

Cenozoic plankton diversity dynamics and the impact of macroevolution on the marine carbon cycle.

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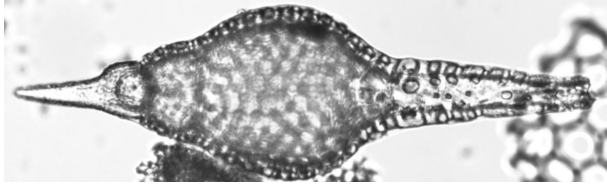
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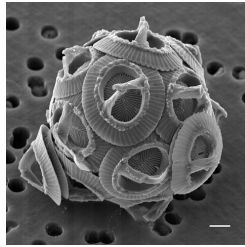
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2020-05-04

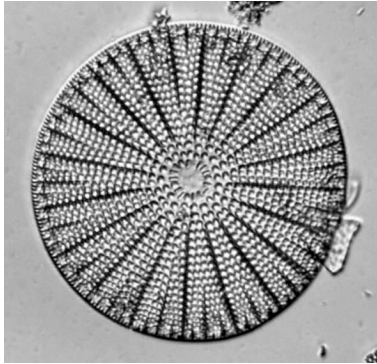
Marine microfossils



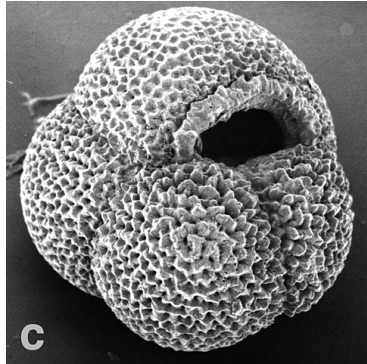
Radiolarians



Calcareous nannofossils



Diatoms



Planktonic foraminifera

The planktonic biome is the world's largest ecosystem. It is also incredibly diverse. Primary productivity in the open ocean accounts today for ca. 45 Pg of Carbon per year, i. e. roughly half of the world's productivity.

The biological carbon pump, i. e. the withdrawal of dissolved carbon from the ocean by marine organisms and its export to the deep-sea and the sediments is the main process for taking carbon out of the cycle for million years at a time.

Four groups of planktonic organisms, because of their mineralized shell, happen to have a very complete and abundant fossil record. In fact most marine deep-sea sediments are mainly composed of at least one of those four groups.

Importantly, they happen to also be four of the most relevant groups as far as the carbon cycle is concerned.

Diatoms and calcareous nannoplankton contribute disproportionately to the biological carbon pump. Diatoms in particular are very effective at capturing carbon. Calcareous nannofossils and planktonic foraminifera are the main source of marine carbonates. They are also the main biological component of the so-called alkalinity pump (i. e. the formation of calcium carbonate shell releases CO_2).

Furthermore radiolarians and foraminifera, being rhizarians, i. e. amoeboid protists, are among the main groups of organisms responsible for the formation of marine aggregates that sink carbon quickly into the deep-sea, and occasionally to the sediments.

Pictures: Johan Renaudie (diatom and radiolarian), Wikicommons user:NEON_ja (calcareous nannofossils) and Hannes Grobe via WikiCommons (planktonic foraminifera).



Neptune (NSB) database

Neptune Sandbox Berlin

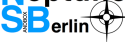
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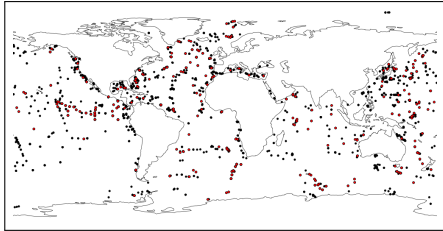
Search for occurrences

Fossil group	<input type="text" value="Dinobirds"/>	Time span	<input type="text" value="0"/>	<input type="text" value="50"/>	<input type="text" value="Ma"/>	Ocean
Genus	<input type="text"/>	Longitude	<input type="text" value="0"/>	<input type="text" value="0"/>	<input type="text" value="°"/>	<input type="text" value="Lat"/>
Species	<input type="text"/>	Latitude	<input type="text" value="0"/>	<input type="text" value="0"/>	<input type="text" value="°"/>	<input type="text" value="Site"/>
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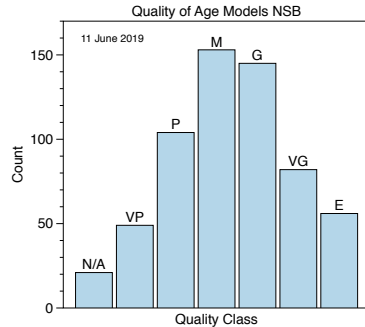
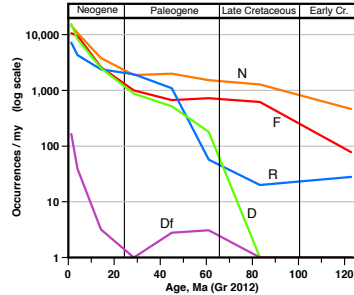
Options

- ☒ Resolve taxonomy using TML
- ☒ Filter out questionable identifications and taxa invalidly included in the fossil group
- ☒ Filter out open-sensu-lata taxa
- ☒ Filter problematic sample/occurrences (reworking...)
- ☐ Choose Age Scale:
- ☒ Filter out sites with age quality less than
- ☐ Perform specimen trimming (top % , bottom %)

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From Renaudie et al. 2020.



