package *rgeos*. Each circular area had a diameter of 1000 km², based on the maximum longitudinal movement reached by the great white shark (*Carcharodon carcharias*), as reported in Domeier & Nasby-Lucas (2008). Given the differences in body size between these two species (maximum total length = *c.* 6 m in *C. carcharias* versus *c.* 18 m in *C. megalodon*; Fergusson *et al.*, 2009; Pimiento & Balk, 2015), our proxy of the home range of *C. megalodon* represents a conservative estimate. Despite the differences in size (and possibly physiology), *C. carcharias* is widely considered to be a modern ecological analogue of *C. megalodon*. This analogy is based on similarities in trophic level (and hence ecological function), overall tooth and vertebral centrum morphology and taxonomic proximity (Applegate & Espinosa-Arrubarrena, 1996; Purdy *et al.*, 2001; Pimiento *et al.*, 2010; Ehret *et al.*, 2012; Pimiento & Balk, 2015), and it is therefore a useful model for studying the extinct species (e.g. Gottfried *et al.*, 1996; Wroe *et al.*, 2008; Pimiento *et al.*, 2010; Pimiento & Balk, 2015).

In order to qualitatively assess *C. megalodon's* pathway to extinction, we calculated the global area coverage, occupancy range and various latitude metrics per time bin. In addition, we built an ecological niche model with a subset of our samples. The global area coverage was the total area (km²) of the home range areas per time bin (calculated using 'gArea' from the *rgeos* package), which was used as a proxy for geographical range (Kiessling & Aberhan, 2007). We only considered marine areas (i.e. we did not include any area projected to be on land), and overlapping home areas were combined and only included in the area calculation once. Furthermore, given the differences in sample size for each time period, we standardized our bins, bootstrapping the data 1000 times and resampling the bins based on the lowest sample size (i.e. the early Miocene had 23 geographically unique records, whereas the middle Miocene had 75, the late Miocene had 65 and the Pliocene had 43).

Occupancy was determined as the ratio of the number of localities where a species was found to the total number of localities sampled, i.e. occurrences/(occurrences + absences) and was used as a proxy of global abundance (Lyons & Smith, 2010). This metric standardizes the occurrence of each time bin in relation to the total number of samples available. For latitude, we calculated the total range, maximum, minimum, mean and modal latitude per time bin.

In order to explore further the relationship between geographical distribution and climate, we carried out two analyses. For the first, we created time bins using the methods described above, but for every 2 Myr and latitudinal bins every 15°. We then calculated the occupancy range per time and latitudinal bin, and generated a raster image (using 'geom_raster' from the *ggplot2* package). We used occupancy rather than occurrence to take into account the difference in total number of sites (= samples) per bin. For the second analysis, we developed an ecological niche model using a subsample from the Pliocene. Our subsample consisted of the 18 occurrences (marked with an asterisk in Table S1) that overlapped with the climatic global circulation model CCSM4 (community climate system model; Peter *et al.*, 2011) and represented a solid estimate of the distribution of the species because it covered its entire latitudinal range. We built the model for the Pliocene using the climatic envelope 'Bioclim' (Busby, 1991), then projected the model into the Last Glacial Maximum, Holocene and Recent to test whether the climatic changes during the glacial–interglacial periods would have been related to changes in the distribution of the species. For a detailed methodology see Appendix S2.

RESULTS

Carcharocles megalodon was distributed globally, with occurrences in the Pacific, Atlantic and Indian oceans. The species had a geographical range from 55.28° N to 43.99° S and from 178.32° E to 122.35° W and it was found mostly in the Americas (Argentina, Chile, Colombia, Costa Rica, Ecuador, Mexico, Panama, Peru, USA, Venezuela and Uruguay), the

Caribbean and western Atlantic (Antigua and Barbuda, Barbados, Cuba, Grenada, Jamaica and Puerto Rico), and Europe (Austria, Belgium, Cyprus, Czech Republic, Denmark, France, Germany, Greece, Italy, Malta, the Netherlands, Turkey, Poland, Portugal, Slovakia and Spain) (Fig. 1). Fossil occurrences were also located in Asia (Japan, India and Myanmar), Africa (Angola, Libya, Nigeria and South Africa) and Oceania (Australia, Fiji and New Zealand). Reports with inadequate or insufficient stratigraphical, geographical or taxonomic information included occurrences from Austria, Colombia, Germany, India, Italy, Japan, Malta, Mexico, UK, USA (California and South Carolina), South Africa, Spain and Venezuela. Areas with a lack of occurrences included Brazil, the Pacific coast of northern Central America, the northern part of the Indian Ocean, the Arctic Ocean and the Southern Ocean (Fig. 1).

