Syst. Biol. 61(1):80–89, 2012

DOI:10.1093/sysbio/syr076
Advance Access publication on August 9, 2011

Taxonomic Structure of the Fossil Record is Shaped by Sampling Bias

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Received 20 September 2010; reviews returned 11 January 2011; accepted 5 April 2011
Associate Editor: Ron DeBry

Abstract.—Understanding biases that affect how species are partitioned into higher taxa is critical for much of paleobiology, as higher taxa are commonly used to estimate species diversity through time. We test the validity of using higher taxa as a proxy for species diversity for the first time by examining one of the best fossil records we have, that of deep-sea microfossils. Using a new, taxonomically standardized, data set of coccolithophorid species and genera recorded from 143 deep-sea drilling sites in the North Atlantic, Caribbean, and Mediterranean, we show that there is a two-stepped change in the ratio of species to genera over the last 150 myr. This change is highly unexpected and correlates strongly with changes in both the number of deep-sea sites yielding coccolithophorids that have been studied and with the number of taxonomists who have published on those sections. The same pattern is present in both structurally complex heterococcoliths and the simpler nannoliths, suggesting that increasing complexity is not the driving factor. As a stepped species-to-genus ratio exists even after subsampling to standardize either the numbers of sites or numbers of papers, both factors must be contributing substantially to the observed pattern. Although some limited biological signature from major extinction events can be recognized from changes in the species-to-genus ratio, the numbers of sites and the numbers of taxonomists combined explain some 82% of the observed variation over long periods of geological time. Such a strong correlation argues against using raw species-to-genus ratios to infer biological processes without taking sampling into account and suggests that higher taxa cannot be taken as unbiased proxies for species diversity. [Coccolithophorids; diversity; fossil record; taxonomy.]

The fossil record provides the only direct evidence we have for how biodiversity has changed over geological time. In order to produce diversity curves, paleobiologists will typically assemble numbers of fossil taxa described and named from each time period. Such curves then go on to form the data for macroevolutionary interpretation. However, although the species is the true level of macroevolution, reasons ranging from pragmatic considerations of worker effort to arguments of taxonomic instability have led to counts of higher taxa (usually families or genera) being used in their stead (e.g., Sepkoski et al. 1981; Benton 1995; Alroy et al. 2001, 2008). Compilations undertaken at these higher taxonomic levels thus form the basis for numerous biodiversity studies, with simple tallies of genera or families present implicitly hoped to be proportionally representative of the underlying pattern of species diversity.

To date, most paleontological species-level diversity curves have only been estimated, using modeling (Lane and Benton 2003), sampling (Signor 1985), or rarefaction (Raup 1975, 1979), with the nonstandardized tabulation of Raup (1976) and the recent curve of Janevski and Baumiller (2009) the only exceptions. Of these last two, the former has been compared with both family-level (Flessa and Jablonski 1985) and genus-level (Alroy 2008) counts, with both authors finding a general trend of increasing species-per-higher-taxon ratio over time. Janevski and Baumiller (2009) show a similar result for species-per-genus in marine invertebrates (their fig. 3). In other words, higher taxa appear to become more speciose over time.

Diversity curves derived from different higher taxonomic levels are also known to be dissimilar (Valentine 1974; Lane and Benton 2003), suggesting at the very least their relationships are not simple. Furthermore, taxonomic counts cannot necessarily be taken at face value because the fossil record is beset by a series of biases that can mask and distort the original pattern (Alroy et al. 2001; Smith 2001, 2007). The question then arises as to whether higher taxa become more species rich over time for biological reasons or because of sampling artifact, as first suggested by Simberloff (1970).

Understanding biases that affect how species are partitioned into higher taxa is critical for much of paleobiology. If we are to uncover the underlying species pattern, we need accurate data on how the taxonomic partitioning of species into higher taxa is affected by various sampling biases, something that is currently hindered by a lack of adequate species-level data (Lane and Benton 2003). To explore these issues, we turn to one of the most complete fossil records—that of the coccolithophorid algae.