The Neptune database (est. 1992) holds microfossil occurrences from deep-sea sediments, combined with a complex stratigraphic layer allowing reliable and precise numerical age calculations for most samples. Its modern implementation is NSB (<http://nsb-mfn-berlin.de>).

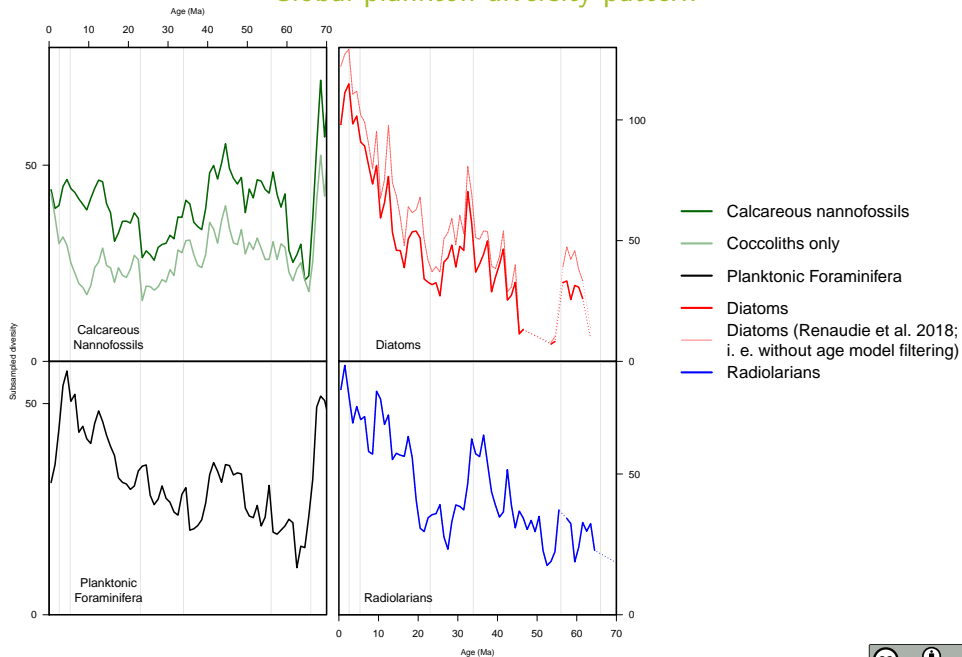
Thanks to the widespread coverage of the DSDP-ODP-IODP expeditions (black and red dots on the map), the database has a very good geographic coverage (red dots), as well as a good stratigraphic coverage: excellent for the Cenozoic, but also good for Cretaceous calcareous microfossils. The database contains currently ca. 800k occurrences for the 4 main taxonomic groups (Radiolarians, Diatoms, Foraminifera and Calcareous Nannofossils). The taxonomy is resolved thanks to IODP Paleo Coordination Group 'Taxonomical Name List' (TNL), an expert consensus.

Samples are given a numerical age via the library of age models relating age vs depth in section, supplemented by a large library of calibrated stratigraphic events needed to produce and maintain age models, and to assess the age model's quality, ranging from VP – very poor– to E – excellent.

Renaudie J., Lazarus D.B., Diver P., 2020. NSB (Neptune Sandbox Berlin): An expanded and improved database of marine planktonic microfossil data and deep-sea stratigraphy.. *Palaeontologia Electronica*, 23(2):a11.



Global plankton diversity pattern



Data for each of the four studied groups (Calcareous Nannofossils, Planktonic Foraminifera, Diatoms and Radiolarians) are drawn from NSB. Samples from sites with very poor (VP) age models are discarded here. Taxonomy is resolved at the species level, and open nomenclature species are discarded.

Subsampled diversity is computed using a single common procedure for all groups: a combination of Shareholder Quorum Subsampling (SQS, with a quota of 0.7 over 100 trials; Alroy, 2010), to correct for geographic disparity and sample size, and D80 (Lazarus et al., 2014) to correct for secular changes in evenness.