Our data-quality screening process and time-binning analysis revealed that the oldest reliable records of *C. megalodon* were early Miocene in age (see Appendix S2). For this time period, fossils of the species were mostly distributed in the Northern Hemisphere, with the majority of the fossil occurrences being in the Caribbean, western Atlantic and Mediterranean Sea, and a few in the central Paratethys (Austria), eastern Atlantic (Portugal), Indian Ocean (India) and USA (California). Southern Hemisphere records only included a few occurrences in Australia (Fig. 2d; see Appendix S2). For the middle Miocene, records of *C. megalodon* were present in the major ocean basins of the world, occurring widely in the Neotropics (the Caribbean and central Eastern Pacific), the western Atlantic (New Jersey and Maryland) and Europe (eastern

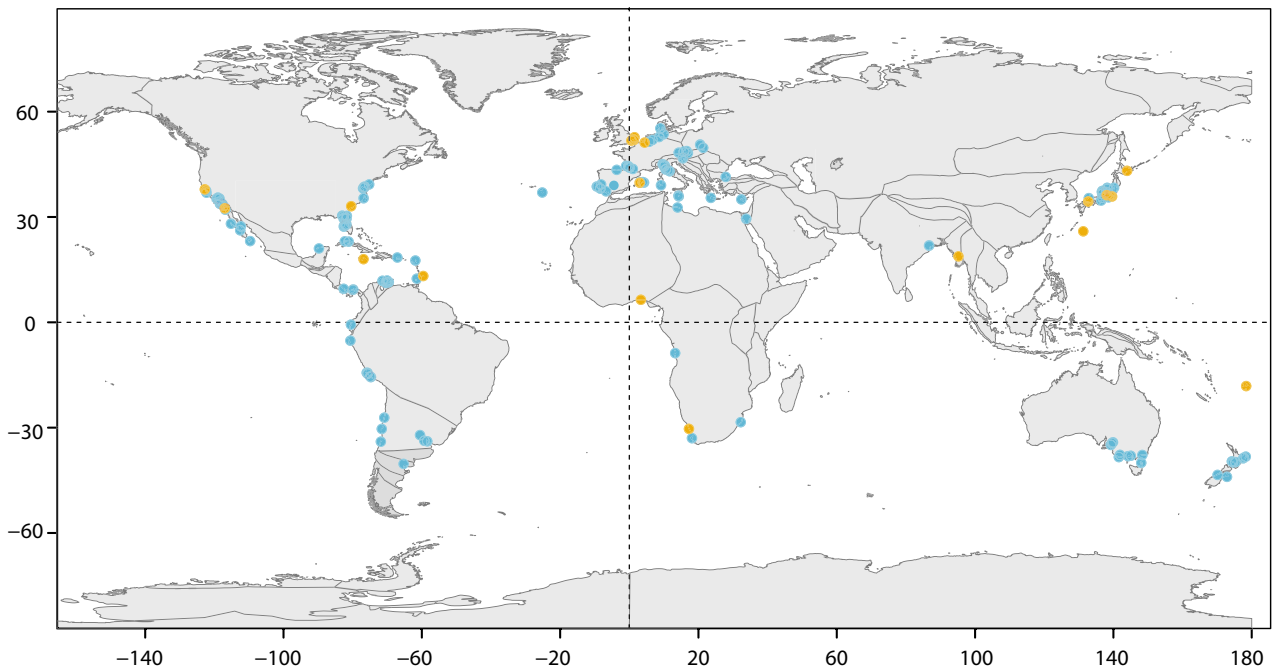


Figure 1 *Carcharocles megalodon* fossil occurrences. Blue dots represent fossil occurrences of the species, yellow dots represent dubious occurrences (i.e. occurrences without adequate associated stratigraphic, taxonomic or geographical information).