MATERIALS AND METHODS

Database

Coccolithophorids are unicellular planktonic algae of the division Haptophyta that have an exoskeleton formed of calcareous plates known as coccoliths (Fig. 1). These coccoliths are produced intracellularly, within a golgi-derived vesicle, and have highly regulated morphologies and crystallographies (Young and

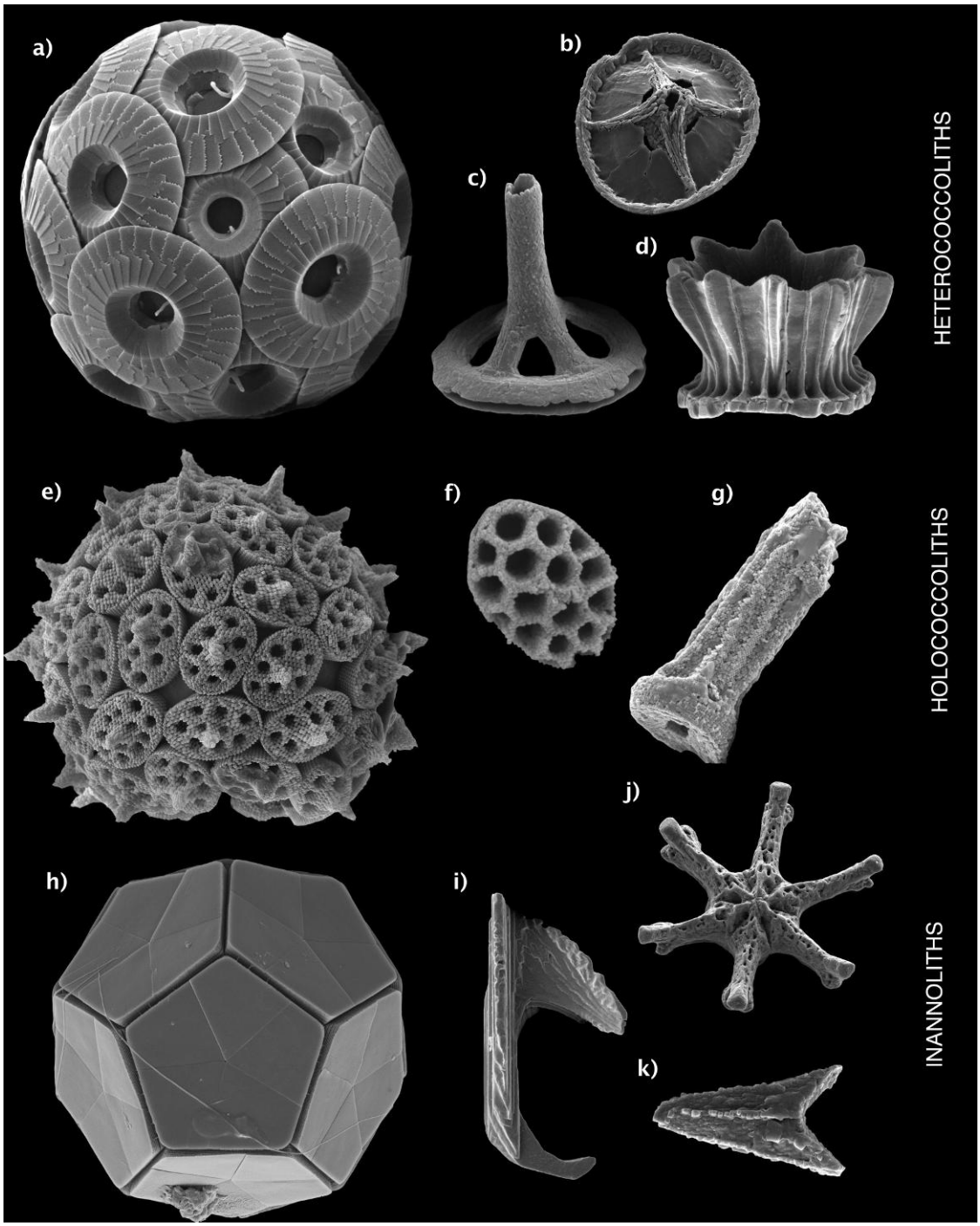

FIGURE 1. Scanning electron micrographs illustrating the main types of calcareous nannofossil comprising our database; all scale bars 1 μm. a–d) Heterococcoliths: a) *Umbilicosphaera foliosa*; b) *Eiffellithus turriseiffelii*; c) *Tetrapodorhabdus decorus*; and d) *Rotelapillus lafittei.* e–g) Holococcoliths: e) *Helicosphaera carteri* holococcolith phase; f) *Syracolithus schilleri*; and g) *Lucianorhabdus cayeuxii*. h–k) Nannoliths; h) *Braarudosphaera bigelowii*; i) *Ceratolithina hamata*; j) *Discoaster surculus*; k) *Ceratolithoides aculeus*.

Henriksen 2003). As a result, coccolith morphology provides excellent taxonomic characters as has been confirmed by comparison of molecular genetic and morphological data (Saez et al. 2004). Coccolithophores are minute (cells are typically 5–10 μm across) but very abundant, and coccoliths are the single most important component of calcareous deep-sea sediments. They form 20–40% of modern deep-sea oozes (Baumann et al. 2004) and a rather higher proportion through most of the fossil record (Late Triassic to Recent); the Late Cretaceous Chalk is predominantly formed of coccoliths. This fossil record has been extensively sampled as a result of

the Deep Sea Drilling Program (DSDP) and its successor the Ocean Drilling Program (ODP) and intensively studied because coccoliths provide the fastest and most reliable means of determining the age of these sediments (Spencer-Cervato 1999). As a result of this activity, detailed records of fossil coccolith occurrence are available for hundreds of sites around the world's oceans, and much of these data are readily accessible. Furthermore, species are considered more stable than genera by coccolith workers and are the basis of previous diversity curves (Bown et al. 1992, 2004).

