

Testing the accuracy of genus-level data to predict species diversity in Cenozoic marine diatoms

Robert Wiese^{1,2*}, Johan Renaudie², and David B. Lazarus²

¹Institut für Geologische Wissenschaften, Freie Universität Berlin, Malteserstraße 74-100, 12249 Berlin, Germany

²Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Invalidenstraße 43, 10115 Berlin, Germany

ABSTRACT

Correlations between past biotic diversity and climate can inform humanity's response to predictions of future global climate change, e.g., extinction risk with global warming. Paleodiversity studies, however, frequently use genera as a proxy for species diversity, a practice that has often been questioned. Tests using actual data of the impact of using species-level versus genus-level taxonomy in paleodiversity-paleoenvironmental studies are also lacking. We conduct such a test, based on a recent study that showed a strong correlation of Cenozoic marine planktonic diatom species diversity to geochemical climate proxies. Using an updated version of the data set, we still find a strong correlation of Cenozoic diatom species diversity to environment. Using identical data but instead genera results in the loss of all significant correlations of diversity to environmental change. This occurs due to the earlier rise and later stability in genus versus species diversity data, a pattern known to be common between taxonomic ranks in the fossil record, and in general models of diversification. We conclude that studies of paleodiversity, particularly those addressing biotic responses to future environmental change, need to demonstrate the adequacy of genera as a proxy for species diversity, or use species-level data.

INTRODUCTION

Reconstructing biodiversity is a major research theme in paleontology. Studies, mostly on taxa richness, have contributed to major debates in evolutionary ecology, such as mechanisms of diversification, coevolution, competition, and the carrying capacity of the environment (Rabosky, 2013). Paleodiversity data document major events in life history, i.e., radiations, mass extinctions, and biologic recoveries (e.g., Sepkoski, 1981; Jablonski, 1986; Alroy et al., 2001; Barnosky et al., 2011), and are essential to understanding the impact of biologic evolution on long-term changes in biogeochemical cycles (Katz et al., 2004; Ridgwell, 2005). Studies of past biodiversity-environment interactions (increasingly under the label conservation paleobiology), by documenting environmentally driven extinction risk, affect economic and political decisions on humanity's response to anthropogenic environmental changes, e.g., global warming (e.g., Committee on the Geologic Record of Biosphere Dynamics et al., 2005; Dietl and Flessa, 2011; Barnosky et al., 2011; Kelley et al., 2013).

Early studies of past biodiversity used high-level taxa, such as families (e.g., Sepkoski, 1981). However, biotas respond to environmental change via their component species, the fundamental entities in evolution, adaptation, and selection (Mayr, 1963; Coyne and Orr, 2004; Hendricks et al., 2014). While simplifying aggregate concepts are sometimes used (e.g., functional groups; Tilman et al., 1997), species-level data are still essential (e.g., keystone species; Simberloff, 1998). Higher level taxa, unlike species, are more hypothetical constructs. This presents a variety of theoretical problems when used in diversity reconstructions, particularly for larger clades or biotas, despite occasional claims that higher taxa may be in some regard superior to species (reviewed in Hendricks et al.,

2014). These include systematic bias in diversity trajectories over time, with higher taxa showing more logistic patterns of early diversity rise and more constant values afterward (Lane and Benton, 2003); biases via aggregation in geographic range, longevity, rates of extinction, and other statistics with taxon size, as well as correlations to environment based on these (e.g., geographic range and environmental variables; Hendricks et al., 2014); and biased comparisons between clades, when criteria for higher taxa definitions are partially arbitrary and clade specific. These concerns have led to a shift from using families to using genera. This has become so widespread that Hendricks et al. (2014) titled their review *The Generification of the Fossil Record*, and reported that 43% of papers published in *Paleobiology* from 1975 to 2013 used genera rather than species. In 124 recently published papers listed as contributions by the Paleobiology Database (<https://paleobiodb.org/#/>), we find 72% of the 81 primary biodiversity studies used genera or even higher taxa, not species (Table DR1 in the GSA Data Repository¹). Genera, however, are still higher level taxa and thus have the same problems listed here (Hendricks et al., 2014). Diversity comparisons of modern biotas, for example, are known to sometimes yield significantly different results when using genera instead of species (Prance, 1994), demonstrating that genera data cannot always be assumed to be adequate proxies for species data. The relationship of genus to species diversity is often systematically correlated to climate or other environmental characteristics (Krug et al., 2008). This results in a systematic data bias that potentially can affect conclusions about diversity-climate relationships. Despite this, using genera instead of species in diversity studies has been justified usually by stating that genera are used due to practical problems with species diversity data quality, including incompleteness, unreliable species determinations of specimens particularly in large data compilations partially from old literature (e.g., the Paleobiology Database), limits to species-level discrimination from only hard parts, and other issues (Padian and Clemens, 1985; Hendricks et al., 2014; Table DR1).