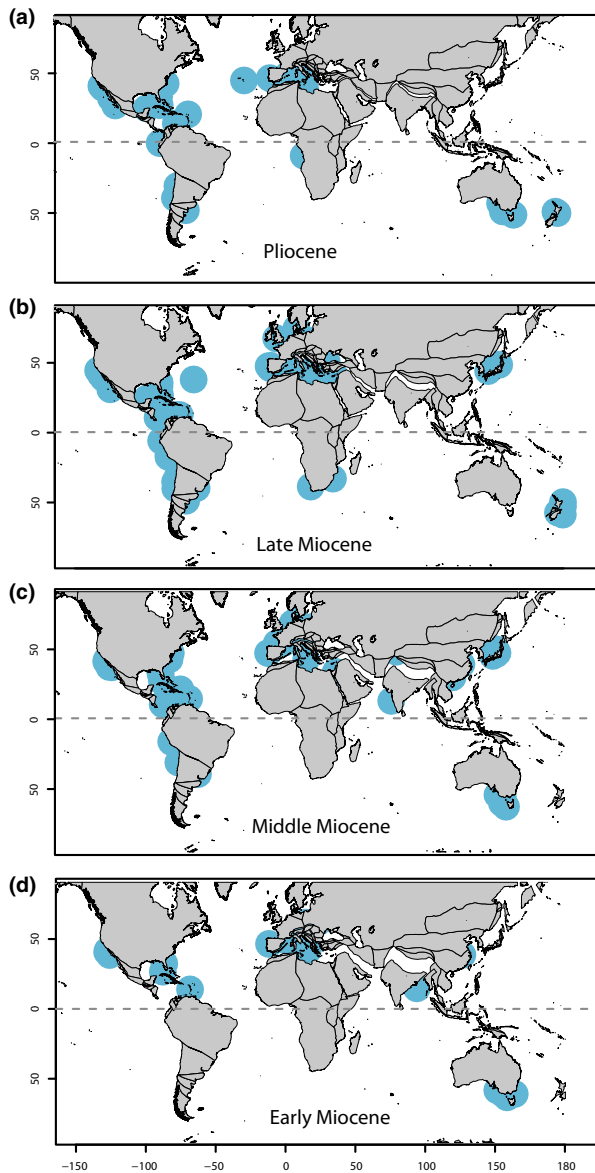


Figure 2 *Carcharocles megalodon* buffer circles area over geological time. (a) Pliocene, (b) late Miocene, (c) middle Miocene, (d) early Miocene.

Atlantic and Mediterranean–central Paratethys). In the Indo-Pacific Ocean, *C. megalodon* occurred in Australia and India, and in the western Pacific it occurred in Japan (Fig. 2c). For the late Miocene, records of *C. megalodon* were distributed along the coasts of the Americas (from California to Chile in the Pacific, and from Florida to Argentina in the Atlantic) and Europe, with some occurrences in southern Africa, New Zealand and Japan (Fig. 2b). For the Pliocene, the fossil record of *C. megalodon* had a scattered distribution along the Americas, with occurrences in Europe, Australia, New Zealand and Angola (Fig. 2a). Taken together, the temporal maps revealed that the Atlantic Ocean (including the Caribbean), California and Australia were persistently inhabited by this species throughout its duration.

Geographical analyses indicated that during the early and middle Miocene *C. megalodon* presented its narrowest coverage (early Miocene median = 20.05 million km²; middle Miocene median = 19.22 million km²; calculated from 1000 randomizations). During the late Miocene it reached its broadest coverage (median = 24.94 million km²), to then decline in the Pliocene (median = 21.91 million km²) (Fig. 3, blue line). Analyses of relative abundance showed that the minimum occupancy range occurred during the early Miocene (25%), and the maximum during the middle Miocene (47%). During the late Miocene and Pliocene, the occupancy of *C. megalodon* decreased (36% and 29% respectively) (Fig. 3, green line). Similarly, latitudinal range estimations showed maximum values during the middle and late Miocene, a tropical modal value in the late Miocene, and mostly tropical mean values overall (Table 1).

