Analysis of Global Diversity Patterns and Dynamics of Selected Mesozoic Marine Invertebrate Groups

Theses of PhD dissertation

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Crucella mijo De Wever 1981. A radiolarian from the Lower Pliensbachian of Haida Gwaii, Canada (formerly Queen Charlotte Islands). SEM image from Goričan et al. (2006)

Introduction

Analyses of large paleontological databases became a standard practice in the field of analytical palebiology in the past couple of decades. Using compilations of age range data, various intriguing concepts were developed on the basis of the stratigraphic distribution of fossils, such as the Red Queen hypothesis (Van Valen 1973) and episodic mass extinctions (Raup and Sepkoski 1982). In the 21st century the Paleobiology Database (PaleoDB) became the standard data source for paleontological analyses and due to its coverage of fossil sampling information, it allows the assessment of previously not addressable macroevolutionary and paleoecological hypotheses.

In this thesis, the research questions focus on the Mesozoic marine biota. This almost 200 Myr long era was bounded by two mass extinctions, witnessed the breakup of the last supercontinent Pangea, the evolution of dinosaurs, birds, mammals and the “Mesozoic marine revolution” (Vermeij 1977), to name but a few events. The two most important biotic crises in the era (the end-Triassic mass extinction and the Toarcian Oceanic Anoxic Event in the Early Jurassic) are recurrent themes in the analyses and interpretations in this work, and two of the case studies focus on their causing factors, killing agents and implications.

The general goal of this dissertation is to demonstrate state-of-the-art approaches to global paleoecological research, and to implement and test recently developed methods (such as the gap-filler turnover rates [Alroy 2014] and the SQS subsampling [Alroy 2010] algorithm) in the R environment (R Core Team 2015) using data from the PaleoDB. Experimenting with improvements on the already established methods, notably the increase of stratigraphic resolution in the binning procedure (assignment of information to stratigraphic units), is also an integral part of the analyses.

Four case studies are showcased in this work, each one dealing with a specific Mesozoic higher-rank taxon that has a fossil record which is reasonably well represented in the PaleoDB. Although the third study is rather explorative (Chapter 5), these individual research projects are designed in general to test specific hypotheses that are to be assessed in the face of the biasing factors of incomplete sampling.

Radiolarian biodiversity dynamics through the Triassic and Jurassic: implications for proximate causes of the end-Triassic mass extinction (Chapter 3)

This study demonstrates an analysis of diversity dynamics in order to better understand the environmental changes during the end-Triassic mass extinction. Radiolarians, as organisms with siliceous tests, have the potential to serve as a control group to the theory of ocean acidification that selectively decimated calcifying organisms (Hautmann et al. 2008). Although a previous analysis (Kiessling and Danelian 2011) supported the hypothesis that radiolarians were not significantly affected by the end-Triassic crisis, this contradicted the results of research focusing on individual sections (Carter and Hori 2005). The primary novelty in this study is the application of finer binning with a biostratigraphically important taxon, where data loss is negligible.

Demise of the last two spire-bearing brachiopod orders (Spiriferinida and Athyridida) at the Toarcian (Early Jurassic) extinction event (Chapter 4)

This is a case study of basic diversity dynamics, with focus on extinction selectivity and on its potential implications. Based on his preliminary analyses on data extracted from the Treatise on Invertebrate Paleontology, A. Vörös noted that groups featuring spiral lophophore support structures went extinct abruptly, at the Early Jurassic extinction event. The study assesses the hypothesis of extinction selectivity, compares the trajectories of diversity dynamics of spire-bearer and other forms, and has relevance in the biological understanding of brachiopod evolution.

The effects of binning and stratigraphic resolution on the statistics of diversity dynamics: a case study of Mesozoic bivalves (Chapter 5)

A rather explorative and theoretical chapter of this thesis focuses on the implications of increased stratigraphic resolution on global diversity analyses. Procedurally generated data are used to assess the effects of increased resolution on the analytical toolkit. Then the general applicability of substage-level resolution in the Mesozoic is tested on PaleoDB data. Fossil occurrence data of Mesozoic bivalves are subjected to stratigraphic binning at various resolution to assess the effects of data loss and the turnover patterns under the stage level of stratigraphic resolution.

