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Global impact and selectivity of the Cretaceous/Paleogene mass extinction among sharks, skates, and rays

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Abstract

The Cretaceous/Paleogene event was the last dramatic biological crisis, yet its impact and long-term effects on species-level marine vertebrate diversity remain largely uncharacterized. We quantified elasmobranch (sharks, skates, rays) speciation, extinction and ecological change resulting from the end-Cretaceous event using >3,200 fossil occurrences and 675 species spanning the Late Cretaceous-Paleocene interval at global scale. Elasmobranchs declined by >62% at the Cretaceous/Paleogene boundary and did not fully recover in the Paleocene. The end-Cretaceous event triggered a heterogeneous pattern of extinction with rays and durophagous species reaching the highest levels of extinction (>72%), while sharks and non-durophagous species were less impacted. Taxa with large geographic ranges and/or those restricted to high-latitude settings show higher survival. The Cretaceous/Paleogene event drastically altered the evolutionary history of marine ecosystems.

One-Sentence Summary

Global fossil data unveil heterogeneous extinction patterns in elasmobranch diversity across the end-Cretaceous event.

Main Text

The most recent biological mass extinction occurred ~66 million years ago (Ma), marking the Cretaceous-Paleogene (K/Pg) boundary. This event caused dramatic worldwide extinctions among a large range of clades and wiped out large metazoan vertebrate groups (1). Although the causes of this mass extinction are intensely debated (2, 3), previous estimates suggest that the K/Pg extinction removed >40% of genera and 55-76% of species (4-6). There is also increasing evidence pointing to a variable degree of severity of this event between clades (1), ecologies (7), and geographical areas (8, 9). However, global estimates of diversity loss are primarily extrapolated from genus- or family-level data on marine invertebrate clades that may not reflect the complexity of extinction patterns at the K/Pg boundary. Global species-level analyses of K/Pg extinction patterns among marine vertebrates, using bias-corrected approaches, are comparatively rare (10). Yet, marine vertebrate clades could provide different tales of extinction and post-extinction recovery due to their higher trophic position. Only a few speciose vertebrate groups crossed the K/Pg. Elasmobranchs (sharks, skates, rays) represent an important component of marine ecosystems since the Mesozoic (11, 12), are further characterized by a dense fossil record matching that of marine invertebrates (12), and developed a wide range of ecologies (13).

To assess the impact of the K/Pg extinction event, we compiled a global species-level fossil occurrence data for elasmobranchs covering a time interval between 93.9 and 56 Ma (most of the Late Cretaceous and Paleocene). This dataset represents 2,582 occurrences for 675 species (3,218 occurrences for 258 genera; table S1, Data S1). We estimated speciation and extinction rates, their temporal shifts, and the magnitude of rate change using Bayesian process-based birth-death models incorporating the temporal and taxon-specific variation of the preservation processes and uncertainties associated with the age of fossil occurrences (14).

