



Climate cooling and clade competition likely drove the decline of lamniform sharks

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Edited by Nils Chr. Stenseth, University of Oslo, Oslo, Norway, and approved August 20, 2019 (received for review February 20, 2019)

Understanding heterogeneity in species richness between closely related clades is a key research question in ecology and evolutionary biology. Multiple hypotheses have been proposed to interpret such diversity contrasts across the tree of life, with most studies focusing on speciation rates to explain clades' evolutionary radiations, while often neglecting extinction rates. Here we study a notorious biological model as exemplified by the sister relationships between mackerel sharks (Lamniformes, 15 extant species) and ground sharks (Carcharhiniformes, ~290 extant species). Using a comprehensive fossil dataset, we found that the diversity dynamics of lamniforms waxed and waned following repeated cycles of radiation phases and declining phases. Radiation phases peaked up to 3 times the current diversity in the early Late Cretaceous. In the last 20 million years, the group declined to its present-day diversity. Along with a higher extinction risk for young species, we further show that this declining pattern is likely attributed to a combination of abiotic and biotic factors, with a cooling-driven extinction (negative correlation between temperature and extinction) and clade competition with some ground sharks. Competition from multiple clades successively drove the demise and replacement of mackerel sharks due to a failure to originate facing the rise of ground sharks, particularly since the Eocene. These effects came from ecologically similar carcharhiniform species inhibiting diversification of medium- and large-sized lamniforms. These results imply that the interplay between abiotic and biotic drivers had a substantial role in extinction and speciation, respectively, which determines the sequential rise and decline of marine apex predators.

extinction | fossils | macroevolution | paleoenvironment

The dynamics of species richness over time is determined by variation in speciation and extinction rates that drive clades to successively thrive, decline, and replace one another (1–3). These variations in rates are further impacted by abiotic and biotic factors shaping these deep-time changes in biodiversity (4–6). Deciphering the roles of how these factors influenced speciation and extinction through time and across clades is a central focus in evolutionary biology (7, 8). Several studies have suggested that environmental forcing such as global temperature variations (9, 10), or sea-level fluctuations (11), played an overarching role in determining the fate of whole clades, but the wax and wane of clades could also be the result of biotic interactions, and in particular, competition for resources and predation (4, 12). Competition is usually assumed to occur mostly among closely related species, but it may also take place among species from different clades with similar ecology (13, 14). The role of competition has been suggested as the main evolutionary mechanism in clade dynamics, either through a passive replacement or active displacement (15). In the former, an incumbent clade initially prevents a competing clade from radiating, which can only radiate after the incumbent clade declines, freeing ecological space (13, 16). In the latter, it occurs when the rise in diversity of a clade drives the decline of another clade by outcompeting it on limited resources (14, 16). Although clade competitive interactions have recently been unveiled over long time scales, few studies have shown an interplay of abiotic and biotic drivers (5, 14, 17).

The shark order Lamniformes (mackerel sharks, Fig. 1A) includes some of the most iconic shark species, such as the great white (*Carcharodon carcharias*) and extinct (†) megalodon (†*Otodon megalodon*), as well as more unusual representatives like the goblin shark (*Mitsukurina owstoni*) and megamouth shark (*Megachasma pelagios*). Currently, this order contains only 15 species distributed in 7 families (Fig. 1A), 4 of which are monospecific (18). Despite the low extant specific diversity, lamniforms have high morphological and ecological disparities (18, 19). Their body size ranges from 1 m for the crocodile shark (*Pseudocarcharias kamoharui*) to 8 m for the basking shark (*Cetorhinus maximus*) and the megalodon is estimated at 17 m (20). Although living mackerel sharks are mostly pelagic, some species are more nectobenthic (*Carcharias taurus*). Lamniforms can be found at different depths, from coastal waters to the bathypelagic zone (up to 1,300 m of depth). Their diet is diverse as this order includes small- to medium-sized carnivorous to large apex predators (great white), but also filter feeders (basking and megamouth sharks), and this diet diversity is even more marked when fossil taxa are included (hypercarnivorous and small nectobenthic species). The fossil record of lamniforms dates back to the Early Cretaceous ~140 million years ago (Mya), and indicates they were diverse during the mid and Late Cretaceous (21, 22).

The low diversity, low number of species per family, and strong morphological and ecological disparity have often been used to characterize living lamniform species as representatives of relict clade that was once speciose and subsequently experienced a diversity decline during their evolutionary history (21, 23, 24), but that has not yet been demonstrated and understood. Drivers of their diversification dynamics and decline are unknown but have

Significance

Many lineages increase in diversity through time, and some of them eventually decline and get replaced. The causes of such diversity decline remain elusive and are especially difficult to understand over a long-time scale and global distribution. Relying on unprecedented species-level fossil datasets spanning the last 140 million years, we investigated the causes of the wax and wane of mackerel sharks (Lamniformes), including the great white shark. We find that both temperature and competition with some ecologically similar members of their sister group, the ground sharks, played a substantial role in the lamniform demise. Our results provide quantitative evidence that the Court Jester and Red Queen can jointly drive the radiation and extinction of entire lineages.

Author contributions: F.L.C. and G.G. designed research; F.L.C., J.R., and G.G. performed research; F.L.C., J.R., and G.G. analyzed data; and F.L.C. and G.G. wrote the paper.