Biodiversity dynamics and environmental occupancy of fossil azooxanthellate and zooxanthellate scleractinian corals (Chapter 6)

Due to the environmental constraints and relatively low preservation potential, the substage-level stratigraphic resolution could not be applied to the time series of scleractinian corals. This study is a complex application of the analytical toolkit to evaluate hypotheses (which were drafted by W. Kiessling) of a broader framework. The autecological and macroevolutionary understanding of the coral group is improved. Beside the other methods applied previously, the utilization of environmental information is the most important feature of this study.

Methods

A comprehensive review and the state-of-the-art of analysis of global diversity dynamics is provided in this chapter of the thesis, which is organized around the concept of the fossil sampling process.

Parameters

The most important parameters that these global analyses try to reveal and interpret are diversity and turnover. Although diversity (Magurran 2004) comprises both richness (the number of categories) and evenness (the distribution of units among the categories), global analyses tend to focus on richness alone and usually use taxa as categories, as the information available to estimate evenness is very scarce.

Turnover represent the degree of changes in a system. In global diversity dynamics, this term includes both originations and extinctions (Foote 2000), which are expressed as rates that represent the speed at which the number of taxa in a predefined group (cohort) decreases (extinctions) or increases (originations) with time.

To illustrate these parameters of diversity dynamics, birth-death simulations were developed to create procedurally generated age range data (which proved to be very useful in the study of the effects of binning on the estimates in Chapter 5).

Fossil sampling

Fossil sampling is heterogeneous and incomplete. These two factors contribute to the random noise and introduce bias in the metrics of diversity and turnover. Heterogeneity means that the extent of sampling varies over time, geographic, lithologic, sedimentary attributes of the fossiliferous localities.

It is now generally accepted that the fossil record is biased by sampling, but empirical corrections are available to allow the assessment of our results in the face of variable sampling extent. Sampling standardization algorithms (Alroy et al. 2001) are necessary to check for the distorting effects of heterogeneous sampling, as intervals with better sampling are expected to exhibit higher richness values, similarly to the derivative counts of taxa affected that we use to estimate turnover rates. The basic idea of sampling standardization is to calculate expected values for the estimates that are to be compared at the same levels of sampling effort (sample size), which are commonly calculated with random resampling. A number of such algorithms were run in all the case studies, although, due to large number of potential estimates and the similarity of their behavior for genera, only representative results are usually presented. As a lower amount of information is used to calculate a subsampled estimate, the function of these correction algorithms is to check the unstandardized ("raw") patterns in the face of heterogeneous sampling.

Incomplete sampling means that (1) organisms without fossilization potential will not be available in such analyses, and (2) even the fossil record of taxa with good preservation potential will be full with gaps. These gaps are usually "filled in" using the range-through assumption (interpolating between first and last appearance dates, [Foote and Miller 2007]), that introduce a number of biases. Occurrence registration, however, allows the application of metrics that are not influenced by these problems (Alroy 2008, 2014). Occurrence-based metrics of diversity dynamics are discussed in detail and contrasted with range-based methods, to provide a background on the applied methodology, and the choice of metrics.

After the application of the correction procedures, the calculated time series of metrics are subjected to statistical analyses. Resampling (e.g. bootstrapping) is frequently used to evaluate model suggested by a null hypothesis. The R programming language and environment was used for every simulation and analysis in this work, and the code produced is made available as electronic supplementary material.

Data

Since its conception in 1998, the Paleobiology Database has provided data for more than 200 official publications, and quickly replaced Sepkoski's (2002) compendium due to its data organization method, international support and increasing size.

The most important feature of the database is that instead of age ranges, the occurrences of fossils are registered in theoretical containers of unique stratigraphic and geographic attributes called collections. These units allow the assessment of sampling extent and the influence of different lithologic, geographic and sedimentary environmental variables on the ecological patterns. The primary publication information is also registered, allowing the continuous update of the database.

For the four case studies data were downloaded at different times between 2013 and 2015 from the PaleoDB both using the current main server in Madison (https://www.paleobiodb.org/), Wisconsin and through the Fossilworks gateway (http://www.fossilworks.org/) in Sydney. The downloaded data were binned to the Mesozoic stages based on the time scale of Gradstein et al. (2012) as the default resolution, which was refined further in three of the case studies.