We found no latitudinal gradient, and no evidence of correlation between occupancy values per latitude and temperature trends over time (Fig. 4). Major events in global climate during the Miocene and Pliocene, such as the high temperature values reached during the Mid-Miocene Climatic Optimum (MMCO; 17–15 Ma) and the subsequent cooling as a result of the re-establishment of a major ice sheet on Antarctica (c. 10 Ma) (Zachos *et al.*, 2001), did not correspond with either an increase or decrease in *C. megalodon* latitudinal abundance (Fig. 4). Finally, our ecological niche models based on Pliocene records indicated that *C. megalodon* inhabited oceans with a mean annual temperature from 12

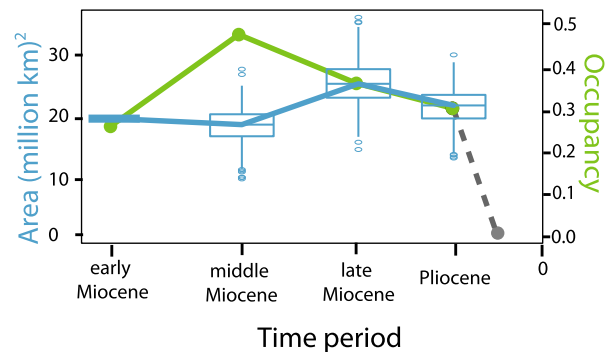


Figure 3 *Carcharocles megalodon* geographical distribution over time. Blue = global area coverage (a proxy of geographical range). The box plot shows the interquartile range of the 1000 randomizations. The line connects the median value of each period. Green = species occupancy (a proxy of global abundance).

Table 1 *Carcharocles megalodon* latitudinal metrics over time.

	Range	Maximum	Minimum	Mean	Mode
Pliocene	87.60°	44.90° N	42.70° S	14.74°	28.00°
Late Miocene	102.50°	55.50° N	47.00° S	13.3°	9.10°
Middle Miocene	102.60°	53.10° N	49.50° S	29.56°	34.50°
Early Miocene	98.20°	48.70° N	49.50° S	19.95°	38.70°

to 27 °C (maximum 18–33 °C, minimum = 1–24 °C; see Table S3). Our projections showed that the global areas climatically suitable for *C. megalodon* would have not been affected significantly by the temperature changes during the Pleistocene, Holocene and Recent. For instance, there was a decrease of only 2% in the predicted area during the Last Glacial Maximum, and an increase of 8% and 9% in the predicted areas during the Holocene and Recent respectively (Fig. 5).

DISCUSSION

Our analyses of fossil occurrences indicate that *C. megalodon* was a cosmopolitan species with a widespread distribution that covered the major ocean basins in the tropical, subtropical and temperate regions (Fig. 1; see Table S3). Analyses of occurrences over time showed that *C. megalodon* originated during the early Miocene (Fig. 3), rather than the middle Miocene as previously assumed (Applegate & Espinosa-Arrubarrena, 1996; Purdy *et al.*, 2001; Pimiento *et al.*, 2010, 2013a,b; Pimiento & Balk, 2015). Furthermore, it has been widely accepted that *C. chubutensis* (or its synonym *Carcharocles subauriculatus*) preceded *C. megalodon* and occurred in the early Miocene (Applegate & Espinosa-Arrubarrena, 1996; Pimiento *et al.*, 2013b). However, our data evaluation process (see Appendix S2) and time-binning analysis indicated that *C. megalodon* also occurred in the early Miocene. These early Miocene records were carefully examined following our evaluation process (see Appendix S2) to corroborate that they were indeed *C. megalodon*, and not *C. chubutensis* (see Materials and Methods). Among these records, those stratigraphically constrained to the stage level reported *C. megalodon* in the Burdigalian (20.43–15.97 Ma). Given that both *C. megalodon* and *C. chubutensis* are chronospecies within the megatooth lineage (Ward & Bonavia, 2001; Pimiento & Balk, 2015), it is possible that *C. chubutensis*

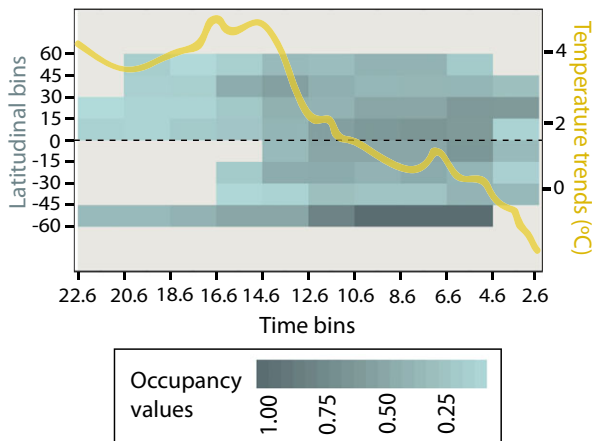


Figure 4 Species occupancy over time and latitude. Blue squares = occupancy values per latitude bin. Grey area = cells with no data. Gold line = temperature trends from Zachos *et al.* (2001).