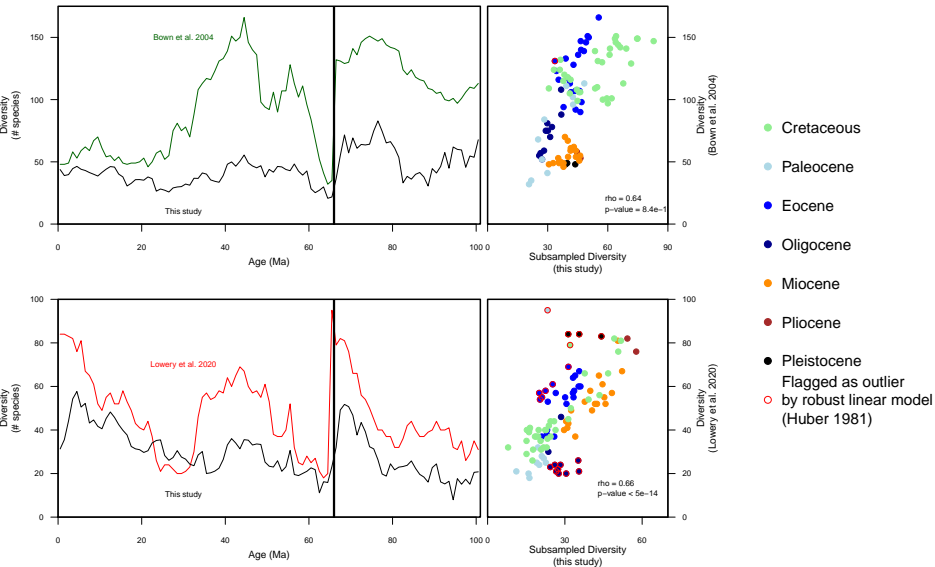
The radiolarian diversity curve shown here is to our knowledge the first sample-standardized estimate for the Cenozoic: it shows a diversification event in the Middle to Late Eocene, a diversity drop in the Oligocene followed by a sharp increase in the early Miocene.

Alroy J., 2010. Geographical, environmental and intrinsic biotic controls on Phanerozoic marine diversification. *Palaeontology*, 53(6): 1211–1235.

Lazarus D.B., Barron J., Renaudie J., Diver P., Türke A., 2014. Cenozoic diatom diversity and correlation to climate change. *PLoS ONE*, 9(1), e84857.

Renaudie J., Drews E.-L., Böhne S., 2018. The Paleocene record of marine diatoms in deep-sea sediments. *Fossil Record*, 21(2), 183–205.

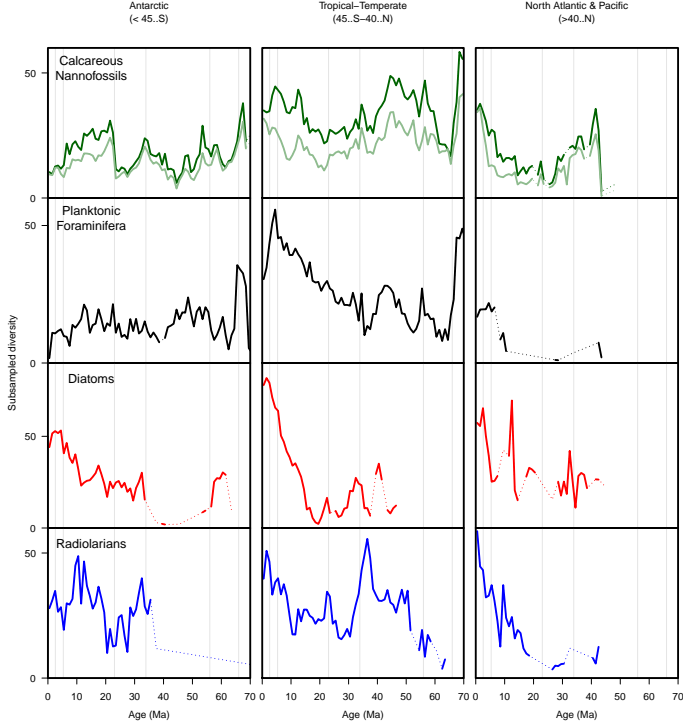
Comparison with previously published estimates



Previous estimates for diatoms were already shown in the previous slide: our new results, using the same database and methods are naturally also near identical, i. e. an increase in diversity in the late Eocene, followed by a drop in the Oligocene and finally a large diversification event in the mid-Miocene. Both the calcareous nannofossils and planktonic foraminifera curves follow a pattern similar to the previously published estimates (Bown et al. 2004; Lowery et al. 2020): a sharp decrease at the KPg boundary, followed by an increase in the Paleocene, a subsequent decrease during the second half of the Eocene and, in the case of foraminifera, a subsequent final increase. However they differ in the timing of changes and their amplitude: in our estimates, both curves show a considerably lower diversity in the Eocene. The drop toward the end of the Eocene happens also sooner, i. e. around ca.40Ma instead of at the Eocene-Oligocene boundary at ca. 34Ma, in the case of the foraminifera. Also as this decrease is more dampened in our results, the subsequent increase is more progressive, starting already at the end of the Eocene instead of starting only at the base of the Miocene.