Theses

Radiolarian biodiversity dynamics through the Triassic and Jurassic: implications for proximate causes of the end-Triassic mass extinction (Chapter 3)

1. Radiolarian turnover rates exhibit a decline over the Triassic and Jurassic periods, which is supported by sampling standardization.
2. The extinction rates of radiolarians in the late Rhaetian, the last time slice of the Triassic, was significantly higher than in its neighboring intervals, suggesting that radiolarians were indeed significantly affected by the end-Triassic mass extinction. The heat sensitivity of radiolarians, implied by experimental autecological research, suggests that a calcification crisis was not the only proximal cause of the end-Triassic mass extinction, temperature increase was also an important stressor.
3. No strong evidence was found for selectivity among the different groups of Radiolaria during the end-Triassic mass extinction.

4. Increased stratigraphic resolution is the sole cause that, in contrast to earlier studies, allowed detection of the latest Triassic extinction peak, suggesting that increased resolution might prove useful in additional global diversity analyses.

Demise of the last two spire-bearing brachiopod orders (Spiriferinida and Athyridida) at the Toarcian (Early Jurassic) extinction event (Chapter 4)

5. Differences in the structure of lophophore support of early Mesozoic brachiopods had a substantial effect on the diversity trajectories of the orders
6. Spire-bearing groups (Athyridida and Spiriferinida) were affected by selective extinctions in two intervals, the Rhaetian and the Toarcian.
7. The final, complete extinction of all spire-bearers happened in the Toarcian, most likely in the Early Toarcian substage, in relation to the oceanic anoxic event.

The effects of binning and stratigraphic resolution on the statistics of diversity dynamics: a case study of Mesozoic bivalves (Chapter 5)

8. Simulation results suggest that the increase of stratigraphic resolution is an important step towards improved recognition of mass extinction events.
9. General application of substage-level resolution of PaleoDB data is feasible on larger intervals such as the Mesozoic, even for a group of low turnover rates and less biostratigraphic importance.
10. The need for the assessment of the feasibility of the increase of resolution is justified by the significant loss of data (more than 40% of collections in the case of bivalves), and the unlikely increase of resolvability to the substage level in the near future.
11. The correlation patterns of the turnover rates with interval durations are suggestive of continuous turnover. Between-stage extinction rates are higher than those within the stages, but the difference is only marginally significant. Simulation results imply that at the sampling completeness of bivalves, a completely pulsed model is unlikely to hold. Instead, a combined turnover model, which better resembles the continuous model than a pulsed one, is suggested. Based on the results, it is very likely that turnover did happen within the stages.

Biodiversity dynamics and environmental occupancy of fossil azooxanthellate (AZ) and zooxanthellate (Z) scleractinian corals (Chapter 6)

12. The apparent difference in the overall turnover rate of Z and AZ genera emerges due to the different sampling intensity of Z and AZ corals. After correction for this bias, turnover of the two groups is shown to be similar even though they have different environmental preferences.
13. AZ corals exhibited smaller extinction rates since the Cretaceous compared to Z corals.
14. During the mid-Cretaceous a critical change occurred in the environmental occupancy of scleractinian corals that is indicated by the proportional diversities of Z and AZ corals. AZ corals started to proliferate in deeper water, siliciclastic and non-reef environments.
15. The environmental change of AZ corals in the Cretaceous is supported by an origination pulse, indicating the higher number of genus originations compared to Z corals.

Conclusions

The dissertation is concluded by a general discussion on the overall stability and reproducibility of the results, along with a brief outlook on the future potential of paleontological data analysis.

As more information is being continuously entered into the PaleoDB, the results of statistical analyses, such as the ones presented in the case studies here, are expected to change. Although paleontology, as a discipline, has some experience with this issue (cf. the diversity curves of Sepkoski [1993]), the stability of the estimates of such detailed analyses have not been assessed yet in the face of time-heterogeneous data amassment. Therefore, these estimations are to be rechecked after a substantial amount of new data is uploaded into the database.

In order to facilitate this, and to encourage the development of the field, the results of the analyses presented in this thesis can be recalculated with the scripts and data that were provided as electronic supplementary material. I also encourage fellow paleontologists to publish occurrence information in a well-documented way that allows the fastest integration of newly described fossils to the dataset. The aggradation of data shall allow a more accurate reconstruction and understanding of the past, with implications for the possible future of our planet’s biota.