Our data come from range charts based on core data from the North Atlantic, Caribbean, and Mediterranean taken from the scientific results of both the DSDP and ODP (freely available from http://www.deepseadrilling.org/i_reports.htm and http://www-odp.tamu.edu/publications/). These record the species of coccolithophorids from 149 DSDP and ODP sites, ranging from Late Jurassic to Quaternary in age. All our data are sampled-in-bin: We only count a taxon in a time bin if a fossil of that age has been observed and we do not use extant data at all. This is to avoid the "Pull of the Recent" (Raup 1972) artifact, which introduces a skewed diversity curve in favor of the almost perfect extant record. Species occurrences were entered into a relational database (Lloyd et al. 2011) and dated using standard nannofossil zonation schemes and dates (Gradstein et al. 2004). Here, we use 3 myr time bins following a pre-existing procedure first suggested by Alroy et al. (2008) and outlined in Lloyd et al. (2011). We also recorded the number of authors (coccolithophore taxonomists) on the papers describing coccolithophores from these sites and the total number of sites sampled, for each successive time bin.

All species names were checked against a standardized taxonomic list compiled for the Neptune database (Spencer-Cervato 1999) and subsequently updated for the ODP database by Jeremy Young, Paul Bown, and Jacqueline Lees. This authoritative and comprehensive list includes all species combinations used in DSDP and ODP nannofossil chapters with tracking of synonyms. (This is available from Dryad along with the other data files here: http://dx.doi.org/10.5061/dryad.8476.) This allowed well-established synonymies to be identified and valid species to be placed into their appropriate genera as currently recognized. The database has 796 valid species names assigned to 203 valid genera. The species-to-genus ratio was then calculated for each time bin and the time series plotted.