The authors declare no conflict of interest.

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This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1902693116/-DCSupplemental.

First Published September 23, 2019.

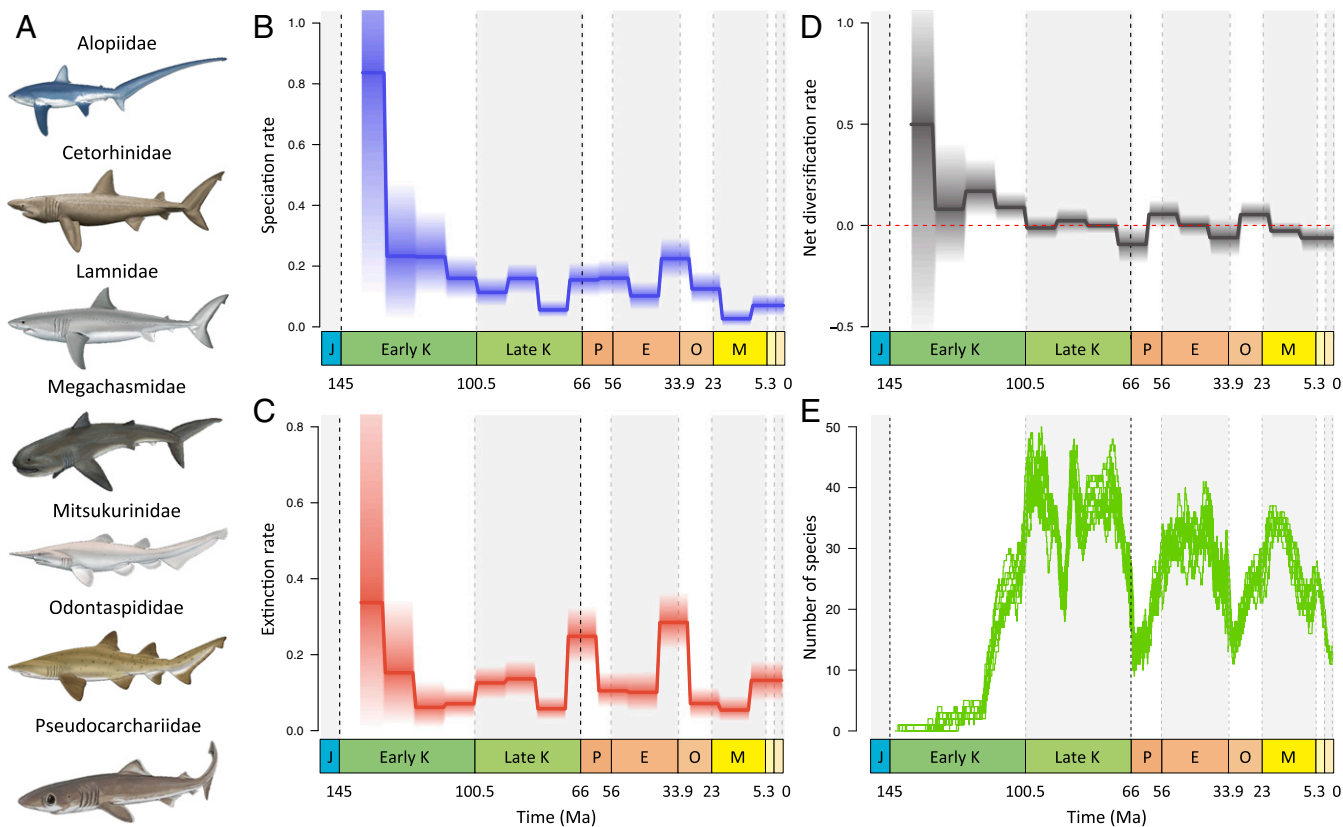


Fig. 1. The rise and fall of lamniforms controlled by time-variable speciation and extinction. (A) Illustration of the 7 extant lamniform families. Shark images courtesy of Marc Dando (artist). Inferences of speciation (B) and extinction (C) rates with analyses at the species level under the birth–death model with constrained shifts. (D) The net diversification rates are the difference between speciation and extinction rates (rates below 0 indicate declining diversity). Solid lines indicate mean posterior rates and the shaded areas show 95% CI. (E) The lamniform diversity trajectories incorporating uncertainties around the age of the fossil occurrences. The results indicate that: 1) diversification of lamniforms was elevated in the Early Cretaceous, 2) net diversification rates decreased through time and were punctuated by high-extinction peaks at the K-Pg and E-O boundaries, 3) species diversity bounced back but did not recover to preextinction levels, and 4) the lamniforms decline since the last 20 My. J, Jurassic; K, Cretaceous; P, Paleocene; E, Eocene; O, Oligocene; M, Miocene.

been tentatively linked to abiotic factors such as temperature (21) or to the Cretaceous–Paleogene (K–Pg) extinction and subsequent filling of their former ecological niches by ground sharks (Carcharhiniformes) (25–27). The elasmobranch fossil record is mainly based on isolated teeth, resulting in a particularly good preservation potential compared to other marine vertebrates (21). However, lack of information on tooth morphology of some living taxa may hamper the identification of some of their fossil representatives (28). As opposed to some elasmobranch groups, lamniforms have most of their living species represented in the fossil record (12 over 15) and their dentition and tooth morphology are well known. With more than 360 fossil species described, the rich and well-identified lamniform fossil record, along with their ecological specificities and long evolutionary history, offers a unique opportunity to study the processes and mechanisms of diversification among marine vertebrates.

