Science Bulletin xxx (xxxx) xxx

Contents lists available at ScienceDirect

Science Bulletin

journal homepage: www.elsevier.com/locate/scib

News & Views

Was there a global Cretaceous terrestrial biodiversity decline?

Xing Xu [a,b]

[a] Centre for Vertebrate Evolutionary Biology, Yunnan University, Kunming 650504, China
[b] Key Laboratory of Vertebrate Evolution and Human Origins, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China

The Cretaceous, lasting from 145 to 66 million years ago, was a time period of major turnover in terrestrial and marine ecosystems when many modern groups of plants and animals appeared for the first time. The Cretaceous was also famously terminated abruptly by the impact of a huge asteroid that wiped out such classic animals as dinosaurs and pterosaurs, but these organisms were supposedly killed in their prime, with no pre-extinction diversity decline [1]. A new study [2] identifies a long-term decline in the pterosaurs, lasting some 60 million years of the middle and late Cretaceous, before their final disappearance.

This result is unexpected for two reasons. First, it recalls an old debate about whether the dinosaurs, and their reptilian kin, disappeared with a whimper, not a bang. The end-Cretaceous asteroid implied sudden disappearance, and the gradual decline model was widely rejected in support of the impact model. However, there has been evidence in recent years that pterosaurs [3] and dinosaurs [4] were indeed declining in biodiversity through the middle and late Cretaceous, and the same seems to have been true of several other vertebrate groups, including non-marine crocodyliforms and rhynchocephalians [2].

The second reason the result is surprising is that the Cretaceous is widely seen as a time during which major groups flourished, including the non-avialan dinosaurs [1]. Further, the decline hypothesis appears to be in conflict with the proposed Cretaceous Terrestrial Revolution (KTR), Angiosperm Terrestrial Revolution (ATR), and Great Divergence (GD) that identify the middle and late Cretaceous as an important time for diversification of many terrestrial groups, most notably the angiosperms, and the origins of modern diversity [5,6]. This GD marks the important global turning point when terrestrial biodiversity for the first time exceeded marine biodiversity [7]. In fact, studies supporting the KTR and ATR noticed the biodiversity decline of some organismal groups during the mid-Cretaceous, but these were interpreted as episodes of faunal turnover [8]. For example, the mid-Cretaceous witnessed the replacement of rhynchocephalians and some early-diverging squamates by modern squamates, non-therian mammals by therian mammals, as well as the replacements of archaic groups by cryptodiran turtles, eusuchian crocodylomorphs, titanosauriform sauropods, and tyrannosaurid theropods, respectively, among others [8].

But explosive evolution of new groups in general can be envisaged at a time when others are indeed in decline. It appears to be true that dominant elements in modern ecosystems such as angiosperms, insects, birds, and mammals were rising in ecological significance during the KTR and ATR, whereas conditions perhaps did not favor other clades such as rhynchocephalians, crocodyliforms, pterosaurs, and dinosaurs. There is no suggestion that the new groups that benefited from the steady build-up of diversity of angiosperms (e.g., coevolving insects and insect-eaters such as spiders, lizards, birds, and mammals) were outcompeting the declining clades; they were doing different things in the mid-Cretaceous ecosystems. Further, biodiversity can be measured by different criteria such as species richness, or genetic, phenotypic, and ecological diversity, and these different measurements do not necessarily change simultaneously (Fig. 1). For example, the mid-Cretaceous witnessed declines in ecological functions but taxonomic increase of therian mammals [9] and a similar pattern has been noted for birds [10].

The clades in decline in the middle to late Cretaceous can be said to mark a collective "Cretaceous terrestrial biodiversity decline" (KTBD). This can be explained in two general ways. Firstly, many of the taxa that appear to have shown long-term biodiversity loss were large (non-marine crocodyliforms, dinosaurs, and pterosaurs). Secondly, climates were changing, with temperatures starting high in the mid-Cretaceous, but declining thereafter, especially in the last 20 million years of the Cretaceous [11]. Possibly, too, the gradual takeover of terrestrial floras by flowering plants and the decline in significance of other plant clades such as ferns, seed ferns, and gymnosperms, denied some herbivores their regular diet, and had upstream effects on their predators. In their study of latest Cretaceous dinosaur decline, Condamine et al. [12] found that the key drivers were global climate cooling and the fact that hadrosaurs outcompeted the other dinosaurian herbivores.

In their new paper, Yu et al. [2] suggest that the biodiversity decline of large-sized terrestrial animals in the middle to late Cretaceous could be attributed to the extremely high sea levels at the time (up to 200 m higher than today) which had the effect of reducing the total area of land; land area is important for biodiversity through the classic species-area effect [13] and particularly for large-sized animals [14]. This is perhaps another reason why comparatively small animals were favored during the KTR and ATR [5,6]. This apparent shift from relatively large animals to relatively

E-mail address: xu.xing@ivpp.ac.cn

https://doi.org/10.1016/j.scib.2023.04.022

Please cite this article as: X. Xu, Was there a global Cretaceous terrestrial biodiversity decline?, Science Bulletin, https://doi.org/10.1016/j.scib.2023.04.022