We identified the K/Pg event in elasmobranch species diversity with an increase in extinction rate starting in the latest Maastrichtian (**Fig. 1**, 66.6 Ma; log Bayes factors [BF] > 6 with a 95% credibility interval [CI]: 66.72-66.27 Ma, fig. S1). The K/Pg extinction rate significantly exceeds background extinction in the Maastrichtian and Paleocene with a mean of 1.763 events/lineage/Myr (95% CI: 0.528-2.762; peaking at 1.949 events/lineages/Myr with 95% CI: 0.976-2.993 at 66.01 Ma with 95% CI: 66.26-65.91) during the K/Pg compared to 0.170 events/lineage/Myr (95% CI: 0.115-0.284) in the Maastrichtian ($t = -27.923$, $df = 15.001$, $P = 2.391e-14$), and 0.156 events/lineage/Myr (95% CI: 0.078-0.295) during the Paleocene ($t = -28.179$, $df = 15.016$, $P = 2.043e-14$). The K/Pg extinction diminished elasmobranch diversity by 62.6% (table 1) as measured by the number of extinct species between 66.6 and 65.8 Ma, at which time extinction rate significantly decreased (BF > 6; 95% CI: 65.82-65.37 Ma). Analyzing the fossil record at the genus level indicates a 44.94% diversity drop across the K/Pg boundary (table 1, fig. S2) (15). According to our data, the K/Pg event was brief at geological scale, and lasted ca. 800 kyrs. The diversity drop at the K/Pg cannot be attributed to a bias in preservation rates (q) because the expected number of species occurrences per lineage per Myr is similar throughout the K/Pg (Maastrichtian: mean $q = 0.890$, 95% CI: 0.787-0.980; and Danian: mean $q = 0.697$, 95% CI: 0.583-0.838; fig. S3). We also evaluated the impact of singletons by excluding taxa represented by a single occurrence. We found very similar extinction intensities for species- (63.97%) and genus-level estimates (42.65%) once singletons were excluded (fig. S4-5) (15), confirming the robustness of the mass extinction pattern identified. Previous work on K/Pg elasmobranch extinction intensity provided equivocal estimates (species: 84% \pm 5% to 45% \pm 9%; genera: 56% \pm 10% to 34% \pm 11%), depending on the inclusion or exclusion of singletons, respectively (11). Such uncertainty in previous extinction percentages may be explained by the absence of correction for paleontological biases. Our estimations take into account fossil record biases and are based on

revised and greatly expanded datasets in the last two decades (12, 13), which further refine estimates of elasmobranch extinction intensity at the K/Pg.

Previous analyses have pointed out heterogeneous extinction within elasmobranchs (11, 12, 16). We analyzed the extinction patterns of the two main elasmobranch clades (sharks and batomorphs) separately and found stronger extinction rates and percentages for batomorphs than sharks (table 1, fig. S6-7; $t = -7.603$, $df = 7.20$, $P = 0.0001$), suggesting phylogenetic selectivity in the extinction pattern. This selectivity during the K/Pg is further exemplified within sharks and batomorphs with some orders being strongly impacted (Lamniformes, Orectolobiformes) and even came close to complete extinction (Rajiformes, Rhinopristiformes), whereas others (Carcharhiniformes, Hexanchiformes, Squaliformes) show no marked shifts in extinction rates (fig. S8-S16). We found similar patterns of extinction heterogeneity with analyses at the genus level (fig. S17-S25) (15). Furthermore, some clades (lamniforms, hexanchiforms) appear to experience a declining phase (negative net diversification) before the K/Pg event, whereas others (rajiforms, orectolobiforms) show a sudden increase in extinction rates while previously in a diversification phase. Comparison of global-scale extinction patterns with regional data is hampered by the rarity of fine-scale samplings from geological sections including the K/Pg boundary. Our results are congruent with the only such analysis of elasmobranch faunas in Denmark (17), where squaliforms and carcharhiniforms are less affected than other clades, whereas none of the two recorded batomorph species cross the boundary.

Taxonomic-level analyses of extinctions provide partial insights into the aftermath of past extinction events over the functioning of paleoecosystems, especially in the case of clades including taxa with a large array of ecologies. The ecological patterns of diversification and extinction events can be decoupled from the associated increase or loss of taxa (18). We therefore complemented our estimates of paleodiversity with an approach using phenotypic traits linked with broad feeding preferences to test for the ecological selectivity of the K/Pg extinction. The elasmobranch fossil record is mainly represented by teeth, which are the main elements involved in the processing of food items (13). We separated our dataset into two dental categories (15), termed ecomorphotypes: durophagous and non-durophagous. The former includes all taxa whose teeth display a crushing or grinding component in their morphology, and encompasses taxa capable of consuming prey with hard exoskeletons such as shelled molluscs and crustaceans (e.g., many skates and rays, heterodontiforms, the extinct ptychodontiforms, some orectolobiforms, and few carcharhiniforms). This group was further divided into two ecomorphotypes to differentiate the degree of specialization to durophagy from generalist durophagous (Crushing type) to specialized durophagous (Grinding type). The non-durophagous group includes taxa with cuspidate teeth that display a wide range of tooth sizes and likely encompasses species with different ecologies (15). We categorized non-durophagous species into three classes (small, medium, and large) based on measurement of tooth crown height (Data S1) (15), following previous work (19).