Given the frequent use of genera, despite these potential problems, one would assume that there have been several studies demonstrating that using fossil genera instead of fossil species data does not affect relative diversity change estimates, or bias correlations between diversity and environmental change data. Surprisingly, this is not so: we know of no studies where this question has been adequately addressed. Most prior studies have used models to simulate species data (e.g., Sepkoski, 1978; Lane and Benton, 2003) or use geographic comparisons of modern diversity (e.g., Prance, 1994; Roy et al., 1996). There are three noteworthy exceptions. Lloyd et al. (2012) documented major differences in species and genus diversity histories in fossil coccolithophores. Liow and Finarelli (2014) found moderate differences in genus versus species diversification metrics in Neogene mammals. In Klompaker et al. (2013), primary trends in

¹GSA Data Repository item 2016350, Table DR1 (survey of use of genus and/or species in recent paleodiversity studie), Table DR2 (species per genus in representative living clades of organisms), and Table DR3 (summary of correlation statistics for species, genus and paleoenvironmental time series), is available online at <http://www.geosociety.org/pubs/ft2016.htm> or on request from editing@geosociety.org.

*E-mail: robert.wiese@fu-berlin.de

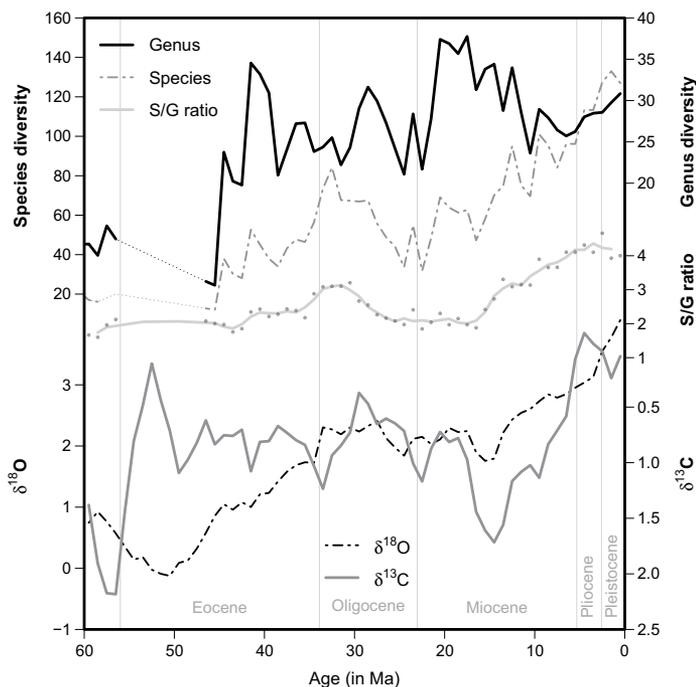


Figure 1. Top: Species (S) and genus (G) diversity of planktonic diatoms from the NSB (Neptune) database (www.nsb-mfn-berlin.de), using shareholder quorum subsampling (SQS) and evenness correction (see text). The gap from ca. 56 to 45 Ma is, as in the Lazarus et al. (2014) subsampling estimates, due to insufficient data in the NSB. Bottom: Syntheses of deep-sea stable isotopes of oxygen (water temperature–ice sheet volume) and carbon (global carbon cycle) are after Zachos et al. (2008). The time scale is from Gradstein et al. (2012).

