1 **Robust evidence for modest diversity loss across the K/Pg in neoselachians: Response to**
2 **Guinot et al.**
3

4 Amanda Gardiner[1,2], Gregor H. Mathes[1,3], Rebecca Cooper[4,5], Kristína Kocáková[1], Jaime A.
5 Villafaña[6], Daniele Silvestro[5,7,8*], Catalina Pimiento[1,9,10*]
6
[1]Department of Paleontology, University of Zurich; Zurich, 8006, Switzerland.
[2]Department of Genetics, University of Cambridge; Cambridge, CB2 3EH, UK
[3]Chair of Physical Geography, University of Passau, Passau, 94032, Germany
[4]Natural History Museum, University of Oslo, Oslo, 0562 Norway
[5]Centre for Planetary Habitability, Department of Geosciences, University of Oslo, Oslo,
0315, Norway
[6]Departamento de Ecología, Facultad de Ciencias, Universidad Católica de la Santísima
Concepción, Concepción 4090541, Chile.
[7]Department of Biosystems Science and Engineering, ETH Zurich, Basel, 4056, Switzerland
[8]Department of Biological and Environmental Sciences and Gothenburg Global Biodiversity
Centre, University of Gothenburg, Gothenburg, 41319, Sweden
[9]Department of Biosciences, Swansea University; Swansea, SA2 8PP, United Kingdom.
[10]Lead contact
*Correspondence: daniele.silvestro@bsse.ethz.ch; catalina.pimientohernandez@pim.uzh.ch

21
22 **Summary**
23

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. 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. 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.

38
39 **Main text**
40
Although our findings contrasts with previous works by Guinot et al.[4,5], 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[6,7]. 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[8], which showed that although neoselachians experienced
extinction rates greatly exceeding background levels, these were accompanied by elevated
origination rates, suggesting rapid diversity turnover[9]. Consequently, we contend that our
results do align with recent research.

Guinot et al. 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[8], 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[10-13]. Methods to infer past biodiversity have evolved, from statistical and Bayesian approaches to deep learning, improving reconstructions of diversity dynamics[3,14-16]. We agree with Guinot et al. 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[17]. 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. 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[18,19]. 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[20]. In line with recent calls to promote open, transparent, and continuously updated biodiversity datasets[21], 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. 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[22] to dinousaurs[23] and angiosperms[24]. 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.

101
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).
109
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, the inferred species
richness loss across the K/Pg remains moderate and incompatible with a catastrophic
diversity decline.
124
125 ***Conclusion***
126
Our evaluation of Guinot et al. 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[6,7], as well as diversification rate analyses, suggesting rapid diversity
turnover[9]. 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[2,6,7,9]. 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.

A Test 1: Uncertain taxonomy excluded; other corrections applied

B Test 2: As test 1; K/Pg extinction explicit model

C Test 3: As test 1; occurrences "without evidence" excluded

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).

Resource availability

Lead contact
Further information and requests for resources should be directed to and will be fulfilled by the lead contacts, Catalina Pimiento (catalina.pimientohernandez@pim.uzh.ch).

Materials availability
This study did not generate new unique reagents.

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).

Acknowledgments
This work was supported by the Swiss National Science Foundation through a PRIMA grant (no. 185798) awarded to CP. DS received funding from ETH Zurich and the Swedish Foundation for Strategic Environmental Research MISTRA within the framework of the research programme BIOPATH (F 2022/1448).

Declaration of interests
The authors declare no competing interests.

Supplemental Information
Supplemental information including procedures, figures, tables, and references can be found online.

References

1. Kocáková, K., Villafaña, J.A., Gardiner, A., Mathes, G.M., and Pimiento, C. (2025). FINS - A global dataset of fossil sharks, rays and skates from the Cretaceous to the Quaternary.

2. Gardiner, A., Mathes, G.H., Cooper, R., Kocáková, K., Villafaña, J.A., Silvestro, D., and Pimiento, C. (2026). Revealing the hidden patterns of shark and ray diversity over the past 145 million years. Current Biology *36*, 1045-1053.e1044. 10.1016/j.cub.2025.12.017.

3. Cooper, R.B., Flannery-Sutherland, J.T., and Silvestro, D. (2024). DeepDive: estimating global biodiversity patterns through time using deep learning. Nature Communications *15*, 4199.

4. Guinot, G., and Condamine, F.L. (2023). Global impact and selectivity of the Cretaceous-Paleogene mass extinction among sharks, skates, and rays. Science *379*, 802-806.

5. Guinot, G., Adnet, S., and Cappetta, H. (2012). An analytical approach for estimating fossil record and diversification events in sharks, skates and rays.