Our results suggest strong ecological selectivity, with durophagous species being much more impacted than non-durophagous (Fig. 2, table 1, fig. S26-32; $t = 10.663$, $df = 5.23$, $P = 9.566e-05$), and this contrast is even more marked based on genus-level data (table 1, fig. S33-39). Extinction rates for durophagous species exceed those of batomorphs, indicating that durophagous sharks and batomorphs responded similarly to extinction (table 1). Conversely, non-durophagous species show a less sharp diversity loss at the K/Pg boundary. Results suggest an increase in species extinction during the end Campanian-Paleocene interval for small and medium-sized species with a weak peak around 66 Ma, and relatively stable extinction for large species. Our results support ecological selectivity of the K/Pg event against species relying on lower parts of the food web. Growing evidence points to high levels of extinction at the bottom of marine food webs linked with strong upheavals in the biogeochemical cycling of the oceans (20–22). The high

extinction rates of durophagous elasmobranchs indicate that the tremendous diversity loss of primary producers and consumers directly impacted elasmobranchs relying on hard shelled invertebrates. More generalist shark clades seem less impacted, whether they are adapted to deep/cool environments (squaliforms) or not (carcharhiniforms), and large sharks taken together do not show marked extinction. This suggests decreasing extinction intensity towards mesopredators. Lamniformes are probably the only strictly non-durophagous clade showing an increase in extinction rates at the K/Pg boundary. The lamniform extinction pattern is not recovered in our ecomorphological datasets (especially the medium and large categories), which suggests a distinct response of this clade to the K/Pg extinction. Nevertheless, lamniforms represent 90% of large and 83% of medium species going extinct at the K/Pg. Late Cretaceous lamniforms are meso- to top predators displaying a wide range of strong ecological specializations (19), which likely makes them more prone to extinction (23). Lamniforms were probably strongly hit by the K/Pg event due to a high trophic position and dietary specialization, which is in line with the pattern found for marine actinopterygians (12, 24). We therefore highlight a bottom-up trophic dynamics of the K/Pg extinction in elasmobranchs, but with lower extinction among generalist mesopredators.

During a mass extinction, the law of constant extinction can be broken (25). Studying marine invertebrate groups generally points to age-dependent extinction (26), such that recently-originated species turn over faster than old species indicating evidence of taxon selectivity for survival. We fit a Bayesian age-dependent extinction model to estimate the probability of extinction to be dependent on taxon age (15). Analyzing all elasmobranchs, we found higher extinction rates in old species than in young species in the Maastrichtian ($\phi = 3.5092$, 95% CI: 1.5442-6.7414), whereas there is no effect in pre- and post-Maastrichtian times (table S2). Separating sharks and rays, we found higher extinction rates in old shark species than in young species in the Maastrichtian ($\phi = 4.6602$, 95% CI: 1.2691-14.3273), and no effect in pre-Maastrichtian and Paleocene, while batomorph species show no age-dependent extinction in all time intervals (table S2). Shark species with long temporal ranges show higher extinction, suggesting a lack of evolutionary novelty or poor fitness to a rapidly changing environment, which is in line with the results that some shark clades were in decline prior to the K/Pg event (e.g. Lamniformes, Hexanchiformes).