We compiled and analyzed the species-level fossil record of lamniforms, which spans the entire existence of the order since the Cretaceous. We used a Bayesian framework (see *Materials and Methods*) to investigate whether and to which extent speciation and extinction rates responded to major environmental changes in Earth history, tooth size evolution (a proxy of body size and trophic levels), and competition with carcharhiniforms (ground sharks). The latter are sister group to lamniforms (29, 30) and are often considered to ecologically replace them after the K–Pg extinction (25–27, but see ref. 21) and display convergent tooth morphologies with some extinct lamniforms. To quantitatively test for the effect of competition of carcharhiniforms over the evolutionary history of

lamniforms, we compiled the fossil record for carcharhiniforms, which harbor high species diversity today (~290 species) (18). Our approach estimates process-based birth–death models while incorporating the preservation process and uncertainties associated with the age of fossil occurrences (31) (*SI Appendix, Table S1*). We thus simultaneously assessed the effect of co-occurring clades on their speciation and extinction rates by quantitatively investigating the passive and active roles of competition among 2 marine vertebrate clades throughout the Cretaceous and Cenozoic.

Results and Discussion

The Boom-and-Bust Diversification of Mackerel Sharks. The fossil record of lamniforms includes 2,051 occurrences assigned at the genus level and 1,698 occurrences assigned at the species level, which represent 82 genera (10 extant and 72 extinct, *Dataset S1*) and 373 species (12 extant and 361 extinct, *Dataset S2*). We inferred the diversification history of lamniforms using a birth–death model with constrained shifts (BDCS) (31, 32) at both the species and genus levels. Shifts were analyzed using predefined time intervals (10 million years [My] or geological epochs), where rates can change between time bins. In all analyses, our results indicate that the diversity dynamics of lamniforms conform to a time-variable birth–death process characterized by decreasing net diversification through time (Fig. 1B and *SI Appendix, Figs. S1–S3*). This pattern is marked by high background extinction rates and is punctuated by peaks of extinction rates at the K–Pg and the Eocene–Oligocene (E–O) boundaries (Fig. 1C and *SI Appendix, Figs. S1–S3*). Net diversification rates (defined as speciation minus

extinction) are particularly high during the Early Cretaceous and generally decreased through time with negative peaks at the K-Pg and E-O boundaries (Fig. 1D), suggesting the group lost species diversity at these events (Fig. 1E and *SI Appendix*, Figs. S1–S3). After the K-Pg event, the lamniform diversity bounced back but did not recover the preextinction levels of diversity, nor did it after the E-O event. More importantly, we find that lamniform diversity is in decline since the last 20 My (Fig. 1D and E and *SI Appendix*, Figs. S1–S3). The taxonomic levels used in the analyses did not alter the inferred pattern of diversification (only the magnitude of rates differs between genus and species datasets). Therefore, our results support the idea that the demise of a clade is controlled not only by an increase in its extinction rate but also by a decrease in speciation through time (1–3).

Ecological and Evolutionary Determinants of a Diversity Decline. Several factors could explain these dynamics, and we tested competing hypotheses (14, 31, 33). We first tested for the hypothesis of an effect of body size on clades' diversity dynamics since it has been shown that fish body size evolution is correlated with diversification rates (34), although this pattern seems absent in other clades (14). We compiled measurements of tooth crown height of 350 lamniform species (96.1% of the nonfilter-feeding species present in the dataset, see *Dataset S3*) and find no evidence that tooth size evolution impacted speciation and extinction for the entire group (*SI Appendix*, Fig. S4 and Table S2). Because fossil and extant lamniforms display a wide range of ecologies, we categorized tooth crown height into 3 classes of lamniform species ("small," "medium," and "large"), which correspond to main ecologies (see *Materials and Methods*). We find that both speciation and extinction rates of large lamniform species correlate negatively with tooth size (*SI Appendix*, Table S2), suggesting that the largest, and hence more ecologically specialized species (18) show lower extinction and speciation rates than other species. This translates into high turnover rates within these specialized ecological niches, which has been reported in other clades (35). The analyses also indicate an extinction selectivity at the K-Pg and E-O events where the extinction rates rose sharply at the K-Pg event for medium lamniforms, while the extinction increased at the E-O event for large lamniforms (*SI Appendix*, Figs. S5–S7). This latter marked extinction event was not reported in previous analyses of elasmobranch diversification patterns and echoes earlier results showing marked diversity drops in marine invertebrates and terrestrial vertebrates, which were linked with global climate cooling (36, 37). Note that the abundance of fossiliferous rock does not exert a bias on our analyses (preservation rates, α_q , in *SI Appendix*, Table S2). By fitting an age-dependent extinction (ADE) model (38), we found strong evidence for ADE in medium and large lamniforms, in which the recently originated species are much more likely to become extinct than older species (*SI Appendix*, Table S3). This means that the extinction rate for a large lamniform species 0.1 My after its speciation is 2.384, whereas the extinction rate is considerably lower (0.459) for a species that has lived 1 My and even reduces to 0.088 for species living after 10 My. These results agree with previous studies on ADE, which mostly found a similar relationship between taxon age and extinction risk (see ref. 39 and references therein, but see ref. 40) including carnivorous terrestrial clades (38). Geographical range may impact extinction probability as widely distributed taxa are buffered against extinction (41). For instance, the megatooth lineage (genus †*Otodus*), which includes a succession of gradually larger apex predators across the Cenozoic and culminating with the megalodon (20), exemplifies this pattern. This lineage includes 18 species of which the median longevity is less than 2 My, but includes the most specialized hypercarnivorous species, which lived over 23 My. Interestingly, the †*Otodus* species that have the longest longevity (>20 My) are those with a cosmopolitan range (†*Otodus angustidens*, †*Otodus auriculatus*, †*O. megalodon*, †*Otodus obliquus*, and †*Otodus sokolovi*), whereas short-lived (~2 My) species are endemic or regionally