Additional modifications of the data before analysis were also made. This includes the removal of other calcareous nannofossils such as dinoflagellates (e.g., *Thoracosphaera*) and ascidian spicules (*Micrascidites*) that were often recorded in the same data tables but were incompletely listed or may have introduced effects peculiar to noncoccolithophore taxa. In addition, we wanted to explore the effect of complexity on species recognition by separating coccolithophores into coccoliths and nannoliths sensu (Young et al. 1997). Coccoliths are further split into heterococcoliths (which are produced in the diploid life cycle phase and are formed of a radial array of complex calcite crystals: Fig. 1a–d) and holococcoliths (which, by contrast, are formed in the haploid life cycle phase and are formed of a mass of minute, ca. 0.1 μm, euhedral calcite crystallites: Fig. 1e–g). Nannoliths (Fig. 1h–k) on the other hand lack unambiguous homologies (Young et al. 1997) but are of similar size and frequently occur with coccoliths. They are highly variable but typically they are formed of one or a few complex calcite crystals. Holococcoliths have low preservation potential so are poorly represented in the fossil record and make up only a few percent of total records in our database; nannoliths however have a rich fossil record and so the distinction between them and coccoliths is potentially important in shaping the observed diversity records.

Model Fitting and Testing

To test whether the resultant time series change gradually or in a step-like way, we applied the punctuated model of Hunt (2008). We compared our data with two models, one involving one step (or two periods of "stasis") and one with two steps (or three periods of stasis). These two punctuational models were then contrasted with three other models (a directional trend, random walk, and complete stasis; Hunt 2007). The best model was chosen by first calculating the AIC_c (Akaike Information Criterion), a sample size-corrected likelihood method that weighs both the fit of a model and its complexity. These values were then used to calculate Akaike weights, which return the relative likelihoods of a set of models (Johnson and Omland 2004). We repeated the fitting of our five models to separate time series of nannoliths and coccoliths and to the ratio of nannolith to coccolith genera over this time. We also record the preservation quality (good, moderate, or poor) of the best sample from each of our database units to test whether this affects the species-to-genus ratio.

We removed the effect of autocorrelation from our time series by calculating generalized differences (McKinney 1990). The data were regressed against time, residuals were taken, the correlation of the residuals with themselves at a lag of one time interval was computed, each of the lagged values was multiplied by this correlation, and the lagged values were subtracted from the data. This technique has a strong and building use in paleobiological studies (e.g. Alroy 2000; Butler et al. 2011), as it does not reject as much potentially legitimate signal as the harsher first differences approach.

Subsampling Method

To assess if the variation in species-to-genus ratio is still present when sampling is effectively level throughout the study interval, we employ a subsampling approach, specifically rarefaction by occurrences (Bush et al. 2004). We prefer it here over other methods, such as shareholder quorum subsampling (Alroy 2010), as it better allows us to subsample against both of our

potential explanatory variables (sites and authors). Our procedure involved first compiling a table of species occurrences per time bin. For subsampling with respect to number of sites, an occurrence is defined as a valid species present at a DSDP or ODP site in that time bin. Unfortunately, subsampling with respect to authors is complicated by a many-to-many relationship, so instead, we subsampled with respect to the number of papers. To do this, an occurrence is defined as a valid species present in a published paper in that time bin. Otherwise, the procedure follows that outlined in Lloyd et al. (2011) where mean and 95% values were taken from 1000 runs. Multiple diversity curves were then produced by setting the sampling level as equal to the worst bin (lowest number of occurrences), before removing this bin, and repeating for the next worst bin until only one bin remained (that with the most occurrences).

All analyses were undertaken in the freely available statistical programming language R (R Development Core Team 2010) using the "paleoTS" package (Hunt 2006, 2008), available from Graeme Lloyd on request.

Results

Taxonomic Structure and Sampling Patterns are Strongly Correlated

The species-to-genus ratio of calcareous nannofossil taxa plotted over the last 150 myr (Fig. 2a) undergoes a striking step-like change after the end Cretaceous. Applying Hunt's (2008) test identifies a two-step model as optimal when comparing Akaike weights (Table 1). Using Hunt's (2008) θ as a guide, initial Cretaceous levels of 1.69 species per genus rise to 3.00 in the Paleogene then 3.98 in the Neogene (Fig. 2a).

