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Response to Comment on “An early Miocene extinction in pelagic sharks”

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Naylor *et al.* argue that the existence of multiple denticle types within a single species precludes the use of this metric as a measure of the decline of multiple shark species. We show that species-level shark diversity would have to decrease by >90% to account for the observed >70% denticle extinction, implying that the early Miocene shark extinction was larger than previously recognized.

Sibert and Rubin (1) found that a >70% extinction in shark dermal denticle morphotype diversity in deep-sea sediments occurred rapidly during the early Miocene, marking a previously unidentified and permanent step change in open-ocean elasmobranch diversity and abundance. Naylor *et al.* (2) assert that this decline in shark dermal denticle morphology cannot be attributed to a substantial change in shark biodiversity, because denticle morphotypes vary across the bodies of individual species, and thus the extinction of a few select species could result in the loss of many morphotypes in the open-ocean fossil record. We agree that dermal denticle morphological diversity is an imperfect metric of shark diversity as a result of substantial overlap in interspecific and intraspecific denticle morphological variation (1, 3–5). However, we note and agree with Naylor *et al.* that there are distinct taxonomic groupings of denticle morphotype diversity, which allows them to be used as broad-scale indicators of elasmobranch evolution (3, 4, 6). Indeed, taxonomically distinct denticles in reef sediments correlate with the relative abundance and presence of those shark species in the local area (7) and have been used to reconstruct historical shark communities on coral reefs (8).

We agree with Naylor *et al.* that “exhaustive documentation of denticle variation from multiple parts of the body across the diversity of chondrichthyans” would be a major contribution and would greatly improve the interpretation of microfossil denticle studies. However, we note that this is the work of years and is ongoing in our laboratory and others. The dataset of published modern elasmobranch denticle morphotype diversity compiled in the original paper (1) provides a reasonable first step in this effort. Of the 152 species in the dataset (representing 62

genera, 30 families, and 10 orders, covering the majority of extant elasmobranch diversity), 53 species had images from multiple skin samples along the body, including some from embryonic forms; among sampling efforts involving multiple skin locations, the mean number of images per species was 9.53. In total, this modern dataset comprised 596 images of shark skin and identified 63 unique denticle morphotypes, many of which were not observed in the fossil record and were restricted to coastal, shallow-water taxa (1). The inclusion of these taxa in our database suggests that the observed extinction is not attributable to a range shift of species leaving the open ocean, nor to a change in ocean circulation (as asserted by Naylor *et al.*), because it captures sharks living in all habitats, not just the pelagic ocean. Of the 63 morphotypes identified, 61 are present in the subset of 53 species that include images from across the body of the shark, and the addition of the remaining 99 species with a single skin patch sampled yielded only two additional morphotypes to the dataset. A rarefaction analysis demonstrates that additional sampling would not significantly increase total observed denticle morphotype richness [figures 1A, S3, and S6 in (1)]. Although we agree that this dataset is by no means “exhaustive,” it is a reasonable compilation to interrogate the central question raised by Naylor *et al.*: What level of species extinction is required to reproduce the observed 70% morphotype extinction in denticle morphotypes?

We performed a series of bootstrap simulations, randomly selecting between 1 and 152 species from the modern dataset, to simulate species extinction from 1% to 99%. From these random subsets, we calculated observed denticle morphotype richness for a given level of species “extinction.” Each level of extinction was simulated 10,000

times (Fig. 1B). Analyses were performed in R version 4.0.0 (9, 10). We found that to reproduce a 70% extinction of denticle morphotypes from this modern dataset, 142 species from the dataset would have to be missing, a 93% extinction (87 to 97% species-level extinction at the 95% confidence level). At genus level—a more common metric in paleontological studies [e.g., (11)]—56 of the 62 genera must disappear (90% genus-level extinction, 81 to 97% at the 95% confidence level) to capture a 70% morphotype extinction (Fig. 1C). Overall, this implies that denticle morphotype extinction underestimates taxonomic extinction.

Naylor *et al.* (2) also question the integrity of the depositional environment of the study system, on the basis of the paucity of shark teeth in the deep-sea microfossil record. Denticles and shark teeth are made of similar material and should both preserve within an unbiased depositional environment. However, as denticles are considerably smaller than teeth and cover the entire surface area of the shark, they are approximately three to five orders of magnitude higher in abundance on an individual shark than are teeth. Although precise denticle shedding rates for most species are poorly constrained, teeth would have to be shed at a rate 1000 to 100,000 times faster than denticles to be as prevalent as denticles in the deep-sea fossil record. In this study comprising 246 sediment samples, there were approximately 1400 denticles; this corresponds to roughly one or two shark teeth. Thus, it is unsurprising that shark teeth are not a prominent part of this dataset.