Bown, P. R., Lees, J. A. and Young, J. R., 2004. Calcareous nannoplankton evolution and diversity through time. *Coccolithophores*, Springer Science:481–508.

Lowery, C. M., Bown P. R., Fraass, A. J., Hull, P. M., 2020. Ecological Response of Plankton to Environmental Change: Thresholds for Extinction. *Annual Review of Earth and Planetary Sciences*, 48:16.1–16.27.



Regional patterns

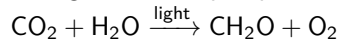
Geographic subsets of the data based on reconstructed paleogeography (using GPlates and Seton et al. 2012 rotation model) show that the global pattern observed for calcareous nannofossils and foraminifera is almost entirely the tropical pattern, while diatom and radiolarian global patterns are a combination of tropic and antarctic trends.

Of particular interest, are the statis-like pattern of Antarctic foraminifera from the Paleocene onwards; the mid-Miocene diversification event in the diatoms which seems to be mostly forced by the tropical/temperate region and the northern hemisphere high latitude; the abrupt decline in tropical radiolarians near the Eocene-Oligocene boundary; and the surge of antarctic calcareous nannofossils at the Oligocene-Miocene boundary.

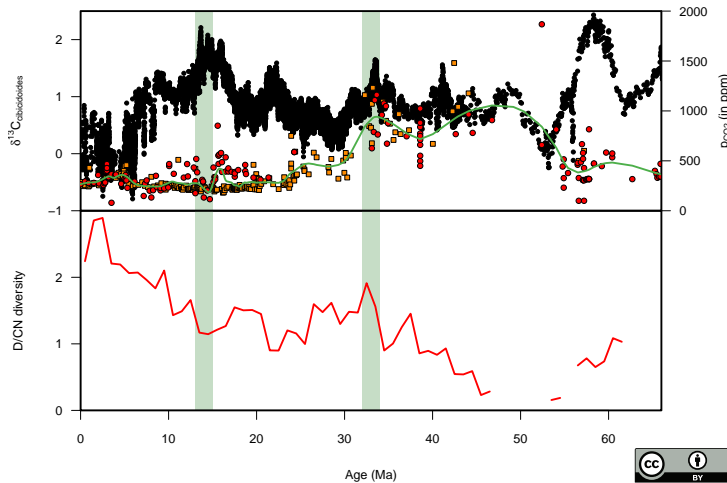
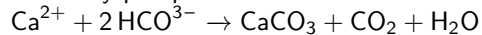
Seton, M., Müller, R. D., Zahirovic, S., Gaina, C., Torsvik, T., Shephard, G., Talsma, A., Gurnis, M., Turner, M., Maus, S., Chandler, M., 2012. Global continental and ocean basin reconstructions since 200 Ma. *Earth-Science Reviews*, 113(3-4):212–270.

Consequences on the carbon cycle

Biological carbon pump :



Alkalinity pump:



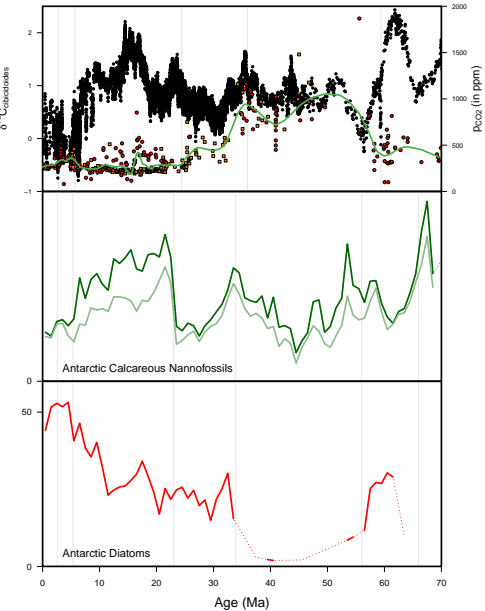
Because calcareous nannofossils contribute both to the biological carbon pump and the alkalinity pump (e. g. Frankignoulle et al. 1994), whereas diatoms only contribute to the former, increase in the diatom-nannofossil ratio should affect negatively $p\text{CO}_2$.

Similarly because rhizarians (planktonic foraminifera and radiolarians) contribute disproportionately to the formation of organic aggregate and thus to carbon export (Guidi et al. 2016), but foraminifera also contributes to the alkalinity pump, increase in the radiolarian-foraminifera ratio should similarly affect $p\text{CO}_2$.