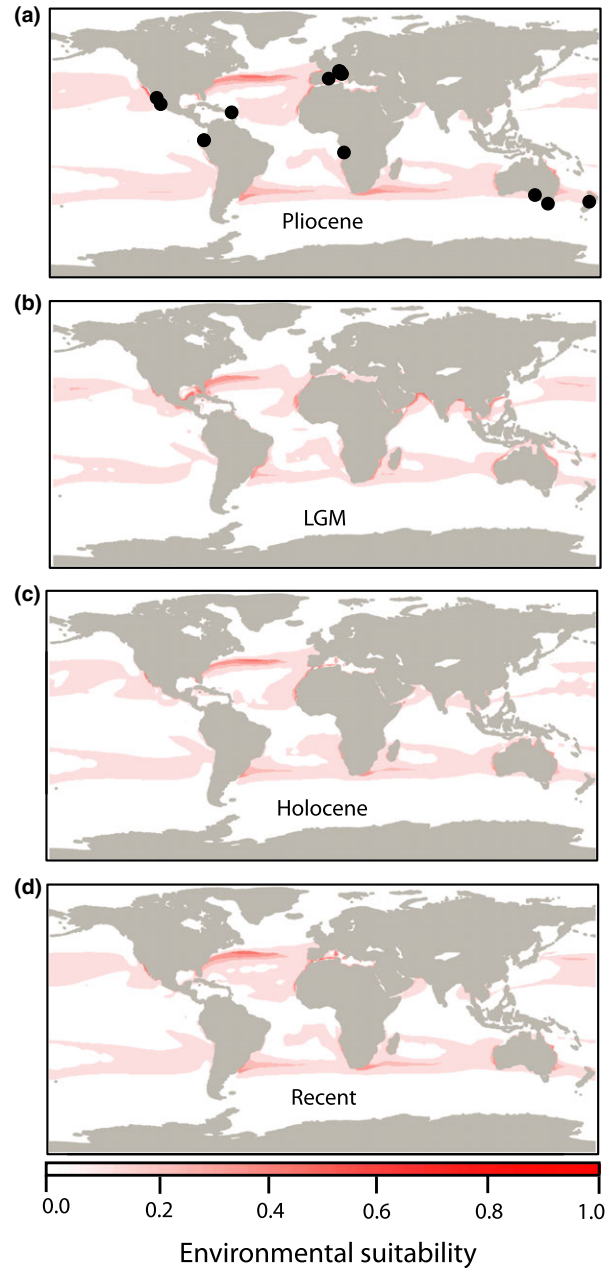


Figure 5 Potential environmentally suitable areas for *Carcharocles megalodon* in the Pliocene, projected to the Last Glacial Maximum (LGM), Holocene and Recent time periods. Black dots indicate the fossil occurrences. Suitability ranges from 0 (not suitable) to 1 (optimum).

occurred during the Aquitanian and *C. megalodon* originated in the Burdigalian. More studies are needed to establish the origination and extinction times of all chronospecies within the megatooth lineage.

Carcharocles megalodon reached its maximum geographical range value (area coverage) in the late Miocene (Fig. 3, blue line). However, at the same time its global abundance started decreasing (Fig. 3, green line). Therefore, *C. megalodon*'s maximum geographical range coincides with a decline in its

global abundance. This discrepancy indicates that the extensive geographical range of *C. megalodon* in the late Miocene could have been a response to a global population decline. This result also suggests that geographical range alone cannot be considered an indicator of extinction vulnerability, as a widespread range can be a response to population decline.