6. Staggl, M.A., Villalobos-Segura, E., Benton, M.J., and Kriwet, J. (2025). Global environmental drivers shape Cenozoic neoselachian diversity and identify modern conservation priorities. Scientific Reports *15*, 38661. 10.1038/s41598-025-25653-6.

7. Staggl, M.A., De Gracia, C., López-Romero, F.A., Stumpf, S., Villalobos-Segura, E., Benton, M.J., and Kriwet, J. (2025). The Drivers of Mesozoic Neoselachian Success and Resilience. Biology *14*, 142.

8. Silvestro, D., Salamin, N., and Schnitzler, J. (2014). PyRate: a new program to estimate speciation and extinction rates from incomplete fossil data. Methods in Ecology and Evolution *5*, 1126-1131. 10.1111/2041-210x.12263.

9. Kocáková, K., Silvestro, D., Mathes, G.H., Villafaña, J.A., and Pimiento, C. (2025). Global extinction events and persistent age-dependency in sharks and rays over the past 145 million years. Proceedings of the Royal Society B: Biological Sciences *292*. 10.1098/rspb.2025.2272.

10. Benton, M.J. (2016). Origins of biodiversity. PLoS biology *14*, e2000724.

11. Alroy, J. (2010). The shifting balance of diversity among major marine animal groups. Science *329*, 1191-1194.

12. Sepkoski Jr, J.J. (1981). A factor analytic description of the Phanerozoic marine fossil record. Paleobiology *7*, 36-53.

13. Niklas, K.J., Tiffney, B.H., and Knoll, A.H. (1983). Patterns in vascular land plant diversification. Nature *303*, 614-616.

14. Flannery-Sutherland, J.T., Silvestro, D., and Benton, M.J. (2022). Global diversity dynamics in the fossil record are regionally heterogeneous. Nature Communications *13*, 2751.

15. Starrfelt, J., and Liow, L.H. (2016). How many dinosaur species were there? Fossil bias and true richness estimated using a Poisson sampling model. Philosophical Transactions of the Royal Society B: Biological Sciences *371*.

16. Alroy, J. (2020). On four measures of taxonomic richness. Paleobiology *46*, 158-175.

17. Louca, S., and Pennell, M.W. (2020). Extant timetrees are consistent with a myriad of diversification histories. Nature *580*, 502-505.

18. Close, R.A., Benson, R.B., Alroy, J., Carrano, M.T., Cleary, T.J., Dunne, E.M., Mannion, P.D., Uhen, M.D., and Butler, R.J. (2020). The apparent exponential radiation of Phanerozoic land vertebrates is an artefact of spatial sampling biases. Proceedings of the Royal Society B *287*, 20200372.

19.   Close, R., Benson, R.B., Saupe, E., Clapham, M., and Butler, R. (2020). The spatial
structure of Phanerozoic marine animal diversity. Science *368*, 420-424.
20.   Pollerspöck, J., and Straube, N. (2025). Bibliography database of living/fossil sharks,
rays and chimaeras (Chondrichthyes: Elasmobranchii, Holocephali) Host-Parasites
List/Parasite-Hosts List. www.shark-references.com.
21.   Dowding, E.M., Dunne, E.M., Collins, K.S., Cryer, K., De Baets, K., Dimitrijević, D.,
Edie, S.M., Finnegan, S., Kiessling, W., and Lintulaakso, K. (2026). The billion-dollar
case for sustaining palaeontology's digital databases. Nature ecology & evolution, 1-
12.
22.   Finnegan, S., Anderson, S.C., Harnik, P.G., Simpson, C., Tittensor, D.P., Byrnes, J.E.,
Finkel, Z.V., Lindberg, D.R., Liow, L.H., Lockwood, R., et al. (2015). Paleontological
baselines for evaluating extinction risk in the modern oceans. Science *348*, 567-570.
10.1126/science.aaa6635.
23.   Dean, C.D., Chiarenza, A.A., Doser, J.W., Farnsworth, A., Jones, L.A., Lyster, S.J.,
Outhwaite, C.L., Valdes, P.J., Butler, R.J., and Mannion, P.D. (2025). The structure of
the end-Cretaceous dinosaur fossil record in North America. Current Biology *35*,
1973-1988.e1976. 10.1016/j.cub.2025.03.025.
24.   Condamine, F.L., Silvestro, D., Koppelhus, E.B., and Antonelli, A. (2020). The rise of
angiosperms pushed conifers to decline during global cooling. Proceedings of the
National Academy of Sciences *117*, 28867-28875. doi:10.1073/pnas.2005571117.
272