Institut des Sciences de l'Evolution-Montpellier

Dear Editors,

This letter accompanies a manuscript entitled "*Drivers of the artiodactyl turnover in insular Europe at the Eocene-Oligocene Transition*" that we are pleased to submit to the *Proceedings of the National Academy of Sciences of the United States of America*.

Context. The Eocene-Oligocene transition (EOT) is regarded as the biggest event in Cenozoic climate evolution and coincides with a marked faunal turnover, referred to as the Grande Coupure (GC). This event is associated in western Europe to an extinction phase of insular European mammals coupled with the arrival of modern Asian clades. However, the extent and magnitude of this faunal turnover remain unclear, and the drivers of the GC around the EOT have never been investigated, with active competition with immigrant clades often being proposed as the main factor of the extinction of endemic European species. Our work attempts to test the impact of the EOT and the GC on the species- and genus-level diversity dynamics of extinct clades of endemic European artiodactyl (even-toed ungulate) mammals, in a context of global and regional environmental changes and biotic turnover. Stemming from more than 50 years of fieldwork in the Quercy Konzentrat-Lagerstätte (SW France), we assembled and analyzed an original high-resolution dataset of more than 2,100 occurrences and 90 species, resulting from the direct systematic revision and determination of the fossil material, along with measurements of morphological and ecological traits for multiple specimens for each species.

Results. Using the state-of-the-art in Bayesian birth-death models, we demonstrate that success and decline of endemic artiodactyl mammals over time are driven by multiple and intertwined factors. We show that their radiation is mainly related to the favorable Eocene tropical conditions, and that the major environmental changes at the EOT are responsible for their spectacular extinction, with the disappearance of 77% of species. We further highlight that the concurrent increase in seasonality in Europe during the Oligocene is likely one of the main drivers of their decline. Contrary to the widely-held hypothesis of active competition between endemic and immigrant clades, our results suggest a passive replacement by Asian species that positively reduced extinction rates of endemic species overturning previous scenarios. By studying species' traits through time, we find a non-overlap of continuous ecological traits over time between endemic and immigrant species, also suggesting a non-competitive interaction between the two ungulate faunas.

Originality/Impact. This study represents one of the first works focusing on the GC while circumventing a number of biases known in the fossil record through Bayesian inferences. We show that the EOT was a severe crisis, by measuring for the first time its precise magnitude for a terrestrial vertebrate group, and which fits the criteria for a mass extinction. We further investigate, with a high regional resolution, the drivers of the GC, and underline the important role of the major environmental upheavals coupled with complex biotic interactions on the diversification of European artiodactyls. Their abundance in the fossil record provides an unprecedented preservation rate for mammals, and the focus on a restricted geographical area, similar to a large island, substantially reduces confounding effects (e.g., preservation biases and differences in climate conditions and biotic interactions), allowing an accurate discussion on their macroevolutionary dynamics on both sides of the EOT. The analysis of continuous ecological traits for a large number of species (four traits on 1,119 specimens for 69 species) provides supports to the soundness of our results in an original and independent way.

Our work represents a fine-scale study to investigate the initial radiation, decline, and recovery of a mammalian fauna during a major crisis context. Our results can impact multiple fields covering macroevolution, mammalogy, vertebrate paleontology, paleoecology, and are of interest for a wide audience. We also make available a large and original database including occurrences and morphological data that will certainly be of interest for future studies.

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We believe that the content and novelty of this study fits the aims and scopes of *Proceedings of the National Academy of Sciences of the United States of America* and we suggest the NAS and Editorial Board member **Dr. Nils Chr. Stenseth** (University of Oslo) as the most relevant person to handle this submission.

Thank you in anticipation for your kind consideration.

Yours sincerely,

Dr. Romain Weppe, on behalf of my co-authors