As a measure of the rock record sampled, we use the number of DSDP and ODP sites with recorded nannofossil-bearing sediments of each time interval. This number rises exponentially towards the present (Lloyd et al. 2011), but when transformed to their log number (to account for outliers) also best fits a two-step model (Fig. 2b). The same pattern is also recovered from plotting the numbers of taxonomists (Fig. 2c) or number of papers (Fig. S2, available from http://www.sysbio.oxfordjournals.org/) recording microfloras from these cores. In all cases, a high degree of correlation was found between the ratio of species per genus and the number of sites with fossiliferous rocks of that age and the number of workers who have published on those microfloras (Spearman $\rho = 0.94$ and 0.92 for the raw data and 0.50 and 0.57 for generalized differences; McKinney 1990, respectively: Fig. 3).

To test whether the amount of fossil-bearing rock also changed in a step-like fashion, we fitted the same models to time series of numbers of DSDP/ODP sites per time bin and the number of authors who have produced distribution charts spanning each time bin. In both cases, the two-step model is preferred (Tables S1 and S2) with jumps occurring shortly after the Cretaceous–Paleogene boundary and in the early Neogene (Fig. 2b,c) in the same up-up sequence of changes.

To determine which, if either, of these two variables was more closely correlated to the changes in species-to-genus ratio, we fitted three simple linear models; one with number of sites as our explanatory variable, another with number of authors, and a third with both sites and authors in combination. As expected, all models showed a high degree of correlation (r-squared $\geqslant 0.8$ in all cases for raw data), although this value drops considerably for generalized differences (r-squared 0.32, 0.35, and 0.35 for sites, authors, and combined, respectively). We then used two different methods for comparing these models, Akaike weights (see Materials and Methods section) and variation partitioning (Desdevises et al. 2003; Kriloff et al. 2008) that, although biased in favor of more complex models, makes an additional estimate of what proportion of the variance remains unexplained. The results (Table 2) split between favoring the sites model, which has the highest Akaike weight, and the combined model, which has the greatest percentage variance explained. Roughly, 18% of the variance remains unexplained in the raw data.

We also took the generalized differences (McKinney 1990) of the species-to-genus time series and compared these with generalized differences of the sites and authors time series (Fig. 4a,b). The curves follow each other in a significantly correlated manner ($P < 0.05$; Spearman $\rho = 0.71$ and 0.66 for sites and authors, respectively) up to about 45 Ma after which correlation breaks down ($P = 0.51$ and 0.18; Spearman $\rho = 0.19$ and 0.38 for sites and authors, respectively), with the distinct dip in species-to-genus ratio in the latest Eocene–early Oligocene not evident in numbers of sites and authors. In addition, the species-to-genus ratio has been dropping since the early Miocene, whereas both the numbers of sites and authors has been increasing. At these times, the species-to-genus ratio is being driven by factors other than those investigated here.

Taxon Complexity, Size, and Preservation Quality Play only a Minor Role in Determining the Pattern

Calcareous nannofossils differ in their structural complexity and size (nannoliths are larger and their outline more variable than coccoliths but are structurally less complex; Young et al. 1997), so any change in the relative abundance of these different groups over time could affect taxonomic practice. When the ratio of nannoliths to coccoliths over time is plotted (Fig. 5), a slight increase in the proportion of nannoliths to coccoliths is evident. Although a two-step model is also favored for this time series (Table S4), the sequence is up-down and the placement of shifts is not coincident with the changes in species per genus. Additionally, the correlation between the proportion of coccolith to nannolith genera in a time bin and the proportion of species per genus is weak (Spearman $\rho = -0.23$ for raw data and 0.06 for generalized differences; $P = 0.13$ and 0.70, respectively). Furthermore, when coccolith and nannolith diversities are plotted separately (Figs. S2 and S3) each still favors a two-step (up-up) three-stasis model