distributed, which lends support to an effect of geographic range on extinction probability. However, these results alone cannot explain the global decline in lamniform diversity.

We investigated the effect of abiotic factors (environmental changes), approximated by global continental fragmentation (42), global sea-level fluctuations (43), and global temperature variations (44, 45), which have been shown to control diversity dynamics (10, 13). We examined whether speciation ($\gamma\lambda$) and/or extinction ($\gamma\mu$) correlate with 1 of these variables using an environment-dependent birth–death model (14, 46) (see *Materials and Methods*). We recovered no signal of continental fragmentation and sea level (*SI Appendix*, Figs. S8 and S9 and Tables S4–S6) on speciation and extinction rates at both species and genus levels, suggesting that tectonic and eustatic changes did not influence the diversification of lamniforms. However, we found that temperature variations significantly correlate negatively and weakly with species-level extinction rate with stronger effect at genus level (Fig. 2, $\gamma\mu_{\text{species}} = -0.0082$ vs. $\gamma\mu_{\text{genus}} = -0.0327$) and positively, albeit not significantly, with speciation/origination rates (*SI Appendix*, Fig. S10 and Table S6). In other words, species (or genus) extinction increased by 0.82% (3.27%) as global temperatures decreased, and conversely. For instance, over the past 5 My, this result translates into a 0.82% increase of species extinction each time global temperatures decreased by 0.92 °C in average. This indicates that the Cenozoic climate cooling slowly increased the extinction of lamniforms up to the point that extinction exceeded speciation, which led to a declining-diversity pattern driven by temperature-dependent macroevolutionary processes. Among environment-dependent models, the best-fit model explaining the global diversification of lamniforms is the temperature-dependent model for both taxonomic levels (*SI Appendix*, Tables S7 and S8).

However, the global extent of a relationship between a given environmental change and diversity is difficult to discern and confounded by issues in linking a single global parameter like sea level with heterogeneous diversity patterns. For instance, changes in sea level can be attributed to a first-order transgressive-regressive cycle driven by the ongoing fragmentation of Pangaea, and geothermal uplift at midoceanic ridges, and has previously been proposed to have driven regional extinctions (11). It is thus possible

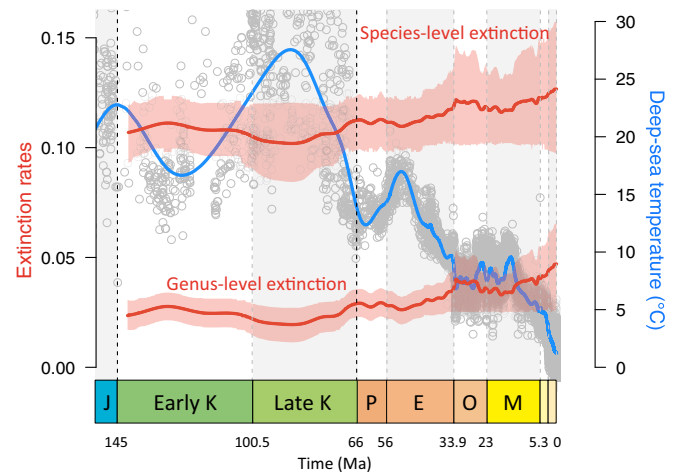


Fig. 2. The Cenozoic climate cooling spurred the extinction of lamniforms. In red are the estimated extinction curves if extinction was exclusively driven by temperature variations as modeled by temperature-dependent birth–death analyses. Superimposed are global variations of past temperature and the extinction rate of lamniforms depending negatively on paleotemperatures (solid line = mean posterior rates and shaded areas = 95% CI). Extinction increased as global climate cooled. More details can be found in *SI Appendix*, Fig. S10 and Table S6. Abbreviations as in Fig. 1.

that multiple environmental variables acted on the diversification of lamniforms. However, when abiotic variables were analyzed simultaneously using a multivariate birth–death (MBD) model (33), results confirmed that continental fragmentation and sea-level fluctuations did not influence lamniform diversification, but that temperature variations correlated positively with speciation and negatively with extinction (*SI Appendix*, Fig. S11 and Tables S9 and S10).