Biotic mechanisms

The pathway to extinction of *C. megalodon* started in the late Miocene, with a drop in its global abundance (Fig. 3). During this time, a number of biotic events occurred that could have been related to this trend. A massive diversity crash of cetaceans took place around this time (Marx & Uhen, 2010; fig. 1). Whether or not *C. megalodon* preyed upon marine mammals remains an open question; however, cetacean fossils [e.g. mysticetes (filter-feeding whales) and odontocetes (toothed whales)] are frequently found together with *C. megalodon* teeth, and *C. megalodon* bite marks have been identified in some cetacean material, leading to the hypothesis of a predator–prey relationship (Spizuco *et al.*, 1993; Morgan, 1994; Allmon *et al.*, 1996; Gottfried *et al.*, 1996; Purdy, 1996; Allmon, 2001; Purdy *et al.*, 2001; Aguilera & De Aguilera, 2004; Aguilera *et al.*, 2008; Antunes *et al.*, 2015). This hypothesis is further supported by the significant increase in mysticete body size after the extinction of *C. megalodon* (Pimiento & Clements, 2014). The coincidental timing of the decline in global abundance of *C. megalodon* and the drop in diversity of mysticetes and odontocetes during the late Miocene suggests that the evolutionary history of cetaceans played a role in the extinction of *C. megalodon*.

Another biotic factor that could have been connected with the decline in global abundance of *C. megalodon* during the late Miocene is the appearance of new potential competitors. During the middle Miocene, raptorial sperm whales appeared and persisted through the late Miocene (Lambert *et al.*, 2010). It has been proposed that these pan-physeteroids occupied feeding niches similar to that of extant killer whale, *Orcinus orca*. If so, some of the largest of these raptorial apex predators probably fed mostly on smaller baleen whales and other marine mammals, and therefore competed with *C. megalodon* for available food resources (Lambert *et al.*, 2010, 2014). Furthermore, *Carcharodon hubbelli*, the ancestor of the modern great white shark (*C. carcharias*), first appeared during the late Miocene (Ehret *et al.*, 2012). Evidence of competition between *C. megalodon* and *C. hubbelli* has not been reported, but the co-occurrence of both has been recorded in the Pisco Formation of Peru (Ehret *et al.*, 2012). Moreover, based on tooth morphology (a good proxy of diet), the great white shark and *C. megalodon* are considered to be ecological analogues (Applegate & Espinosa-Arrubarrena, 1996; Purdy *et al.*, 2001; Pimiento *et al.*, 2010; Ehret *et al.*, 2012; Pimiento & Balk, 2015). It therefore can be inferred that, when they co-occurred, these two closely related sharks were competing for some of the same

resources (e.g. smaller cetaceans such as small whales and dolphins).

In the Pliocene, the relative abundance of *C. megalodon* not only continued to decrease, but its geographical range also declined (Fig. 3). At the end of the late Miocene and during part of the Zanclean (early Pliocene), there was a temporary increase in the diversity of cetaceans (Morgan, 1994). However, during the rest of the Pliocene, mysticete diversity declined again (Allmon *et al.*, 1996; Allmon, 2001; Marx & Uhen, 2010). Lindberg & Pyenson (2006) noted the permanent attenuation of mysticete diversity coincident with the last records of *C. megalodon* during the Pliocene. Although odontocetes also declined during the first half of the Pliocene, they had a slight recovery at the end of the Pliocene and throughout the Pleistocene (Marx & Uhen, 2010). In addition, the appearance and diversification of other potential competitors for *C. megalodon* also occurred during the Pliocene, including large delphinids, for example, the killer whale (*Orcinus*) (Lindberg & Pyenson, 2006), and the modern great white shark, *C. carcharias* (Ehret *et al.*, 2012).

Previous studies have found that macro-evolutionary trends in large sharks are linked to the origin and diversification of marine mammals (Adnet & Martin, 2007). Because the predator–prey and competitive interactions of *C. megalodon* have not been rigorously studied yet, we cannot know for certain whether *C. megalodon* fed directly upon filter-feeding whales, or competed directly with large odontocetes and the great white shark (e.g. Morgan, 1994). However, the evidence from the marine fossil record suggests that biotic factors in the late Miocene (a drop in potential diversity of cetaceans and the appearance of new competitors) and Pliocene (a persistent diversity drop in mysticetes and the appearance and diversification of new apex predators) coincide with the continued and prominent decrease in geographical distribution of *C. megalodon* prior to its extinction at the Pliocene/Pleistocene boundary. Future studies are needed to clarify the identity of species interacting with *C. megalodon*.

