Robust evidence for modest diversity loss across the K/Pg in neoselachians: Response to Guinot et al.

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Summary

We reconstructed the neoselachian diversity over the past 145 million years using new occurrence dataset and DeepDive[1-3]. We recovered a small decline through the K/Pg following a steady increase during the Cretaceous, and a prolonged, substantial decline towards the present following a mid-Eocene peak[2]. Guinot et al.[4] argue that our conclusions are compromised by problems in the underlying data and by the way extinction magnitude across the K/Pg was quantified. They cast doubt particularly on the pattern across the K/Pg, which they consider to be at odds with all previous analyses. They raise no issue with the Cretaceous trend, even though it was recovered with the same dataset and methods. We audited the alleged data issues reported in Guinot et al.[4] and found that they mostly reflect operational choices (see Supplementary Information). However, we applied their data treatment and ran sensitivity tests to evaluate how this approach affects our results, specifically around the K/Pg. None of our tests recovered a diversity collapse for neoselachians during this interval. As such, we demonstrate that our findings are robust and consistent across different data treatments.

Main text

Although our findings contrasts with previous works by Guinot et al.[5,6], they are not unprecedented. Two recent studies found patterns that align remarkably well with our diversity trajectory, including a small decline across the K/Pg[7,8]. Such results were found using an independently compiled dataset, different methodology, and were based on genus-level occurrences, which are more taxonomically stable than species-level. The absence of a diversity collapse across the K/Pg is further corroborated by a reconstruction of neoselachian diversification rates using PyRate[9], which showed that although neoselachians experienced extinction rates greatly exceeding background levels, these were accompanied by elevated origination rates, suggesting rapid diversity turnover[10]. Consequently, we contend that our results do align with recent research.

Guinot et al.[4] argue that estimating diversity trajectories is an inappropriate methodology to understand the evolution of biodiversity in deep time. While we demonstrably appreciate the value of modelling speciation and extinction dynamics[9], we emphasize that the reconstruction of diversity trajectories has greatly advanced our understanding of the evolution of life on Earth through hundreds of studies published over many decades. These include some of the most influential research in the field of paleobiology, which have revealed the rise and fall of major clades in the history of life[11-14]. Methods to infer past biodiversity have evolved, from statistical and Bayesian approaches to deep learning, improving reconstructions of diversity dynamics[3,15-17]. We agree with Guinot et al.[4] that "a multitude of evolutionary histories can produce similar diversity trajectories", which indeed can even lead non-identifiability of speciation and extinction rates in some cases[18]. Yet, this does not invalidate research on past biodiversity trajectories as a key biological indicator of macroevolutionary dynamics.

Importantly, our goal was to reconstruct biodiversity trajectories through time. We contend that Guinot et al.[4] attempts to move the goalposts by focussing on extinction magnitude alone. Furthermore, when estimating extinction across the K/Pg, they use raw taxonomic counts without accounting for biases inherent to the fossil record. However, up to 50–60% of apparent diversity changes in shallow marine fossils can be attributed to sampling biases, and even methods traditionally used to mitigate them fail to fully account for spatial and temporal heterogeneities[19,20]. When explicitly accounting for such biases, we recovered a diversity trajectory displaying a small drop in diversity across the K/Pg[2], providing an analytically robust insight into neoselachian evolutionary history.

Embracing the fossil record through analytical evaluation

Our dataset (herein, FINS) was designed as a transparent synthesis of current knowledge of the neoselachian fossil record, with the goal of representing the published literature consistently and reproducibly. As such, each occurrence is traceable to its primary source facilitating verification[1]. Furthermore, each taxonomic name is harmonised based on the taxonomy from Shark-References[21]. In line with recent calls to promote open, transparent, and continuously updated biodiversity datasets[22], FINS includes detailed documentation to enable its reuse, and allows users to contribute additional occurrences and to implement alternative taxonomic approaches[1]. Our ambition is therefore for this dataset to evolve as new discoveries are made and taxonomic interpretations are refined.

Upon inspection, the dataset issues reported in Guinot et al.[4] largely reflect an overly restrictive interpretation of occurrence data that is not consistent with the methodological advances enabling large-scale palaeobiological analyses. The issues regarding uncertain nomenclature (~7% of our data) represent an operational decision rather than taxonomic interpretation. The suggestion that records lacking illustrations or taxonomic descriptions (i.e., "without evidence", ~40% of our dataset) should be excluded conflicts with 1) the purpose of occurrence datasets, which compile published reports of taxon presence rather than taxonomic diagnoses; and 2) their widespread use in palaeobiology to investigate macroevolutionary dynamics in diverse clades, from marine vertebrates[23] to dinousaurs[24] and angiosperms[25]. Finally, we found the issues regarding age and taxonomy to include both valid indications for corrections (~70% of cases) and claims that were proven unfounded after verification (~30%). Importantly, most corrections involved minor taxonomic harmonisations and had limited impact on the composition of the analysed dataset. A detailed response to each issue is provided in the Supplementary Text and Table S1.