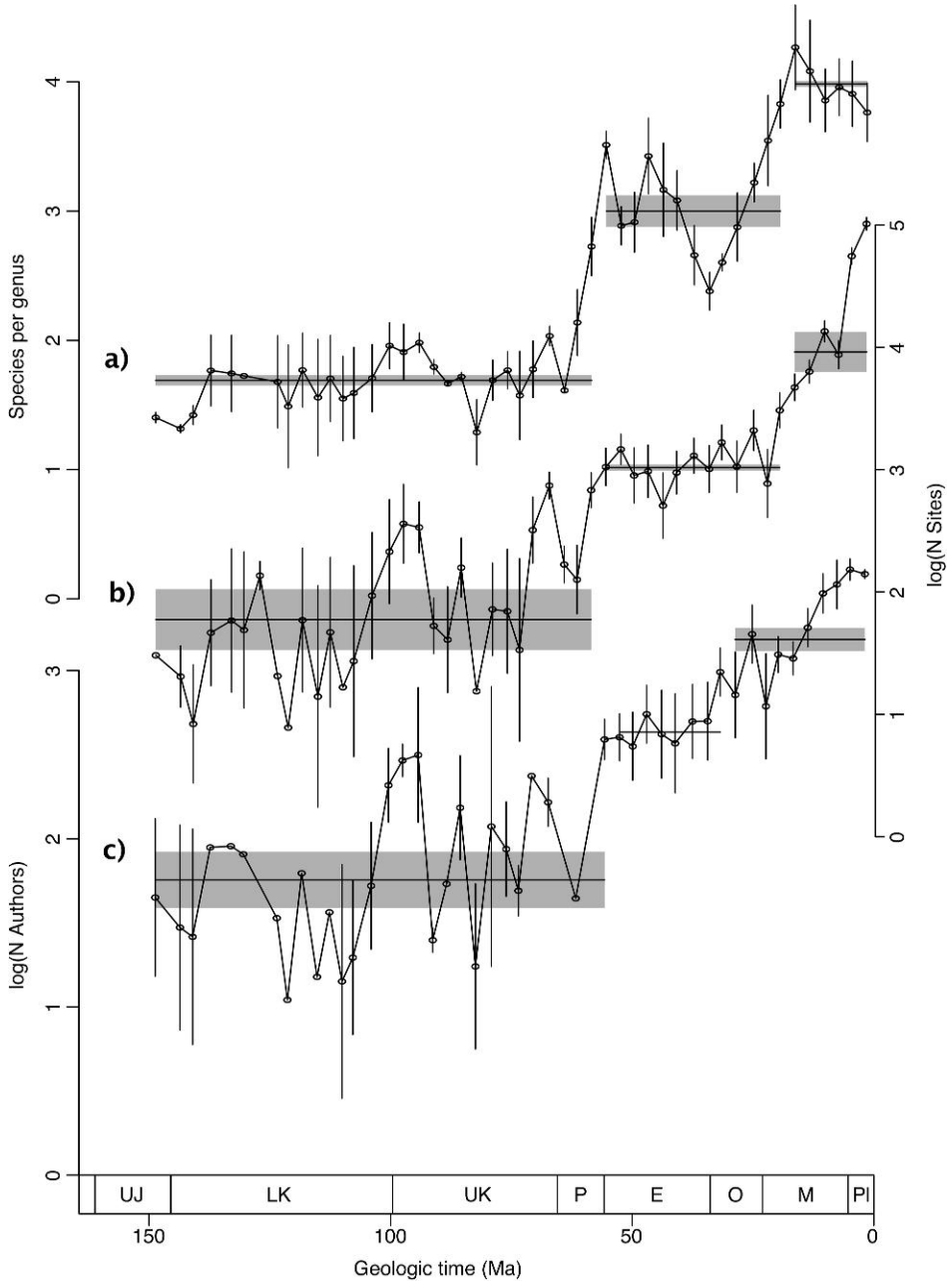

FIGURE 2. a) Plot of species per genus through time with the three-step model. Points indicate mean values and vertical lines 1.96 standard deviations indicating uncertainty over dating. Horizontal lines indicate the values of θ for each step and the gray bars $\theta \pm \omega$ (Hunt 2006). b) The same plot for number of DSDP/ODP Atlantic sites through time. c) The same plot for the number of individual authors publishing on the taxonomy of coccolithophorids from these sites. Geologic epoch abbreviations are as follows: UJ = Upper Jurassic; LK = Lower Cretaceous; UK = Upper Cretaceous; P = Paleocene; E = Eocene; O = Oligocene; M = Miocene; Pl = Plio-Pleistocene.