raw species and genus diversity data for Mesozoic decapods are the same but detrended series are very different; they found a coherent pattern only after rebinning the data to a very low time resolution. Although some fossil diversity studies have begun to use species rather than genera (28% of studies in our literature survey, of which 74% are of vertebrates; Table DR1), comparisons between genera and species data are usually absent, or very brief (e.g., Orzechowski et al., 2015). Many of these studies (particularly on vertebrates) have per time bin species:genus ratios $\ll 2$, and often nearly 1. The species:genus ratios for living representatives of the same clades are generally much higher (4.5 for mammals, 7 to >10 for other groups; Table DR2), suggesting that the large majority of species diversity has not been sampled in the fossil record. In these studies species are little more than alternate name tags for genus resolution data. These data only underline the arguments cited here on the limits of using species in many fossil diversity studies. Even if our supposition about causes is wrong, with species and genus data so highly correlated due to very low species:genus ratios, it is mathematically impossible to have, and thus test for, cases where species and genus diversity yield different results.

To our knowledge there has been no study of fossil diversity data where (1) both genus and species diversity data are thought to be of good (if by no means perfect) quality; (2) the ratio of species to genera is high enough that the two variables can in principle vary independently; and (3) diversity and environmental data are compared. With such data one can test the essential assumption behind using genus data to study past diversity dynamics, and particularly diversity–environment interactions, i.e., that even if good species diversity data were available and were used instead of genera, no significant changes in a study’s conclusions (e.g., extinction risk with environmental change) would occur. Here we carry out the first such test, which underlies a broad range of paleontologic research. We use Cenozoic planktonic marine diatom species occurrence data from deep-sea drilling sections, as compiled in the NSB (Neptune Sandbox

Berlin) database (Lazarus 1994; www.nsb-mfn-berlin.de). These data are well suited to our goals (Lazarus, 2011). Taxonomic knowledge of both genera and species are well developed (if still far from perfect): genera are clusters of similar species defined using multiple distinct synapomorphic morphologic characters, and confirmed with molecular data in selected genera (Round et al., 1990; Medlin et al., 1993, 2008; Bruder and Medlin, 2007, 2008). Fossil species taxonomy is unusually good; it has been carefully defined and standardized as the species definitions have been used for numerous high-resolution biostratigraphic and paleoceanographic studies (Starratt, 2007; Smol and Stoermer, 2010). The deep-sea fossil planktonic diatom record is not complete at the species level, although how much so cannot be accurately determined due to uncertainties in living species diversity and lack of estimates specific to the marine plankton (Lazarus, 2011; Table DR2). However, the species:genus ratio in the fossil data ranges between 2 and 4 per time bin (Fig. 1), which permits tests of genus versus species data behavior. Marine planktonic diatoms also are an ecologically important group. The observation in Lazarus et al. (2014) of a strong inverse correlation of species diversity to temperature, and thus a possible risk of significant species extinction with global warming, is an example of how conclusions from fossil biodiversity studies can be of broader significance. Here we test if the diversity patterns, and the correlations to environment reported in Lazarus et al. (2014) using species, are also found using genus-level data.

METHODS

We use a standard subsampling method: SQS (shareholder quorum subsampling; Alroy, 2010; quota = 0.7), and a linear equation for evenness correction, calculated for each sampled time bin using the D(80) evenness index (Lazarus et al., 2014). The equation’s coefficients are calculated from the effect of actual differences in evenness (summed Paleogene versus summed Neogene data) on subsampled diversity estimates of model populations of identical actual diversity, using sample sizes in the range employed by the SQS procedure (for full details, see Lazarus et al., 2014). The NSB database now has 115,000 diatom occurrence records (versus 64,000 in Lazarus et al., 2014), plus updated taxonomic lists (Lazarus et al., 2015). We therefore compute new values for species diversity and correlations to environmental parameters (stable isotopes of oxygen and carbon; Zachos et al., 2008). We then repeat the identical analyses on these new data, but use genera instead of species. Comparing the latter results to the former tests the effect of using genera instead of species. Analyses were done in R version 3.2 (base modules only) for Apple® operating system OS X.