Establishing a relationship between climate and evolutionary processes stems from elucidating the role of temperature on clades' diversification (47). The observation that climate change has a role over biodiversity dynamics is not surprising in light of recent research that has demonstrated substantial temperature-dependent variations in other marine groups (5, 10, 17, 46, 48, 49), but also on terrestrial groups (9, 49). However, our study extends previous results that reported the impact of temperature on speciation rates (sometimes on extinction rates) as we report that temperature-driven extinction, exceeding speciation, could have participated in the evolutionary decline of lamniforms. Accumulating evidence indicates that warm climates provide the energetic foundation for increased biodiversity by fostering greater population size and thus higher extinction resistance (50), increase metabolic scope (51), allow more species to exploit specialized niches as a result of greater available energy (52), and generate faster speciation and/or lower extinction rates (53). To cope with the effects of environmental temperature fluctuations, endothermic organisms maintain a relatively warm and constant body temperature, whereas most vertebrates are ectothermic and conform to their thermal niche, compromising performance at colder temperatures (51). However, several extant (Lamnidae, Alopiidae) and extinct (Otodontidae, Cretoxyrhinidae) lamniforms have evolved anatomical and physiological adaptations that enable them to keep their body warmer than the environment (54–56). Our macroevolutionary study proposes a positive relationship between lamniform diversification and temperature, suggesting that warming of the oceans increases their potential to support lamniform biodiversity over geological times, and alternatively the cooling increases the erosion of this biodiversity, in particular over the last 20 My.

The results on continental fragmentation and sea-level fluctuations are surprising because it has previously been shown that long-term sea-level fluctuations driven by plate tectonics likely influenced biodiversity (7). Increases in continental fragmentation during the Cretaceous breakup of Gondwana and Laurasia (57) could have created more niches akin to more coastlines created when continents broke up, and thus positively impacted species diversification (58). Our study does not support that continental fragmentation has exerted a first-order control on the long-term trajectory of lamniform diversity (42). A positive relationship between sea level and marine diversity can be expected through species-area effect (59) where rising sea levels increase epicontinental and shelf areas, leading to increasing diversity. As we do not find evidence for a correlation between sea level and diversification, these potential relationships between sea level and marine diversity remain elusive and our results contradict findings showing that sea-level fluctuations were a primary driver of extinction, controlling biodiversity through availability of shallow marine environments (11). Lamniforms are wide-ranging sharks and globally distributed (18). Their fossil record also indicates that such geographic range pattern prevailed in the past for most species and genera, although some small- to medium-sized fossil species were likely more endemic (e.g., some †*Squalicorax*, †*Eoptolamna*, some †*Striatolamia*). As broad geographic range probably buffers clades from extinction (41), it is thus possible that most lamniforms were resilient to past tectonic and sea-level changes. It is also likely that lamniform diversification was heterogeneous as we show with tooth-correlated diversification (*SI Appendix*, Figs. S4–S7), and that some species (particularly small lamniforms) were more sensitive to such changes. However, this hypothesis remains

difficult to test because the small lamniforms are not diverse enough to perform the analyses.

Biotic Interactions within and between Shark Clades. We investigated within-clade diversity dependence throughout the whole lamniform dataset (MBD) but also on the 3 tooth-size categories using a multiple clade diversity dependence (MCDD) model (14). We also investigated between-clade interactions, here represented by competition, which usually occurs among closely related species and/or among species from different clades with similar ecology. Carcharhiniformes, more specifically requiem and hammerhead sharks, display similar ecologies to lamniforms (60, 61) and have been regarded as filling ecological niches freed by lamniform extinction in the aftermath of the K-Pg (25–27). We compiled the fossil record of Carcharhiniformes that includes 1,261 fossil occurrences assigned at the genus level and 1,061 fossil occurrences assigned at the species level, which represent 67 genera (22 extant and 45 extinct, *Dataset S4*) and 328 species (32 extant and 296 extinct, *Dataset S5*). We also measured tooth size for 307 carcharhiniform species (93.6% of the carcharhiniform species in our dataset, see *Dataset S3*), categorized in the same 3 “ecological” classes. We estimated their diversification pattern using the BDCS model (31, 32) at both the species and genus levels and geological epochs as time intervals, which shows an overall diversity increase toward the present (Fig. 3A and *SI Appendix*, Figs. S12 and S13 and Table S1).

The MBD analyses reveal that within-clade diversity-dependent processes played a role over lamniform diversification (Fig. 3B). We find a negative correlation between clade diversity and speciation rates at both species and genus levels (*SI Appendix*, Tables S9 and S10), meaning that lamniform speciation rates decreased as they diversified through time. Within-clade competition for resources (niche) probably imposed some ecological constraints in lamniforms, thus limiting their species diversity. The MCDD analyses bring further evidence on how within-clade interactions acted in lamniforms as we find an effect of negative within-clade interactions for the medium lamniforms at the species level ($g\lambda = 0.0282$, *SI Appendix*, Table S11). This means that medium lamniforms decrease their own speciation rates by 2.82% each time a new medium lamniform species originates. Finally, we inferred substantial levels of diversity dependence within the carcharhiniforms as all 3 ecological types have negative diversity-dependent speciation rates (Fig. 3B and *SI Appendix*, Table S11). This may indicate that the carcharhiniform radiation is in part controlled by ecological limits to diversification or may conform to a pattern of adaptive radiation, as suggested by the post-Eocene radiation of living carcharhiniform species (Fig. 3A) (29).