One of the characteristics of mass extinctions is that they are geographically widespread (27), as opposed to background extinctions (28), although it does not require that high extinction be uniform at global scale (4). We compiled the latest (chiefly Maastrichtian) geographic occurrences before the K/Pg extinction for genera that survived the K/Pg event and for those that went extinct (see Data S1-2). We performed paleogeographic coordinate reconstructions (29) for each of the 822 genus-level occurrences fitting these criteria in our dataset and computed three geographic range measures using standardized numbers of geographic occurrences per genus (15). We found significantly larger mean paleogeographic ranges for surviving than for extinct genera (table S3) (15), which supports a positive relationship between large geographic range and survival for elasmobranchs during the K/Pg event. Furthermore, we found that genera restricted to lower paleolatitude settings show much lower survival than their high-paleolatitude congeners, whatever the splitting value between high and low latitudes (**Fig. 3A**). This biogeographic selectivity is also recovered when singletons are excluded from the analysis and held after various sensitivity tests (tables S4-6) (15). Although this pattern is also found for durophagous and non-durophagous genera separately (tables S7-10), the high proportion of durophagous taxa in lower-latitude settings provides clues to the higher extinction of durophagous species recovered in our analyses (**Fig. 3B**). This result suggests that high-latitude settings were either more resistant to extinction, or that the intensity of the K/Pg upheavals decreased from low to high latitudes. Such a biogeographic

selectivity towards higher survival of high-latitude taxa has rarely been reported for the K/Pg event (30). Interestingly, this extinction pattern was reported for bivalves (8) and other benthic invertebrates (31), which likely represented main prey items of durophagous elasmobranchs. We therefore tested for a potential link between diversification of durophagous elasmobranchs and bivalve diversity along with six abiotic proxies across the 83.6-57 Ma time-interval. We used a multivariate birth-death model to simultaneously evaluate correlations with explanatory variables and diversification processes of durophagous species (15). Among seven tested variables, we found that extinction rates of durophagous species are mainly explained by the diversity dynamics of bivalves (fig. S40-42, table S11) (15), such that drops in bivalve diversity led to higher extinction in durophagous species. Comparing the contribution of elasmobranch orders to the ecomorphotypes (**Fig. 2**, fig. S43-45, tables S12-13) further highlights the effects of the K/Pg extinction over the evolution of the ecological structure of global elasmobranch communities. We show that this event produced a major shift in the proportion of elasmobranch clades within the durophagous ecomorphotype. Our data indicates high proportions of durophagous rajiforms (especially the extinct *Sclerorhynchoidei*) and rhinopristiforms in the Maastrichtian, while the contribution of these clades to the durophagous ecomorphotype is inconspicuous in the Paleocene. Conversely, the proportion of durophagous myliobatiforms strongly increased in the post-K/Pg. This suggests that the strong extinction suffered by rajiforms and rhinopristiforms freed ecological niches, which were subsequently filled by the myliobatiforms (especially dasyatoids) in the Paleocene. The K/Pg extinction also impacted the ecological equilibrium in non-durophagous elasmobranchs, most notably through an increase in the proportion of small carcharhiniforms in the post-extinction fauna. The dominance of small carcharhiniforms in the Paleocene occurred mainly at the expense of squaliforms, whose diversity shifted toward medium non-durophagous in the Paleocene. Similarly, the hexanchiforms, another cool/deep environment clade, also increased in proportion among medium-sized - and, to a lesser extent, large - non-durophagous categories.

Post K/Pg recovery was more rapid for sharks and particularly for non-durophagous taxa (table S14). However, our analyses point to a delayed recovery of durophagous elasmobranchs, which did not reach pre-K/Pg diversity during the Paleocene and account for a lower proportion of the total Paleocene fauna (tables S12-13, fig. S43) than in the Maastrichtian (40% vs. 52%). Previous works showed a slow post-K/Pg recovery in marine bivalves (32), and results of our multivariate birth-death analyses indicate that the pattern for durophagous elasmobranchs is probably due to a lagged recovery in primary consumers. Conversely, although lamniforms suffered high extinction, they account for a large proportion of non-durophagous post-extinction elasmobranchs, supporting rapid turnover for this clade (19). Taken together, our results point to a role of the K/Pg event in reshaping the taxonomic composition of the main elasmobranch ecologies along with a long-term lag in recovery for hard-shell prey consumers.