(Akaike weight > 0.9 in both cases). There is no convincing evidence, therefore, that change in the species-to-genus ratio is being driven primarily by changes in the proportion of nannoliths in the microflora.

Another possibility that we investigated is whether changes in the quality of preservation of coccolithophorids over geological time might be driving the observed pattern. For example, morphological characters that identify genera might be more easily preserved in the fossil record than those that aid finer species-level discrimination, thus resulting in preservation quality driving the species-to-genus ratio. However, the relative proportion of preservation quality over the last 150 myr (Fig. 6) does not show that preservation was worse in the Mesozoic when the species-to-genus ratio was low nor significantly good in the Neogene when the ratio is high. Because the preservation quality ratio has three components, we could not fit Hunt's models;

TABLE 1. Results of model fitting (Hunt 2006, 2008) to the species-to-genus time series (Fig. 2a)

Model	AIC	AIC_c	Akaike weight
Directional trend	22.18	22.45	0.00975
Random walk	21.51	21.60	0.01495
Stasis	125.54	125.81	$\ll$0.00001
Punctuation (one step)	30.59	32.06	0.00008
Punctuation (two steps)	9.45	13.24	0.97523

Note: All numerical values are shown to two decimal places.

however, individual correlation with the proportion of good, moderate, or poor preservation is extremely weak ($\rho = -0.02$, 0.16, 0.03 and $P = 0.88$, 0.28, 0.82, respectively). Consequently, we can reject the idea that the species-to-genus ratio is being driven by shifting preservation quality.

The Relative Strengths of Biases Vary Through Time

Partitioning of the data into the more poorly sampled Mesozoic and better sampled Cenozoic (Tables S14–S17) reveals interesting differences. In both partitions, the correlations with numbers of sites and numbers of authors for raw data (Spearman $\rho = 0.88$ and 0.78, respectively, in the Mesozoic and 0.64 and 0.69, respectively, in the Cenozoic) is lower than when all the data are combined. That both sets of raw values should give weaker correlations indicate the importance of the major shift in values across the Cretaceous–Paleogene boundary. This is to be expected as the strong correlation when the data is pooled is created by the cluster of low Mesozoic values (at bottom left) and high Cenozoic values (at top right) in Figure 3a,c. This shift is further reflected by an increase in the proportion of variance in the raw data that is unexplained (from 17.68% when the data are pooled to 28.49% for the Mesozoic and 44.94% for the Cenozoic, when separated). Correlations of generalized differences are also higher in the Mesozoic (Spearman $\rho = 0.74$ and 0.80 for sites and authors, respectively) and lower in the Cenozoic (Spearman $\rho = 0.34$ and 0.42, respectively) than the pooled data. As expected, then, the proportion of variance left unexplained (66.38% for pooled data) is reduced in the Mesozoic-only partition (34.05%) but increased in the Cenozoic (81.86%). More interesting perhaps is the shift in Akaike weights that show a clear dominance of the sites model in the poorly sampled Mesozoic with a shift in favor of the authors model in the Cenozoic.

Both the Number of Sites and Taxonomic Effort are Important in Setting Species-to-Genus Ratios

The number of sites yielding coccolithophorids and the number of workers describing coccolithophorids are not independent variables, as more sites necessitate more independent taxonomic recording. To further test whether the number of sites sampled or the number of publications generated could be the predominant driver of the observed species per genus curve, we carried out subsampling analyses (see Materials and Methods section). Of the curves produced, that where sampling is set to 109 occurrences was deemed the most useful as