Although the MCDD analyses show that clade competition did not affect the diversification dynamics of small lamniforms, results indicate that competition with some carcharhiniforms played a major role in the diversification dynamics and clade replacement of medium and large lamniforms (*SI Appendix*, Table S11). Specifically, we provide evidence for an effect of competition from large carcharhiniforms over the speciation of medium ($g\lambda = 0.0652$) and large ($g\lambda = 0.084$) lamniforms (i.e., negative between-clade interactions, Fig. 3B). These results imply that, each time a new large carcharhiniform species originates, it decreased the speciation rates of medium and large lamniforms by 6.52% and 8.4%, respectively, suggesting that increasing species diversity of large carcharhiniforms inhibited speciation rates of medium and large lamniforms. As these carcharhiniforms ecologically similar to lamniforms such as extinct relatives of living tiger, hammerhead, and bull sharks diversified from the Eocene to the present (Fig. 3A and *SI Appendix*, Figs. S12 and S13) (21), they progressively increased their tooth size overlap with both medium and large lamniforms. The increase in ecological similarity of ground sharks likely imposed a long-term competition between the 2 orders, but only during the second half of the existence of lamniforms and probably not during

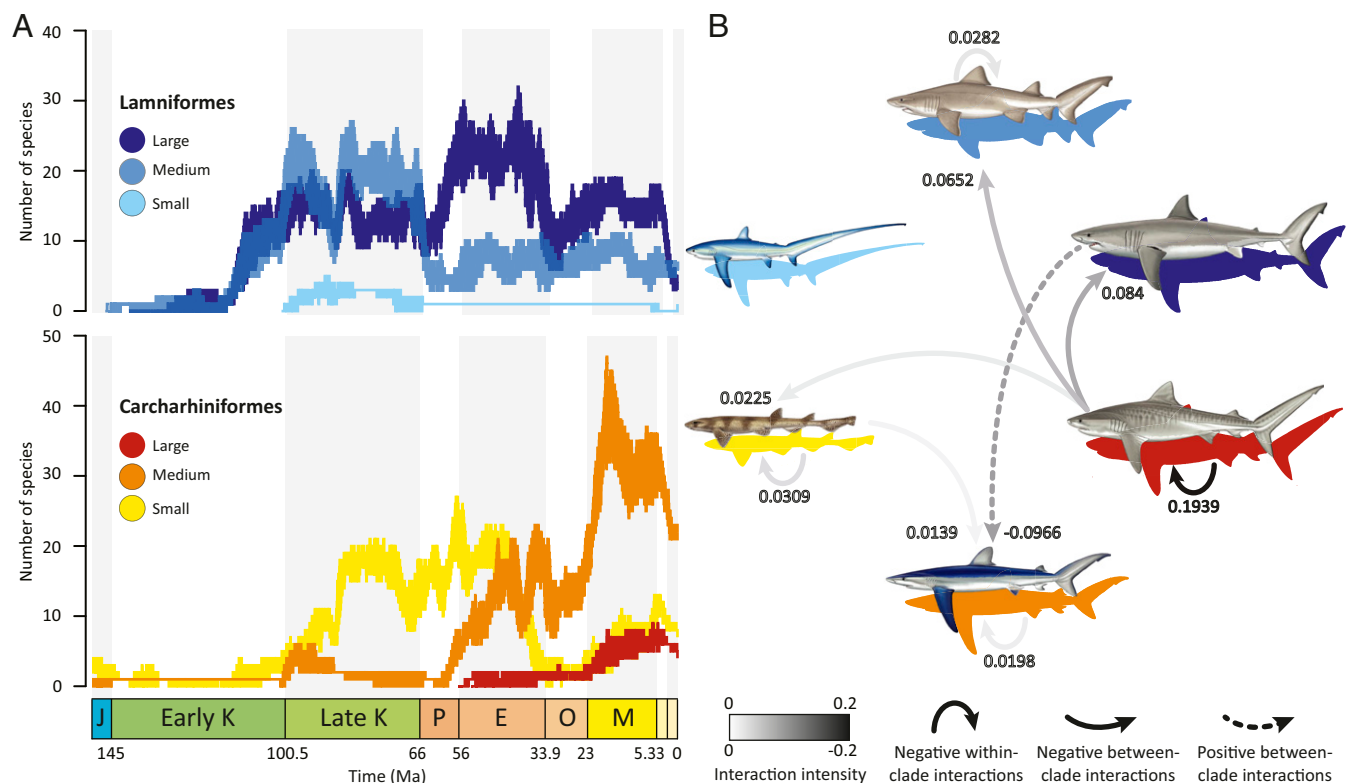


Fig. 3. Diversity trajectories and the effect of competition on speciation rates of shark groups. (A) The diversity trajectories of the 3 lamniform and 3 carcharhiniform groups at global scale. Reconstructions of diversity trajectories are replicated 10 times, incorporating uncertainties around the age of the fossil occurrences. (B) Network showing the diversity-dependent effects within and between clades on speciation rates (only significant correlations are shown). Each arrow indicates the intensity of interaction imposed by a given group toward another one, which quantifies the proportion of rate change (decrease for speciation) associated with the addition of 1 species of the competing group. Shark images courtesy of Marc Dando (artist). Abbreviations as in Fig. 1.