RESULTS

Our new diversity curves, plus the paleoclimate proxies $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$, are shown in Figure 1. Species diversity closely resembles the result of Lazarus et al. (2014) of Cenozoic increase, with minor differences that reflect the greater amount of data used in our current study (e.g., 47–42 Ma). As our study, unlike that of Lazarus et al. (2014), uses only subsampled NSB data, there is a gap in coverage from 56 to 48 Ma. Generic diversity also increases over the Cenozoic, but most of the more detailed changes are different from the species history (raw values of two time series are significantly correlated but detrended series are not; Table DR3). Relative to species diversity, genus diversity increases more during the middle Eocene, peaks ca. 40 Ma, settles to a lower, only gradually changing value from the late Eocene to the end of the Oligocene, followed in the early Miocene by a sharp increase (with a maxima ca. 20 Ma). After the early Miocene increase, genus diversity progressively decreases until the end of the Miocene, when the diversity pattern starts slightly increasing until the Holocene. By contrast, species diversity shows a more gradual increase over the Cenozoic, and a particularly strong rise since the middle Miocene.

We find the same strong correlations between diatom species diversity and environmental proxies as in Lazarus et al. (2014) (all values in

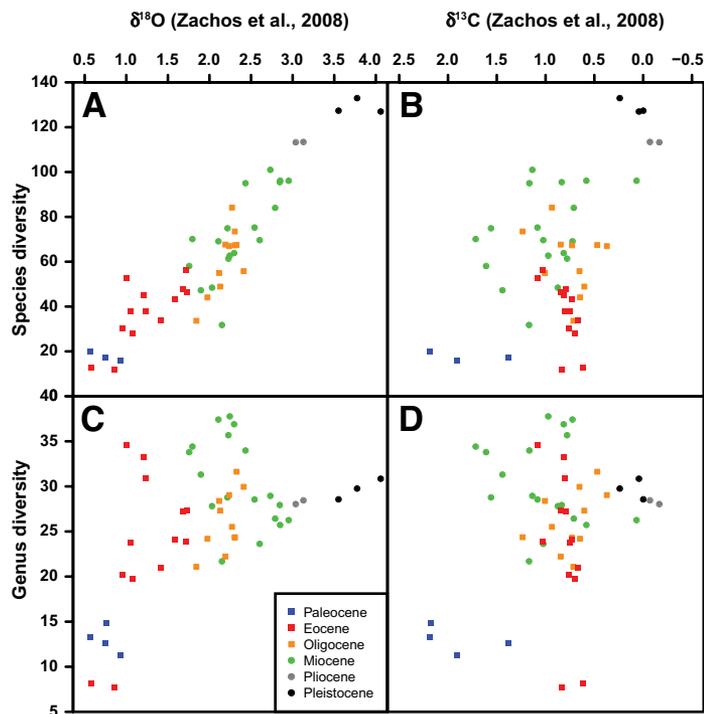


Figure 2. Species and genus diversity versus oxygen and carbon isotopes (data sources as in Fig. 1).

Spearman's ρ ; see also Table DR3, detrending via linear regression on untransformed data): $-\delta^{18}\text{O}$ ($\rho = 0.914$, $p < 2.0 \times 10^{-16}$, detrended $\rho = 0.617$ and $p = 2.53 \times 10^{-6}$; Fig. 2A); $\delta^{13}\text{C}$ ($\rho = -0.306$, $p = 0.03$, detrended $\rho = 0.278$, $p = 0.048$; Fig. 2B). However, these correlations are lost when using generic diversity (Figs. 2C and 2D). While the direct correlation with $\delta^{18}\text{O}$ still holds ($\rho = 0.439$, $p = 0.001$), it is completely lost when detrended ($\rho = -0.043$, $p = 0.762$), and the correlation with $\delta^{13}\text{C}$ is lost in both cases (raw: $\rho = -0.066$, $p = 0.6433$; detrended: $\rho = 0.103$, $p = 0.4717$). These differences are even more striking when looking at the younger part of the record. In the middle Miocene to Holocene species diversity, $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ show continuous parallel trends (toward higher diversity, colder climate and toward a lower carbon isotope ratio, i.e., an increase in exported carbon production) (Fig. 1). Generic diversity shows the opposite pattern: decreasing diversity with cooling and increased carbon export.