Indeed, a back-of-the-envelope calculation (here the ratio of diatom to calcareous nanofossil diversity) seem to match roughly the known history of the carbon cycle: in particular, both the drops in $p\text{CO}_2$ (Beerling & Royer 2011) and benthic foraminifera $\delta^{13}\text{C}$ (Zachos et al. 2008) at the E-O boundary and during the middle Miocene match increase in that ratio.

- Beerling, D.J. and Royer, D.L., 2011. Convergent cenozoic CO_2 history. *Nature Geoscience*, 4(7):418–420.
- Frankignoulle, M., Canon, C., Gattuso, J.-P., 1994. Marine calcification as a source of carbon dioxide: Positive feedback of increasing atmospheric CO_2 . *Limnology and Oceanography*, 39.
- Guidi, L., Chaffron, S., Bittner, L. et al., 2016. Plankton networks driving carbon export in the oligotrophic ocean. *Nature* 532:465–470.
- Zachos, J.C., Dickens, G.R. and Zeebe, R.E., 2008. An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. *Nature*, 451(7176):279–283.

The Southern Ocean planktonic biome



$p\text{CO}_2$ after Beerling & Royer 2011; $\delta^{13}\text{C}$ after Zachos et al. 2008.

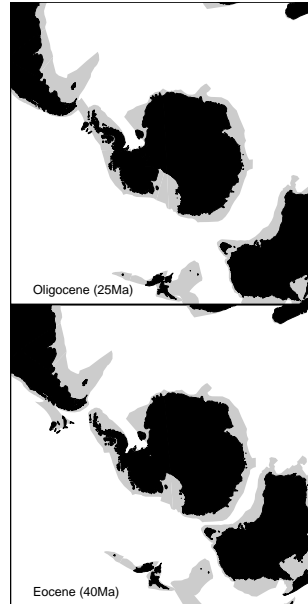


Plate reconstruction after Seton et al. 2012.

Today the Southern Ocean planktonic biome contributes disproportionately to the global carbon budget. It has unique physical and chemical characteristics (such as being separated from other oceans not by a land mass but by a system of fronts and a strong circumantarctic current; a deeper mixed layer, etc.).

It is also a unique planktonic biome characterized in particular by a high endemism, and an ecological dominance of diatoms. It is also home of some of the diatom species that have the most influence on the carbon budget (e.g. *F. kerguelensis*).

This ocean however only appeared with its current physical properties some-when toward the end of the Eocene, so we have here the possibility to study the development of this planktonic biome.

Seton, M., Müller, R. D., Zahirovic, S., Gaina, C., Torsvik, T., Shephard, G., Talsma, A., Gurnis, M., Turner, M., Maus, S., Chandler, M., 2012. Global continental and ocean basin reconstructions since 200 Ma. *Earth-Science Reviews*, 113(3-4):212–270.

Beerling, D.J. and Royer, D.L., 2011. Convergent cenozoic CO_2 history. *Nature Geoscience*, 4(7):418–420.

Zachos, J.C., Dickens, G.R. and Zeebe, R.E., 2008. An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. *Nature*, 451(7176):279–283.

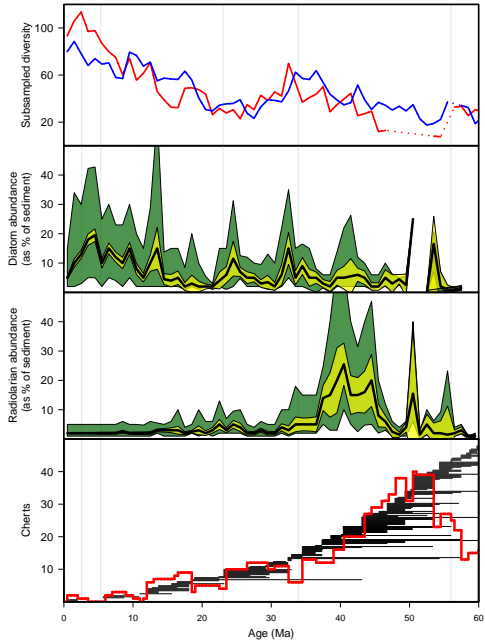
Time-series analysis

model	AICc	Δ_{AICc}	Akaike weight
Diatom diversity			
~ AR	626.6	8.237	0.044
~ AR + lag($\delta^{18}\text{O}$,1)	621.7	3.259	0.184
~ AR + lag(nannos div,1)	626.5	8.130	0.016
~ AR + lag(nannos div,1) + lag($\delta^{18}\text{O}$,1)	619.9	1.464	0.156
~ AR + lag(antarctic nannos div,1)	620.8	2.444	0.277
~ AR + lag(antarctic nannos div,1) + lag($\delta^{18}\text{O}$,1)	618.4	0	0.324
Antarctic Calcareous Nannofossils diversity			
~ AR	473.8	155.005	0.000
~ AR + lag($\delta^{18}\text{O}$,1)	357.8	38.959	0.000
~ AR + lag(diat div,1)	322.0	3.163	0.374
~ AR + lag(diat div,1) + lag($\delta^{18}\text{O}$,1)	318.8	0	0.626