the recovery of the K-Pg extinction and the whole Paleocene (Fig. 3A) (21). This strongly suggests a passive replacement of marine clades as shown by our correlation with speciation rates of medium and large lamniforms with their ecologically similar carcharhiniforms, when they coexisted. Although medium carcharhiniforms were present since the Early Cretaceous, we find no evidence for competition. This might be partly due to niche partitioning as 38% of extant carcharhiniform species that would mainly fall within the medium class (i.e., most carcharhinids and sphyrnids) are associated to reefs (62). This dominant ecology among carcharhiniforms is conversely scarce among lamniforms as only the sand tiger shark (*C. taurus*) regularly frequents reefs (62). However, it is also possible that current knowledge on the fossil of extant carcharhiniforms prevents an accurate testing of the effect of medium carcharhiniforms. Whereas our coverage of the fossil record of extant nonfilter feeding lamniform species is high (11 sampled species out of 13 known), many living carcharhiniform species that would fall within the small- and medium-sized classes have currently no fossil representatives and hence, could not be included in the analyses. Phylogenetic data indicate that the diversification of medium carcharhiniforms occurred after the Paleocene (21, 29) and it is likely that this partly undetected diversification would result in a more marked diversity increase than observed (Fig. 3A), which would produce stronger antagonistic diversity patterns between medium carcharhiniforms and medium lamniforms. Instead, we unveil a case of “co-diversification” (i.e., positive between-clade interaction), where speciation rates in medium carcharhiniforms are positively correlated with diversity of large lamniforms (Fig. 3B). We attribute such result to a similar evolutionary response to climate change (SI Appendix, Fig. S14 and Table S12) rather than direct positive interactions between these groups.

Here we offer an entirely biological explanation of lamniform diversity variations through time, which relies on both abiotic (temperature) and biotic (competition) factors, although our results may depend on our choice and availability of environmental and biological variables used as predictors. As a major goal of evolutionary biology (1–3, 6), we provide insights into the processes linking changes in species richness with abiotic and biotic environmental change over a major marine vertebrate clade. Two-thirds of extant Lamniformes are currently threatened with extinction. A recent study surveying global conservation priorities of sharks, rays, and chimaeras reported they dominate the top 20 imperiled species list, and should be prioritized for targeted conservation (29). Thus, studying the impact of environmental change and marine exploitation on current lamniform diversity may benefit from insights into what factors have influenced their past diversity.

Materials and Methods

Additional data and methodology are described in SI Appendix.

Fossil Record of Lamniform and Carcharhiniform Sharks. We compiled all species-level fossil occurrences of lamniform and carcharhiniform sharks from the literature, which resulted in an unprecedented database (established on January 2017) for Lamniformes and Carcharhiniformes. This extensive work resulted in genus-level and species-level datasets spanning the Early Cretaceous to Recent interval for the lamniforms and Middle Jurassic to Recent for carcharhiniforms.

Tooth Measurements. Measures of tooth crown height were made following a line running from and perpendicular to the crown/root edge up to the apex of the main cusp, in labial view (SI Appendix, Fig. S15). Measurements were made on anterior teeth only in order to exclude size differences related to

heterodonty. Fossil and living lamniforms and carcharhiniforms have a wide array of diets and directly testing for competition between the entire diversity of these 2 clades would not reflect real biological interactions. The shark fossil record is mainly represented by isolated teeth but it appears that shark tooth morphologies can hardly be associated to a precise diet (63, 64). Instead, sharks' diet is most probably determined by prey size and predator/prey co-occurrence in ecological distribution. We selected our measures of tooth crown height as a size proxy to categorize lamniform and carcharhiniform species using model-based clustering for parameterized Gaussian mixture model estimation and selected optimal model according to Bayesian information criterion for parameterized mixture models (65). The optimal model was the 3 classes model that are here defined as small, medium, and large (*SI Appendix, Fig. S16*).

Dynamics of Speciation and Extinction. We analyzed the fossil datasets with PyRate (31) under the BDCS (32) to simultaneously estimate: the preservation process, the times of speciation (T_s), and extinction (T_e) of each taxon, the speciation and extinction rates and their variation through time. We ran PyRate for 10 million Markov chain Monte Carlo (MCMC) generations with time bins of 10 My or geological epochs. All analyses were set with a homogeneous Poisson process of preservation and accounted for varying preservation rates across taxa using the Gamma model (31). We replicated the analyses on 10 randomized datasets of each clade and combined the posterior estimates of the speciation and extinction rates across all replicates to generate rates-through-time plots (speciation/origination, extinction, and net diversification). We also obtained 10 posterior estimates of the T_s and T_e for all taxa. We estimated the past diversity dynamics by calculating the number of living taxa at every point in time based on the T_s and T_e . For the subsequent analyses, we used the estimated T_s and T_e of all taxa, which avoids remodeling the heterogeneity of preservation, and reestimated times of speciation and extinction.

Trait-Related Diversification Model. We tested whether the diversification dynamics of lamniform sharks is linked with changes in tooth size over time, using the Covar birth-death model (31). Under this model, changes in speciation and extinction rates (and preservation rate) correlate with changes in tooth size through the correlation parameters (α_λ , α_μ , and α_q), which are estimated from the data. The birth-death rates are therefore transformed on a lineage-specific basis, rather than through time (31). An $\alpha > 0$ indicates a positive correlation between the trait value and the birth-death rates, and $\alpha < 0$ indicates a negative correlation. Correlation was significant when the 95% credibility intervals (CIs) do not overlap with 0.