We agree with Naylor *et al.* that more comprehensive taxonomic work on denticle morphology is necessary to determine the precise taxonomic extent of this early Miocene event; however, we find that even with this uncertainty, the extinction presented in (1) is robust and is not due to migration or changes in ocean circulation. Improved taxonomic control on denticle morphology could provide insight into the potential mechanisms of extinction and ecological turnover in open-ocean sharks throughout their evolutionary history. Overall, denticle morphotype diversity is a reasonable proxy for broad-scale diversity patterns in elasmobranchs, opening up the deep-sea ecosystem to high-resolution evolutionary study of this charismatic group of vertebrates.

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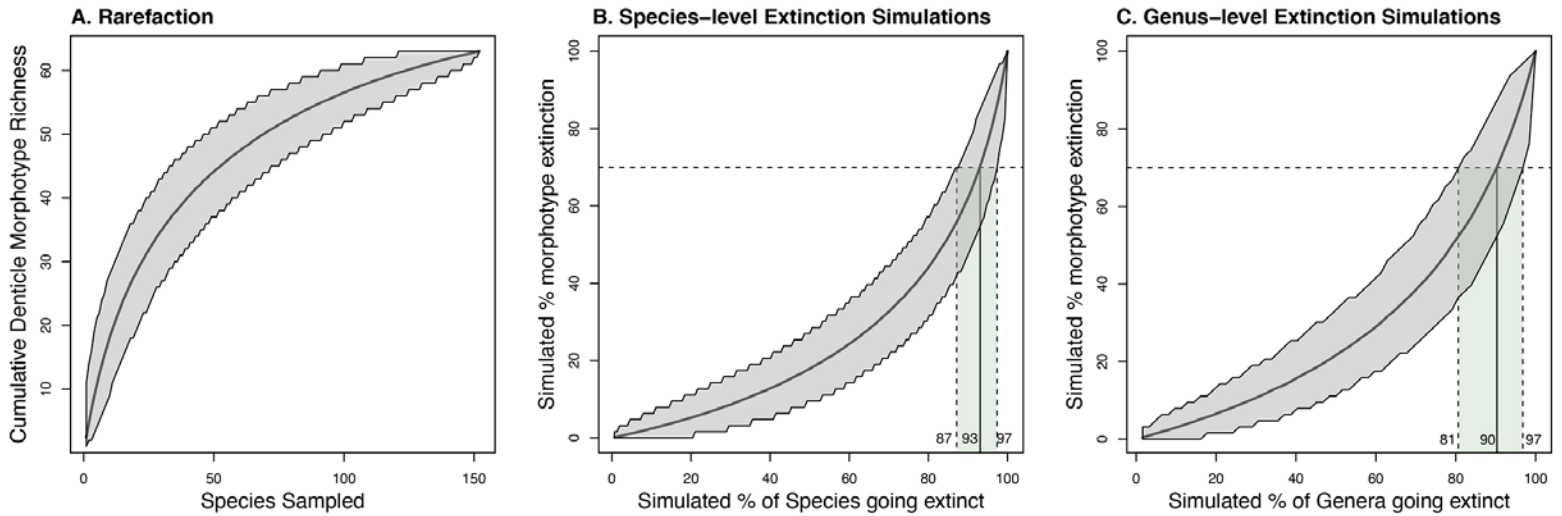


Fig. 1. Species extinction simulation studies. (A) Simulated rarefaction of morphotype diversity showing that the modern dermal denticle database has adequately captured most of modern dermal denticle morphology. (B) Estimated denticle morphotype extinction at varying levels of species-level extinction. The horizontal dotted line marks a 70% morphotype extinction—the conservative estimate of denticle morphotype extinction in the Early Miocene reported by Sibert and Rubin (1). The green box highlights the 93% species-level extinction necessary to reach the 70% morphotype extinction, bounded by the 2.5% and 97.5% quantiles, which are labeled as 87% and 97% species-level extinction. (C) Estimated denticle morphotype extinction at varying levels of genus-level extinction. The horizontal dotted line represents the 70% morphotype extinction threshold, and the green box highlights the 90% genus-level extinction necessary to reach the 70% morphotype extinction, bounded by the 2.5% and 97.7% quantiles, labeled on the figure as 81% and 97% genus-level extinction. On all panels, the gray shaded region represents the 97.5% and 2.5% quantiles from 10,000 bootstrap resampling simulations.

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