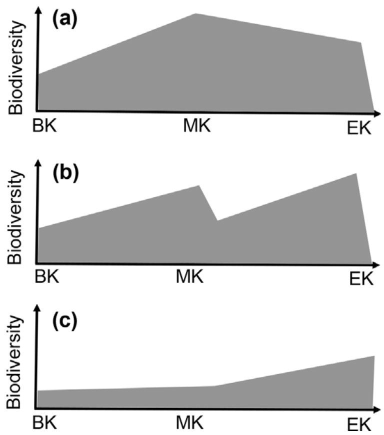

Fig. 1. Hypothetical Cretaceous terrestrial biodiversity evolution patterns based on three different parameters. (a) Diversification rate; (b) phylogenetic diversity/taxic diversity; (c) ecological diversity. BK, beginning of Cretaceous; MK, middle Cretaceous; EK, end of Cretaceous.

small animals during the KTR and ATR can be tested by comparing mean animal body sizes of Cretaceous terrestrial ecosystems through time at global, regional, and local scales.

Admittedly, the available evidence is not yet enough to support the presence of the KTBD. The strongest evidence for the KTBD is derived from biodiversity studies on non-avialan dinosaurs [4], and these studies measure biodiversity using diversification rate (i.e., speciation rate minus extinction rate, also termed net speciation rate; Fig. 1a), a parameter widely used in studying biodiversity evolution based on neontological data but not commonly used in paleontological studies [2]. Worthy of mention is that phylogenetic diversity/taxic diversity (Fig. 1b), which is widely used in macroevolutionary studies based on fossil data, often suffers from sampling issues [5,8]. Some methods for calculating diversification (PyRate, SFBD) consider sampling issues, and thus are likely to remove the sampling bias [2], but still the usage of diversification rate to estimate biodiversity based on paleontological data needs additional testing.

Evidence for the Cretaceous biodiversity decline of pterosaurs is strong given that it is supported by analytical results using several different parameters, including diversification rate, phylogenetic diversity/taxic diversity, and morphological disparity [2,3]. If a biodiversity decline in the latest Cretaceous can be supported by the results of similar analyses on non-avialan dinosaurs and some other groups, the KTBD could be justified as a real evolutionary pattern. It is especially important to compare patterns of diversity evolution from different measurements and parameters such as diversification rate, phylogenetic diversity/taxic diversity and morphological and functional disparity [15], and to explore how these different parameters are related to each other and how they differ in revealing different aspects of biodiversity change in deep time.

Conflict of interest

The author declares that he has no conflict of interest.

Acknowledgments

This work was supported by the National Natural Science Foundation of China (42288201) and Yunnan Revitalization Talent Support Program (202305AB350006). The author thanks Michael James Benton of the University of Bristol for his constructive comments.

References

[1] Brusatte SL, Butler RJ, Barrett PM, et al. The extinction of the dinosaurs. Biol Rev Camb Philos Soc 2015;90:628–42.
[2] Yu Y, Zhang C, Xu X. Complex macroevolution of pterosaurs. Cur Biol 2023;33:1–10.
[3] Butler RJ, Brusatte SL, Andres B, et al. How do geological sampling biases affect studies of morphological evolution in deep time? A case study of pterosaur (Reptilia: Archosauria) disparity. Evolution 2012;66:147–62.
[4] Sakamoto M, Benton MJ, Venditti C. Strong support for a heterogeneous speciation decline model in Dinosauria: a response to claims made by Bonsor et al. (2020). R Soc Open Sci 2021;8:202143.
[5] Lloyd GT, Davis KE, Pisani D, et al. Dinosaurs and the Cretaceous Terrestrial Revolution. Proc R Soc B 2008;275:2483–90.
[6] Benton MJ, Wilf P, Sauquet H. The Angiosperm Terrestrial Revolution and the origins of modern biodiversity. New Phytol 2022;233:2017–35.
[7] Vermeij GJ, Grosberg RK. The Great Divergence: when did diversity on land exceed that in the sea? Integr Comp Biol 2010;50:675–82.
[8] Benson RBJ, Mannion PD, Butler RJ, et al. Cretaceous tetrapod fossil record sampling and faunal turnover: implications for biogeography and the rise of modern clades. Paleogeogr Paleoclimatol Paleoecol 2013;372:88–107.
[9] Grossnickle DM, Polly PD. Mammal disparity decreases during the Cretaceous angiosperm radiation. Proc R Soc B 2013;280:20132110.
[10] Mitchell JS, Makovicky PJ. Low ecological disparity in Early Cretaceous birds. Proc Biol Sci 2014;281:20140608.
[11] Huber BT, MacLeod KG, Watkins DK, et al. The rise and fall of the Cretaceous hot greenhouse climate. Glob Planet Change 2018;167:1–23.
[12] Condamine FL, Guinot G, Benton MJ, et al. Dinosaur biodiversity declined well before the asteroid impact, influenced by ecological and environmental pressures. Nat Commun 2021;12:3833.
[13] Rosenzweig ML. Species diversity in space and time. Cambridge: Cambridge University Press; 1995.
[14] Cardillo M, Mace GM, Jones KE, et al. Multiple causes of high extinction risk in large mammal species. Science 2005;309:1239–41.
[15] Benton MJ. Exploring macroevolution using modern and fossil data. Proc R Soc B 2015;282:20150569.

Xing Xu is a Donglu Professor at Yunnan University and a senior researcher at Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences. His main research interest includes dinosaur vertebrate paleontology and Mesozoic stratigraphy and ecosystems.