When analyzing the diversity time-series, it appears that while calcareous nannofossils evolution might have had as much an impact on diatom diversity than climate change (though the statistical results are inconclusive), antarctic calcareous nannofossil's diversity trajectory can be significantly better explained by an auto-regressive model (AR) combined with lagged values of diatom diversity and climate evolution (here simplified as benthic foraminifera $\delta^{18}\text{O}$).

In more simple terms, our analysis means that diatoms, at least in the Southern Ocean, outcompeted calcareous nannofossils, and that this competition drove diversity decrease in the calcareous nannofossils.

Consequences on the carbon cycle: diversity & abundance



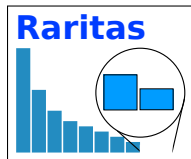
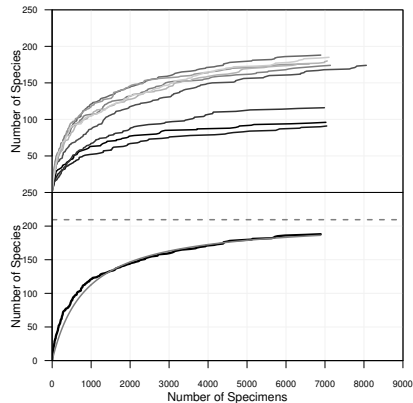
Top panel: Radiolarian (blue) and diatom (red) diversity (this study). Two middle panels: Diatom and radiolarian relative abundance in sediments based on DSDP-ODP-IODP smear slide descriptions (black line: median value per time-bin, yellow: 95% confidence interval on median, green: interquartile range; Renaudie 2016). Bottom panel: Chert cumulative abundance in deep-sea sites (modified after Muttoni & Kent 2007).

Beyond diversity, what connects carbon removal and plankton is its flux of biomass. Obviously this is difficult if not impossible to estimate. However a first order estimate, for siliceous microfossils at least, is their abundance in sediments, granted chertification doesn't overprint the pattern. What we observe in the Cenozoic is, for diatoms, a pattern remarkably close to that followed by their diversity, with a peak in their sediment abundance at the E/O boundary, and a sustained abundance increase from the mid-Miocene onwards. For radiolarians however, as was already noted in the literature, the pattern is dominated by a massive pulse in the Eocene. However the Early Eocene and Paleocene (global) patterns are difficult to interpret due to a large chertification event (Muttoni & Kent 2007).

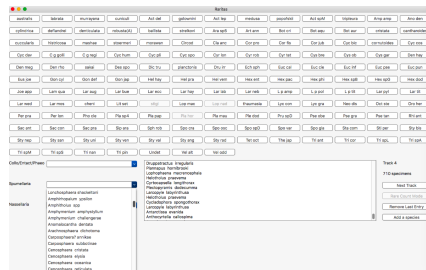
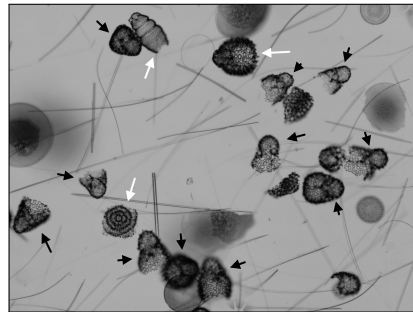
Calcareous microfossils abundance patterns in sediments are considerably more complex to follow at a global scale due to the varying depths of the CCD (carbon compensation depth), below which they are not preserved.

Muttoni, G. & Kent, D. V., 2007. Widespread formation of cherts during the early Eocene climate optimum. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 253(3-4):348–362.
Renaudie, J., 2016. Quantifying the Cenozoic marine diatom deposition history: links to the C and Si cycles. *Biogeosciences*, 13(21).

Studying diversity with exhaustive surveys



From Lazarus et al. 2018.



How accurate are literature database-driven diversity reconstructions, given that the publications usually do not report full diversity?

In order to test our literature data synthesis approach, we have carried out a long-term program to newly count full-fauna/flora deep-sea microfossil diversity.

We use stratified counting (Lazarus et al. 2018) of randomly settled slides, where after a few 'all specimens-counted' tracks, common species are only estimated (from the mean abundance of these species in prior tracks), thus freeing time to focus on rarer species. Counting then continues until the species accumulation curve actually flattens (typically a few thousand specimens).