Paleoenvironment-Dependent Diversification Model. We quantified the effect of environmental variables on diversification rates such that speciation and extinction rates can vary through time, and both can be influenced by 1 or several environmental variables that also vary through time, for instance past variations of global temperature (46). PyRate can test for a correlation between speciation and extinction rates and changes in environmental variables (14). We analyzed the lamniform dataset by fixing the T_s and T_e to the ages estimated from the 10 replicated datasets under the BDCS model. We derived functional forms of λ (μ) as exponential or linear functions of temperature, where λ_0 (μ_0) and γ_λ (γ_μ) are the parameters to estimate. The estimation of a positive γ_λ (γ_μ) indicates that higher temperatures increase λ (μ), whereas a negative γ_λ (γ_μ) indicates that higher temperatures decrease λ (μ). We ran 10 million MCMC iterations with sampling frequency of 1,000 and combined the posterior samples of the parameters from the 10 replicates after excluding the first 20% of the samples as burnin. Posterior samples of the parameters were summarized over all replicates as mean values and 95% CI (significant correlation when 0 was not included in the CI).

Selection of Abiotic Variables. We examined the link between past environment and speciation/extinction rates over their evolutionary history. We focused on the role of 3 abiotic variables, which have been linked to biodiversity change in marine invertebrates (7, 10) and spanning the full time range of Lamniformes (*Dataset S6* and *SI Appendix, Fig. S17*). Major trends in global

climate change through time are estimated from relative proportions of different oxygen isotopes ($\delta^{18}\text{O}$) in samples of benthic foraminifer shells (45). We merged $\delta^{18}\text{O}$ data from the global temperature data for the Mesozoic (44) and Cenozoic (45) periods. The fluctuations in sea levels have also been proposed as a possible driver of marine diversity dynamics (11). Trends in global sea-level changes over time were obtained from $\delta^{18}\text{O}$ data indirectly recorded in the chemistry of foraminifers, thus informing on the growth and decay of continental ice sheets causing eustatic changes (43). The continental fragmentation, as approximated by plate tectonic change, has often been proposed as a driver of marine biodiversity dynamics (7, 42, 58). We retrieved the index of continental fragmentation developed by Zaffos et al. (42) using paleogeographic reconstructions for 1-million-year time intervals. This index approaches 1 when all plates are not touching (complete plate fragmentation) and approaches 0 when there is a maximum aggregation.

MBD Model. We used the MBD model to assess whether multiple factors explain temporal variations in speciation and extinction rates (33). Under the MBD model, speciation and extinction rates can change through correlations with time-continuous variables and the strength and sign of the correlations are jointly estimated for each variable. PyRate jointly estimates the baseline speciation (λ_0) and extinction (μ_0) rates and all correlation parameters (G_λ and G_μ) using a horseshoe prior to control for overparameterization and for the potential effects of multiple testing (33). We ran the MBD model using 20 million MCMC iterations and sampling every 20,000 to approximate the posterior distribution of all parameters (λ_0 , μ_0 , 4 G_λ , 4 G_μ , and the shrinkage weights of each correlation parameter). We summarized the results of the MBD analyses by calculating the posterior mean and 95% CI of all correlation parameters and the mean of the respective shrinkage weights, as well as the mean and 95% CI of the baseline speciation and extinction rates.

ADE Model. We fitted the ADE model (38) to compute the probability for a lineage to become extinct as a function of its age (the elapsed time since its origination). We ran PyRate for 10 million MCMC generations with a time-variable Poisson process of preservation, while accounting for varying preservation rates across taxa using the Gamma model. We replicated the analyses on 10 randomized datasets for each tooth class and combined the posterior estimates across all replicates. We focused on the shape (Φ) of the Weibull distribution knowing that $\Phi < 1$ indicates that extinction rate is higher for young species and decreases with species age, and $\Phi > 1$ indicates that extinction rates increase with species age (no effect of age if $\Phi = 1$) (38).

MCDD Model. We used the MCDD model (14) to assess the effect of competition on the diversification of Lamniformes, in which their speciation and extinction rates are correlated with the diversity trajectory of Carcharhiniformes. Under competitive interactions, increasing species diversity has the effect of suppressing the speciation rates and/or increasing the extinction rates. The MCDD assesses the effects of competition within and between clades by jointly analyzing all clades and estimating the baseline speciation and extinction rates for each clade and competition parameters that quantify the intensity of the diversity dependence between each pair of clades. Each competition parameter expresses a diversity dependence relationship between the diversity of a clade and the speciation or extinction rates of the other clade. We ran 20 million MCMC iterations of the MCDD model with sampling frequency of 10,000. We repeated the analyses on the 10 replicates, using the T_e and T_s estimated under the BDCS model for each shark group (as defined by tooth categories). For each of the 6 shark groups we computed median and 95% CI of the baseline speciation and extinction rates (λ_i and μ_i), the within-clade diversity-dependence parameters g_{λ_i} and g_{μ_i} , and the between-clade diversity-dependence parameters $g_{\lambda_{ij}}$ and $g_{\mu_{ij}}$. We used the mean of the sampled diversity dependence parameters (e.g., $g_{\lambda_{ij}}$) as a measure of intensity of competition (if positive) or positive interaction (if negative) between each pair of groups.

ACKNOWLEDGMENTS. We thank S. Adnet, T. Couvreur, F. Delsuc, and L. Hautier for comments on the study. We also thank D. Silvestro for assistance with PyRate.

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