Extant elasmobranchs are facing strong human-driven pressures leading to high extinction risk for most species (33). Understanding how this clade responded to past mass extinctions helps identify the features of extinction victims and survivors. Our analyses provide a profiling of extinction victims during the K/Pg event where batomorphs, durophagous and strictly low-latitude species with restricted geographic ranges, as well as old shark species show higher extinction than other elasmobranch species. We further report a lagged recovery of durophagous species, associated with a deep restructuring of clade contributions within this ecomorphotype. Causal hypotheses for the K/Pg mass extinction are still debated: while some data suggest a primary role of bolide impact (2), others support a combined effect of the latter with longer-term climatic upheavals and massive volcanism (3). The elasmobranch extinction pattern reported here cannot reject any of these hypotheses, but provides important clues on the putative causal mechanisms of the K/Pg extinction.

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SUPPLEMENTARY MATERIALS

Materials and Methods

Extended Results

Figs. S1 to S50

Tables S1 to S17

References (34–113)

Data S1 to S3

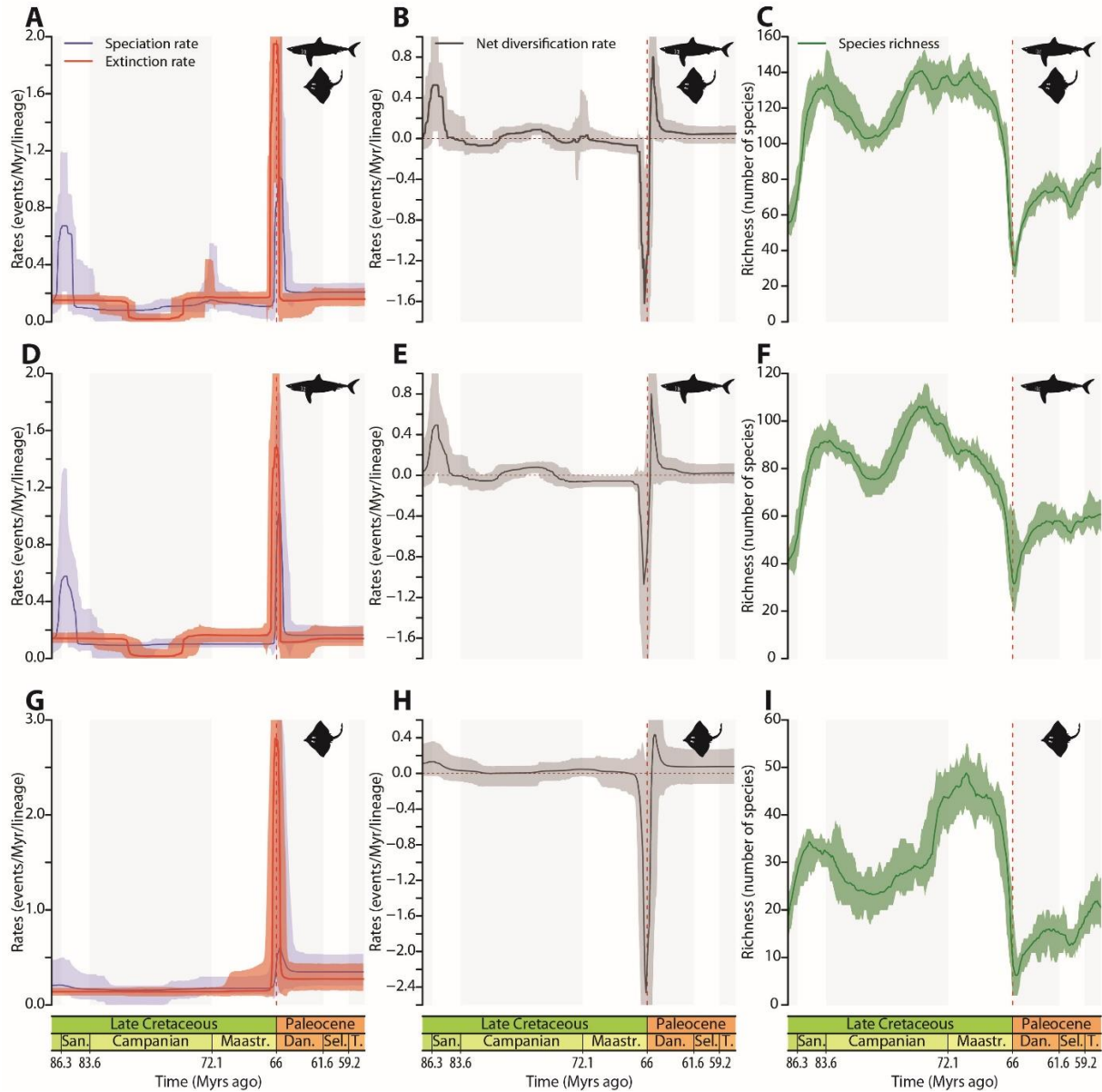


Fig. 1. Diversification and diversity dynamics of elasmobranchs (sharks, rays and skates) across the K/Pg mass extinction. Bayesian inferences of temporal variations of speciation and extinction rates, net diversification rates (speciation minus extinction), and number of species for all elasmobranchs (A-C), sharks (D-F), rays and skates (G-I). Extinction rates (A, D, G) increase sharply at the K/Pg boundary (red dotted vertical line), with significant rate shifts determined by log-Bayes factors > 6 (see fig. S1, S6-7). Net diversification rates (B, E, H) become strongly negative during the K/Pg event, reaching 1.95 extinction events per lineage per million years for all elasmobranchs (see table 1 for details). The number of species through time (C, F, I) quickly drops at the K/Pg, in particular for rays and skates, and we did not find evidence for a post-extinction recovery until the end of the Paleocene. Similar trends are found at genus level (fig. S23-25). San. = Santonian; Maastr. = Maastrichtian; Dan. = Danian; Sel. = Selandian; T. = Thanetian. [for full page width]