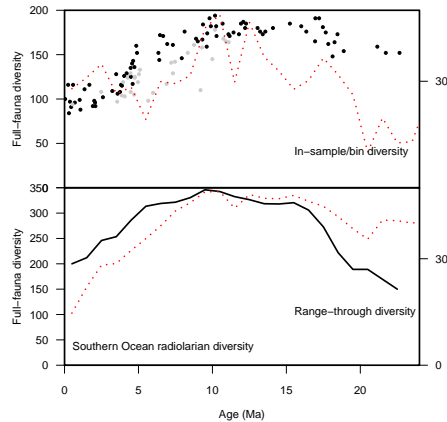
Extrapolation from these accumulation curve, as well as more classical coverage estimator (Good's u , Chao's ACE, etc.), show that 80 to 95% of the preserved diversity is likely to be indeed sampled in these countings.

Further, Cenozoic deep-sea microfossil sedimentation is such that most, if not all, species at least for radiolarians are preserved in the sediments.

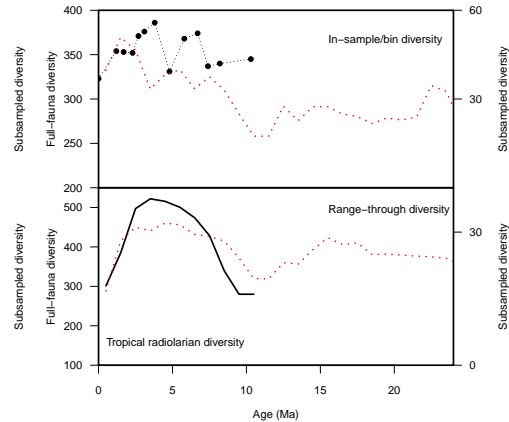
Renaudie J., Lazarus D.B., 2012. On the accuracy of paleodiversity reconstructions: a case study in antarctic radiolarians. *Paleobiology*, 39(3), 491–509.

Lazarus D.B., Renaudie J., Lenz D., Diver P., Klump J., 2018. Raritas: a program for counting high diversity categorical data with highly unequal abundances. *PeerJ*, 6, e5453.

Studying diversity with exhaustive surveys



Modified and recalculated from Renaudie & Lazarus 2012.



Modified after Trubovitz et al., *submitted*.

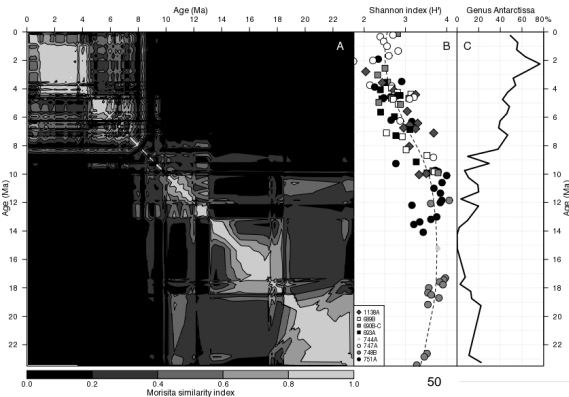
Full-fauna investigation on Southern Ocean and Equatorial Pacific radiolarians (Renaudie & Lazarus 2012 and Trubovitz et al. *submitted* respectively) showed that literature-driven reconstruction usually manages to correctly estimate the pattern (though 1 to 3Myr-lags are fairly common; see Renaudie & Lazarus 2012).

What it also shows is how drastically the absolute (numerical) diversity is underestimated in published literature data. Radiolarian diversity in full survey counts oscillates between 100 and 200 species per sample in the Southern Ocean (with a total of 490 species in the full Neogene of the region, including ca. 100 new to science) and up to 400 per sample in the Equatorial Pacific (with ca. 1k species in total in the last 10Ma)! By contrast, within-sample radiolarian diversity in literature data typically is between 10 to 30 species. Although polycystine radiolarians are an unusually diverse group, literature data similarly severely under-reports absolute diversity for the three other groups mentioned.

Renaudie J., Lazarus D.B., 2012. On the accuracy of paleodiversity reconstructions: a case study in antarctic radiolarians. *Paleobiology*, 39(3), 491–509.

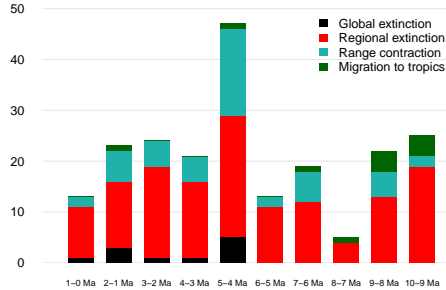
Trubovitz S., Lazarus D., Renaudie J., Noble P., *submitted*. Marine plankton show threshold extinction response to Neogene climate change.