DISCUSSION

Genus diversity in diatoms shows only a weak correlation to environmental change over the Cenozoic and this only in raw data, and only for $\delta^{18}\text{O}$. Detrended genus diversity shows none of the correlations to environmental change present in the species data. Furthermore, the pattern is uncorrelated, or even shows the opposite correlation to environmental proxies over the past 20 m.y. As this interval contains an increasingly modern flora, it is particularly relevant to estimating future biodiversity responses to climate change. The use of genus instead of species diversity thus results in the loss of any signal of sensitivity of diatom diversity to past climate change, and consequently the ability to derive any of the conclusions reached in Lazarus et al. (2014), and most important, their inference of the potential for diversity loss due to climate warming in the future.

The reason for this is that the genus diversification curve is fairly step-like, with most diversification in two short intervals: the late mid-Eocene and basal Neogene, and with near maximum values already by the mid-Eocene. The species diversity curve shows more continuous, incremental change (mostly increase) over time. As a result only the primary trend is present in both data sets: the detrended species and genus series are not

significantly correlated. Detrending of time-series data is normally done in paleobiology, to avoid spurious correlations due to autocorrelation or other problems (Alroy et al., 2001). Rapid early diversification and subsequent plateaus are an often observed pattern of higher taxa (Raup, 1983; Lane and Benton, 2003; Lloyd et al., 2012), a pattern that emerges also in general simulations of diversity change over time in taxonomic hierarchies, particularly when coupled with incomplete sampling (Sepkoski, 1978; Raup, 1983). Differences between (detrended) species and genus-level diversity data, and thus their correlation to environmental histories, may thus be expected in many, if not most, groups of organisms.

CONCLUSIONS

Paleontologic diversity reconstructions are important components of research in evolutionary ecology, biotic control of global geochemical cycles, and conservation paleobiology. These reconstructions largely depend on an essential assumption, that genera (or even higher level taxa) can be used as a proxy for species diversity. However, there are many potential problems with generic data, and to our knowledge, no prior studies with actual fossil data that confirm that generic diversity data work as a substitute for species data when examining paleodiversity-environmental sensitivity. We have thus tested to see if strong correlations between species diversity and environmental change seen in marine Cenozoic diatom data are still seen when genera are used instead. It is disturbing that in our first test of this essential assumption, it fails: while weak correlations are still seen in raw data, none of the correlations seen between species diversity and environment are seen in more typical detrended genus data series, nor are the detrended species and genus diversity series correlated with each other.

Our test of this assumption is only a single study of a single taxonomic group, and clearly cannot in itself invalidate the many analyses done with other taxa and geologic time intervals. However, our results suggest that in the future the adequacy of generic diversity for species diversity cannot simply be assumed, but should be positively documented for the taxa and material under study. This can be done, e.g., by comparison to genus-species diversity patterns in living representatives. If the adequacy of genera cannot be documented, we suggest that generating a better quality, species-level data set may be essential to understanding past biodiversity change and its correlation to the environment. In particular, species-level data may be essential for those studies that use past diversity-environment patterns as guides for understanding modern biodiversity responses to future global warming. Extinctions over the next few decades to centuries due to climate change and other aspects of human impact are expected to be less severe than in past mass extinctions, if still substantial (Barnosky et al., 2011), and the strength of the signal of extinction at higher taxa levels as a result will likely be much weaker. Understanding how such less severe species extinction events are related to environmental change may thus be more difficult to study in the fossil record using only genus or higher level taxonomic data.

ACKNOWLEDGMENTS

We thank several colleagues who provided advice or information that assisted us in this study: Masao Iwai and Dave Harwood for their work on the Integrated Ocean Drilling Program diatom taxonomy name list; Martin Aberhan, Johannes Müller, and Jorg Fröbisch for discussions on macrofossil data; Mandy Schmolh for entering data into NSB (Neptune Sandbox Berlin); and Mimi Katz, Graeme Lloyd, and three anonymous reviewers of an earlier version of the manuscript.

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Manuscript received 11 July 2016

Revised manuscript received 30 September 2016

Manuscript accepted 3 October 2016

Printed in USA