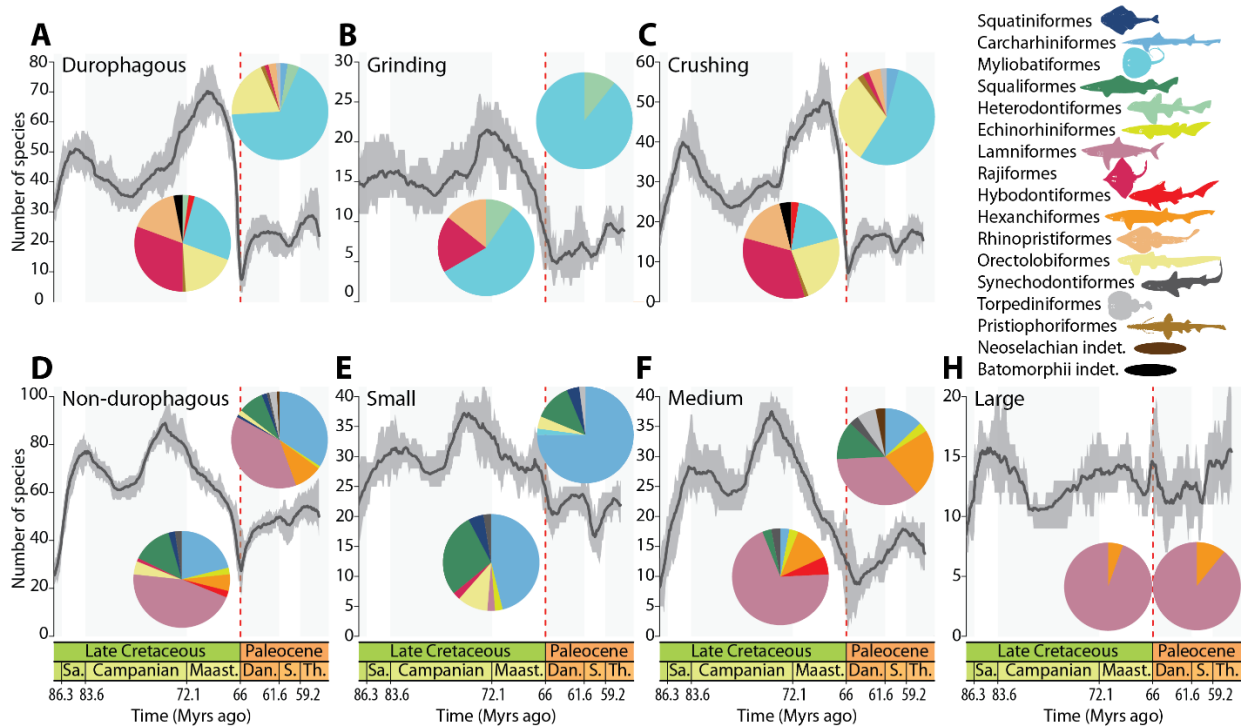


Fig. 2. Evolution of species richness among dental ecomorphotypes across the K/Pg boundary. Estimated paleodiversity variations are represented by the grey curves (mean richness) and associated grey shadings (95% CI) for all durophagous (A), Grinding (B), Crushing (C), all non-durophagous (D), small non-durophagous (E), medium non-durophagous (F), and large non-durophagous (H) ecomorphotypes. Pie charts represent clade contribution to the species diversity of each ecomorphotype before (Maastrichtian) and after (Paleocene) the K/Pg event (fig. S43-45, tables S13-14) (15), which is represented by the red dotted vertical lines. Sa. = Santonian; Maastr. = Maastrichtian; Dan. = Danian; S. = Selandian; Th. = Thanetian. [for full page width]