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We applied the corrections deemed to be valid (Table S1) to FINS (Version v2), applied our
filtering protocol[2] (Data S1), and ran three sensitivity tests: 1) removing all occurrences with
uncertain nomenclature (8% and 1% of occurrences removed from original dataset at the
species and of the genus level, respectively); 2) training DeepDive to explicitly model the
K/Pg extinction; and 3) applying the same approach as the first test, but also removing
occurrences "without evidence" (36% and 39% of occurrences at the species and genus level,
respectively) (Table S2).
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Under our first test, we recovered a diversity change of $-22.9 \pm 1.1\%$ (Table S2; Data S2-S3).
Although this contrasts with the $-10\% \pm 9\%$ reported originally, it lies close to the upper
range of the original estimate. Fundamentally, the magnitude still corresponds to a moderate
decline rather than a catastrophic collapse (Figure 1). Under our second test, which explicitly
models the K/Pg extinction, we recovered a decline of $-29.7 \pm 8.4\%$ and under our third test,
which is the most restrictive, the magnitude of the decline remains within a comparable range
$(-33.1 \pm 3.9\%)$. At the genus level, the original analysis recovered a diversity increase of
$+15\% \pm 4\%$ across the K/Pg boundary. Under the first test, this increase is reduced to $+7.3 \pm$
5.7%, and under the second to $+7.2 \pm 4.7\%$. Under the third test, the result shifts to a small
decline of $-3.5 \pm 3.7\%$ (Figure 1, Table S2). However, because the uncertainty interval spans
zero, this estimate is statistically consistent with no net change in diversity. Together, our
sensitivity tests indicate that even under Guinot et al.'s data approach[4], the inferred species
richness loss across the K/Pg remains moderate and incompatible with a catastrophic
diversity decline.
124
125 *Conclusion*
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Our evaluation of Guinot et al.[4] revealed that the diversity trajectory originally recovered for
neoselachians remains consistent (Figure 1), supporting a modest diversity decline through
the K/Pg. This interpretation is corroborated by independent diversity reconstructions using
different approaches[7,8], as well as diversification rate analyses, suggesting rapid diversity
turnover[10]. Taken together, these multiple lines of evidence indicate that high origination rates
buffered net loss through the K/Pg, resulting in a smaller diversity decline than previously
thought[2,7,8,10]. Our results therefore do not deny elevated extinction across the K/Pg; rather,
they add an important missing piece to the puzzle of neoselachian evolution. We further
contend that the diversity trajectories originally reported[2] remain credible because the data
treatment applied in the sensitivity tests is unnecessarily restrictive, with as much as 38% of
the data (over 11,000 occurrences) excluded. Although ensuring the accuracy of primary data
is a fundamental standard that must be upheld, advocating increasingly restrictive data
filtering, including suggestions that would exclude almost half of published occurrences,
risks discarding the accumulated work of palaeontologists worldwide, limiting the scope of
macroevolutionary research. Our understanding of past evolutionary dynamics benefits from
embracing the available data and applying robust analytical frameworks capable of explicitly
evaluating uncertainty, while ever improving quantitative methods and sensitivity analyses
allow the biases in occurrence data to be tested directly. In our view, the advancement of the
field will come from integrating the richness of the fossil record with increasingly
sophisticated quantitative methods that allow these data to be critically assessed and
interpreted at large temporal and spatial scales.

Figure 1. Diversity trajectories reconstructed using the DeepDive framework under alternative data treatments (Table S1) at the species- (pink) and genus-level (blue). **A**. Sensitivity test 1, whereby we removed all occurrences with uncertain nomenclature, applied the corrections deemed to be valid after our own evaluation, and retained occurrences classified as "without evidence". **B.** Same as A, but K/Pg extinction is explicitly modelled in the simulations. **C.** Same as A, but occurrences classified as "without evidence" are excluded. Solid lines represent the mean reconstructed richness across simulations, and shaded envelopes indicate the uncertainty around the estimates (maximum deviation between minimum and maximum predicted richness values across simulations).

158 **Resource availability**
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160 **Lead contact**
161 Further information and requests for resources should be directed to and will be fulfilled by
162 the lead contacts, Catalina Pimiento (catalina.pimientohernandez@pim.uzh.ch).
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164 **Materials availability**
165 This study did not generate new unique reagents.
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Data and code availability
• The full FINS dataset used is accessible at Zenodo (Version v2):
https://doi.org/10.5281/zenodo.17371410
• The filtered data, which is used in the analyses is included in the Extended data (Data
S1)
• All code and data used this study are publicly available at Zenodo
(https://zenodo.org/records/19259194). These include:
○ The raw data
▪ The code to filter the FINS dataset
▪ The filtered dataset, divided in subsets for the analyses
▪ The paleo-oceans assigned to each occurrence and their time range
○ The data and code to perform the DeepDive analyses:
▪ The codes to generate the input files to process the data in DeepDive
▪ Input files, including .csv occurrence data and .ini configuration files
▪ The codes to perform the DeepDive analyses
▪ The outputs from DeepDive
○ The codes and data to create all tables and figures included in this manuscript.
• The resulting diversity estimations over time using DeepDive at the species level
(Data S2)
• The resulting diversity estimations over time using DeepDive at the genus level (Data
S3).
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195 **Declaration of interests**
196 The authors declare no competing interests.
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198 **Supplemental Information**
199 Supplemental information including procedures, figures, tables, and references can be found
200 online.
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