References

Alroy, J. 2008. Dynamics of origination and extinction in the marine fossil record. Proceedings of the National Academy of Science 105:11536-11542.

Alroy, J. 2010. The shifting balance of diversity among major Marine animal groups. Science 329:1191-1194.

Alroy, J. 2014. Accurate and precise estimates of origination and extinction rates. Paleobiology 40:374-397.

Alroy, J., C. R. Marshall, R. K. Bambach, K. Bezusko, M. Foote, F. T. Fürsich, T. A. Hansen, S. M. Holland, L. C. Ivanyi, D. Jablonski, D. K. Jacobs, D. C. Jones, M. A. Kosnik, S. Lidgard, S. Low, A. I. Miller, P. M. Novack-Gottshall, T. D. Olszewski, M. E. Patzkowsky, D. M. Raup, K. Roy, J. J. J. Sepkoski, M. G. Sommers, P. J. Wagner, and A. Webber. 2001. Effects of sampling standardization on estimates of Phanerozoic marine diversification. Proceedings of the National Academy of Science 98:6261-6266.

Carter, E. S., and R. S. Hori. 2005. Global correlation of the radiolarian faunal change across the Triassic–Jurassic boundary. Canadian Journal of Earth Sciences 42:777-790.

Foote, M. 2000. Origination and extinction components of taxonomic diversity: General Problems. Paleobiology 26:74-102.

Foote, M., and A. I. Miller. 2007. Principles of Paleontology. W. H. Freeman and Company, New York.

Goričan, Š., E. S. Carter, P. Dumitrica, P. A. Whalen, R. S. Hori, P. De Wever, L. O'Dogherty, A. Matsuoka, and J. Guex. 2006. Catalogue and Aystematics of Pliensbachian, Toarcian and Aalenian Radiolarian Genera and Species. Zalozba ZRC.

Gradstein, F. M., J. G. Ogg, and M. Schmitz. 2012. The Geologic Time Scale 2012, 2-Volume Set. Elsevier Science & Technology Books.

Hautmann, M., M. J. Benton, and A. Tomašových. 2008. Catastrophic ocean acidification at the Triassic-Jurassic boundary. Neues Jahrbuch für Geologie und Paläontologie 249:119-127.

Kiessling, W., and T. Danelian. 2011. Trajectories of Late Permian - Jurassic radiolarian extinction rates: no evidence for an end-Triassic mass extinction. Fossil Record 14:95-101.

Magurran, A. E. 2004. Measuring Biological Diversity. Blackwell, Oxford.

Raup, D. M., and J. J. J. Sepkoski. 1982. Mass Extinctions in the Marine Fossil Record. Science 215:1501-1503.

Sepkoski, J. J. J. 1993. Ten years in the library: New data confirm paleontological patterns. Paleobiology 19:43-51.

Sepkoski, J. J. J. 2002. A compendium of fossil marine animal genera. Bulletins of American Paleontology 363:1-560.

Team, R. C. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Van Valen, L. 1973. A new evolutionary law. Evolutionary Theory 1:1-30.

Vermeij, G. J. 1977. The mesozoic marine revolution: Evidence from snails, predators and Grazers. Paleobiology 3:245-258.

List of publications related to the PhD Thesis

Pálfy, J. and **Kocsis, Á. T.** 2014. Volcanism of the Central Atlantic Magmatic Province as the trigger of environmental and biotic changes around the Triassic-Jurassic boundary. In Keller, G., Kerr, A. C. (eds), Volcanism, Impacts and Mass Extinctions: Causes and Effects. Geological Society of America Special Paper 505: 245–261.

Kocsis, Á. T., W. Kiessling, and J. Pálfy. 2014. Radiolarian biodiversity dynamics through the Triassic and Jurassic: implications for proximate causes of the end-Triassic mass extinction. Paleobiology 40(4): 625-639.

Kiessling, W. and **Kocsis, Á. T.** 2015. Biodiversity dynamics and environmental occupancy of fossil azooxanthellate and zooxanthellate scleractinian corals. Paleobiology, doi: 10.1017/pab.2015.6

Kocsis, Á. T., Sághi, K., Pálfy, J. 2015. The Paleobiology Database as a reasearch tool for modern palaeontology. Földtani Közlöny 145(1), 85-98.