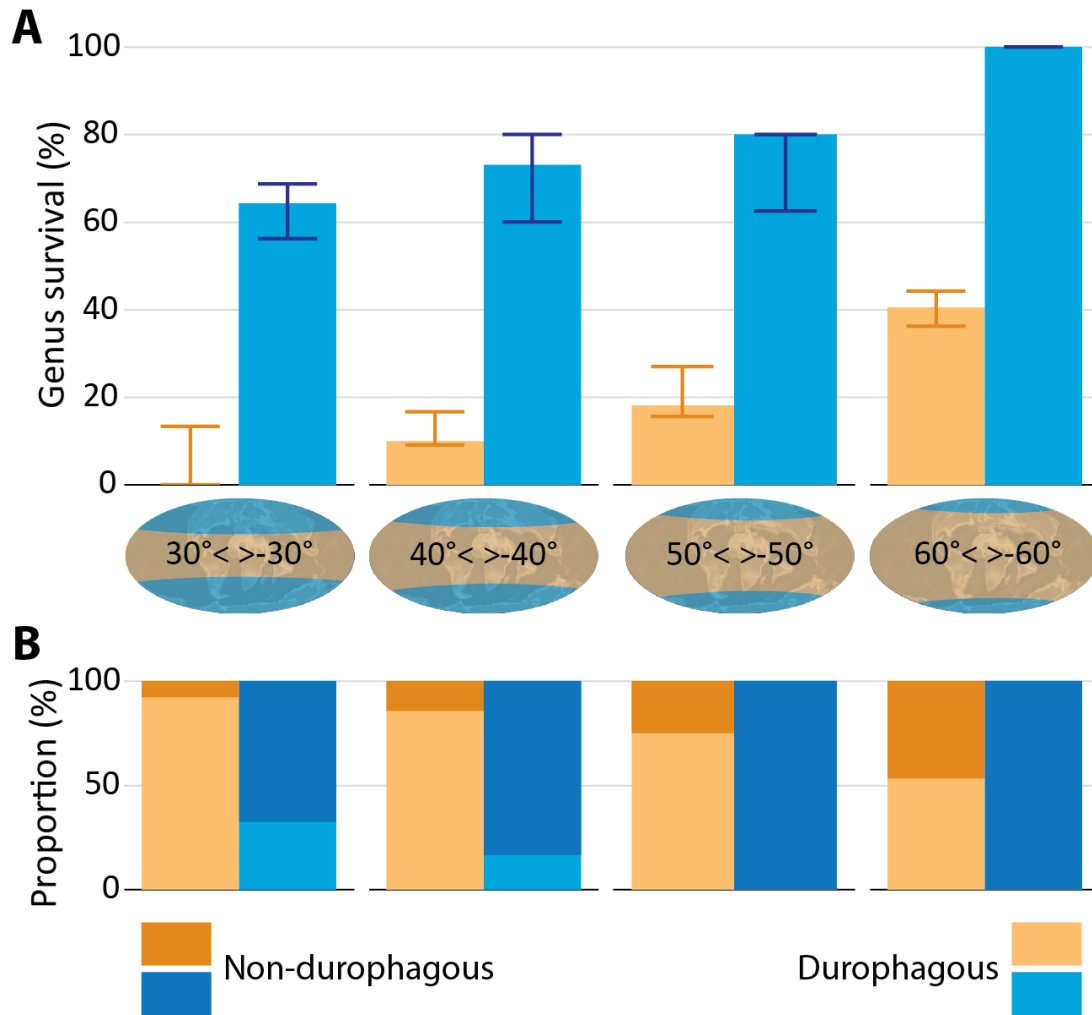


Fig. 3. The paleo-latitudinal pattern of elasmobranch genus extinction and survival at the K/Pg event. Histograms represent the proportion (median) of survival for genera occurring exclusively in low (orange) and high latitudes (blue) according to four values splitting high- and low-latitude settings (table S4) (15) as represented on paleomaps. Orange and blue bars indicate range between minimum and maximum values. B) Proportion of non-durophagous (dark orange and blue) and durophagous (light orange and blue) genera in higher- and lower-latitude settings (see table S9). Paleomaps shows K/Pg paleogeography (used with permission © 2020 Colorado Plateau Geosystems Inc). [for column width]

Table 1. Impact of the KPg event on the diversity of sharks and rays. We identified when the extinction rate upshifted before the K/Pg extinction and downshifted after the K/Pg based on log Bayes factors > 6 (15). Times of upshift and downshift determine the duration of the extinction event. We obtained the mean diversity (species or genus) at the upshift and calculated the number of victims (species or genus) between