Climatic mechanisms

It has been suggested that the extinction of *C. megalodon* was associated with climate change (Gottfried *et al.*, 1996). Various climatic events can be associated with the distributional trends of this species over time. For instance, the maximum global abundance of *C. megalodon* during the middle Miocene (Fig. 3) overlaps with the exceptionally warm climates of MMCO. Moreover, its subsequent drop in global abundance during the late Miocene coincides with the relatively cooler climates that occurred thereafter. During the Pliocene, the continuing decline of *C. megalodon* corresponds with the well-known oscillation of warm and cold temperatures (Fig. 4; Zachos *et al.*, 2001). Thus, it is possible that *C. megalodon* benefited from warmer climates and was negatively affected during colder (or transitional) periods, as

previously proposed (Gottfried *et al.*, 1996; Purdy, 1996). If this was the case, then during cold periods higher occupancy values should be expected towards the tropics compared with temperate regions. Even when we found a higher frequency of occurrences in tropical latitudes during the late Miocene (modal value; Table 1), our analysis of occupancy range per latitude and time did not show such a gradient (Fig. 4). Moreover, we found that the distribution of *C. megalodon* did not contract during cold periods, nor did it expand during warm periods (Fig. 4).

Distributional shifts in marine mammals, i.e. cetaceans (Gaskin, 1982) and pinnipeds (Deméré *et al.*, 2003: fig. 3.7), to anti-tropical latitudes have been proposed as another potential cause of the extinction of *C. megalodon* (Gottfried *et al.*, 1996). This hypothesis implies that this shark was physiologically unable to follow its prey to higher latitudes. Conversely, our results indicate that *C. megalodon* occurred in a wide geographical and temperature range, including anti-tropical latitudes (Figs 2 & 5; Table 1; see Table S3). Most importantly, our ecological niche models show that global temperature changes (such as the extreme cold climate of the Last Glacial Maximum) would not have affected the distribution of *C. megalodon*. These results are in agreement with the physiological capability of large sharks (such as the great white shark, an ecological analogue of *C. megalodon*) to conserve metabolic heat by maintaining a higher body temperature than the surrounding water, i.e. mesothermy or regional endothermy (Bernal *et al.*, 2001; Grady *et al.*, 2014), which in turn gives them the capacity to exist in colder waters (Goldman, 1997; Bonfil *et al.*, 2005) and have a widespread distribution (Fergusson *et al.*, 2009; Dambach & Rödder, 2011). Taken together, our results demonstrate that the pathway to extinction for *C. megalodon* was not driven directly by temperature limitations.

CONCLUDING REMARKS

The study of the geographical distribution of *C. megalodon* over its temporal range reveals that the pathway to extinction of this species started in the late Miocene with a decline in its global abundance. During the Pliocene both its geographical range and the global abundance showed a final drop (Fig. 3). We interpret the overall decline in the distribution of *C. megalodon* to be a response to prey availability and other factors that indirectly regulated prey abundance, such as competition from other predators. Although these biotic factors could have been driven by oceanographic changes (Allmon *et al.*, 1996; Allmon, 2001; Deméré *et al.*, 2003; Marx & Uhen, 2010) we found no correlation between temperature and distribution. Furthermore, the coincidental timing between the maximum values for geographical range and the initial decrease in global abundance during the late Miocene (Fig. 3) demonstrates that, in cosmopolitan species, geographical range alone cannot be considered an indicator of extinction vulnerability, as range broadening can be a long-term response to population decline. This study reveals

clues regarding the pathway to extinction for the largest shark that ever lived. Further studies of predator–prey interactions in relevant ancient marine ecosystems are needed to identify the causes of its extinction.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Occurrences of *Carcharocles megalodon* included (Table S1) and excluded (Table S2) in the analyses.

Appendix S2 Additional methodological information.

BIOSKETCH

Catalina Pimiento is a postdoctoral researcher interested in the macroecology of apex predators. She studies long-term diversity dynamics, environmental constraints, biogeography, body size and the extinction of marine mega-fauna.

Author contributions: C.P., B.M. and B.S. conceived the ideas; C.P., C.C., S.V. and C.J. designed the analyses; C.P. collected the data; C.P., C.C. S.V. and J.V.J. analysed the data; C.P. led the writing.

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