Studying diversity with exhaustive surveys



Similarity index between radiolarian samples from the Southern Ocean, Shannon index and abundance of genus *Antarctissa*, showing a significant community turnover predating the loss of species by ca. 3Myr (from Renaudie & Lazarus 2012).

What actually happened to species disappearing from the Southern Ocean, based on comparison between full-fauna surveys of Southern Ocean and Equatorial Pacific radiolarians; Modified after Trubovitz et al. *submitted*.



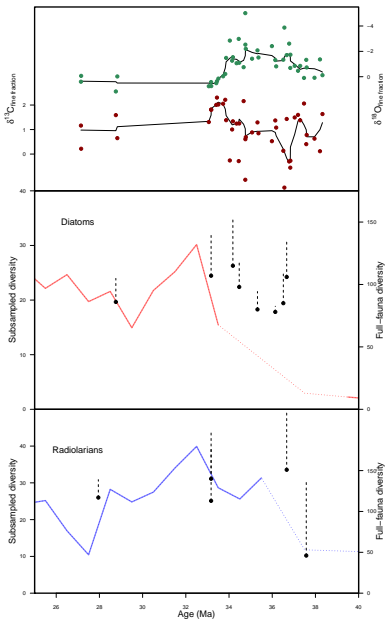
Full-fauna, exhaustive diversity counts allow us to study the community structure, and to compare for each species the modality of their extinction. For example, in the case of the Southern Ocean Neogene radiolarians (Renaudie & Lazarus 2012), full diversity counts highlighted a significant turnover ca. 3Myr prior to the end-Miocene extinction event, coupled with the ecological rise of a single genus: *Antarctissa*.

A comparison of contemporaneous faunas (Trubovitz et al. *submitted*) shows that a handful of species that had disappeared in the Southern Ocean during the late stage of the Southern Ocean cooling were still alive afterwards in the Equatorial Pacific. The locally observed Southern Ocean disappearances were in fact just shrinkages of the species' latitudinal ranges, which is in accord with the current 'migration' paradigm for plankton response to (future) climate change. Most of the polar species however failed to migrate and actually went extinct – which is not in accord with current biologic models!

Renaudie J., Lazarus D.B., 2012. On the accuracy of paleodiversity reconstructions: a case study in antarctic radiolarians. *Paleobiology*, 39(3), 491–509.

Trubovitz S., Lazarus D., Renaudie J., Noble P., submitted. Marine plankton show threshold extinction response to Neogene climate change.

Ongoing studies



Preliminary results for the Eocene-Oligocene siliceous plankton diversity of the Southern Ocean.

Top panel: $\delta^{13}\text{C}$ (dark red) and $\delta^{18}\text{O}$ measured on fine fraction (here calcareous nannofossils) of ODP Site 1090B (subantarctic); with LOWESS fitting.

Middle panel: In-sample diatom diversity from ODP Site 1090B vs literature-based diversity estimate for the Southern Ocean.

Bottom panel: In-sample radiolarian diversity from ODP Site 1090B vs literature-based diversity estimate for the Southern Ocean.

Dotted segments show extrapolated diversity based on the asymptote of a curve fitting the species accumulation curve for each sample (thus showing the estimated coverage of the counting so far).

We are currently studying the changes in the Southern Ocean planktonic biome at the Eocene-Oligocene boundary (with an emphasis on diatoms and radiolarians), and their relationship with the climatic and oceanographic changes that occurred at the time.

In particular we are trying to estimate diatom species' extinction sensitivity to climate change; and quantify the impact of the developing Southern Ocean diatom belt on the carbon cycle, while disentangling the sequence of events that led to its development.

For this purpose we are collecting diversity and abundance data for radiolarians and diatoms in a variety of sites from the Southern Ocean, together with carbon and oxygen isotopes on fine fraction (i. e. coccoliths) in an attempt to constrain the conditions in the uppermost layer of the water, where the biological carbon pump originates.

Find out more about the preliminary results of this project on display EGU2020-5924 (Rodrigues de Faria et al. 2020).

Rodrigues de Faria G., Lazarus D., Struck U., Asatryan G., Renaudie J., Özen V., 2020. Paleogene Polar Plankton and export productivity changes between the Eocene and Oligocene. *EGU General Assembly 2020*, EGU2020-5924.



Thanks for reading this.

The authors would like to thank Sylvia Salzmann (MfN) for preparing the microscopic slides for the faunal/floral surveys; as well as many volunteers and students who have helped maintaining the NSB database in Berlin in the last 8 years (namely M. Schmohl, D. Panning, S. Boehne, E.-L. Drews, R. Wiese, R. Seeger and N. Maier).

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