upshift and downshift times (note that no taxa originate in this time interval), which both allow computing the percentage of extinction (number of victims over mean diversity). The estimations of extinction rates during the K/Pg event show the magnitude of the event and its heterogeneity among elasmobranchs.

| Clade | Taxonomic level | Mean diversity before extinction | Number of victims during extinction time | % of extinction | Extinction rate |
|---------------------|-----------------|----------------------------------|--|-----------------|-------------------|
| All elasmobranchs | Species | 92.6 | 58 | 62.63 | 1.95 (0.98-2.97) |
| | Genus | 89 | 40 | 44.94 | 1.14 (0.53-1.85) |
| All sharks | Species | 59.4 | 35 | 58.92 | 1.48 (0.16-2.26) |
| | Genus | 58.5 | 17 | 29.06 | 0.05 (0.02-0.76) |
| All rays | Species | 30.3 | 22 | 72.61 | 2.80 (0.31-5.812) |
| | Genus | 24.5 | 21 | 85.71 | 1.13 (0.11-2.75) |
| All durophagous | Species | 43.6 | 32 | 73.39 | 3.55 (1.33-5.93) |
| | Genus | 42.7 | 26 | 60.89 | 1.17 (0.245-2.43) |
| All non durophagous | Species | 43.5 | 26 | 59.77 | 1.25 (0.16-2.19) |
| | Genus | 49.4 | 13 | 26.32 | 0.05 (0.021-0.31) |