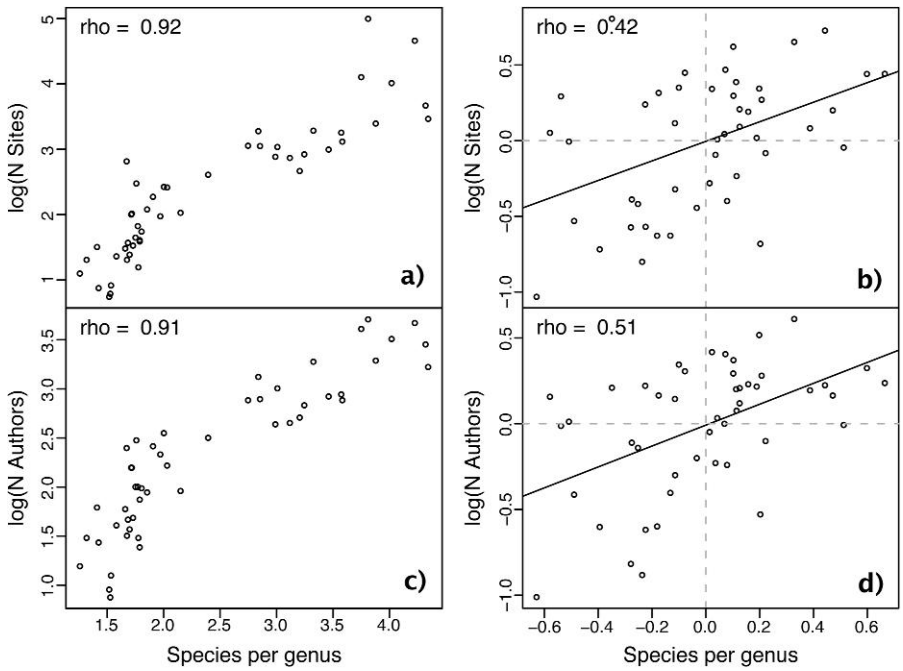

FIGURE 3. a) Correlation plot of the ratio of species per genus versus number of DSDP/ODP sites with recorded coccolithophorid microfloras. b) The same but for generalized differences (McKinney 1990). c) Correlation plot of the ratio of species per genus versus number of named authors on taxonomic papers describing the coccolithophorid microfloras of each time bin. d) The same but for generalized differences. Lines represent a simple least squares fit and all values of Spearman ρ reported are significant at $P < 0.05$.

TABLE 2. Results of species per genus explanatory model comparisons

Explanatory variable	Model (formula)	AIC	AIC_c	Akaike weight	Percentage variance explained
N_{sites}	$(0.82 \times \log(N_{sites})) + 0.38$	49.49	49.77	0.54	2.59
$N_{authors}$	$(1.13 \times \log(N_{authors})) - 0.17$	54.09	54.37	0.05	0.66
$N_{sites} + N_{authors}$	$(0.55 \times \log(N_{sites})) + (0.39 \times \log(N_{authors})) + 0.16$	49.80	50.37	0.40	79.06
Unexplained	—	—	—	—	17.68

Note: All numerical values are shown to two decimal places.

sampling was high enough to record variation but low enough to return a result for all consecutive bins from 150 to 0 Ma (Fig. S4). Similarly, for subsampling against papers, 75 occurrences produced an almost complete sequence (missing just one bin in the Early Cretaceous, Fig. S5). In both cases, the result is extremely similar to that shown in Figure 2a—the best model (highest Akaike weight) is also two steps and three stases in both cases (Tables S7 and S8), and both steps are closely coincident with those of the unmodified data (Fig. 2a), again, in both cases. However, the absolute values do cover a narrower range with Hunt's θ ranging from 1.63 species per genus in the Cretaceous, via 2.36 in the Paleogene, to 2.87 in the Neogene, for the subsampling against sites, and similarly from 1.53 on the Cretaceous to 2.31 in the Paleogene and to 2.71 in the Neogene for subsampling against papers. Critically, the stepped pattern remains when either the signal from sampling or papers (a proxy for *N* authors) is removed, suggesting that both factors must be contributing substantially to the observed pattern.

DISCUSSION

The species-to-genus ratio has long been used in ecological circles to describe community structure and infer evolutionary patterns and processes. Recent examples include Qian and Ricklefs (2000), Ulrich et al. (2009), Kruger et al. (2009), and Harnik et al. (2010) who

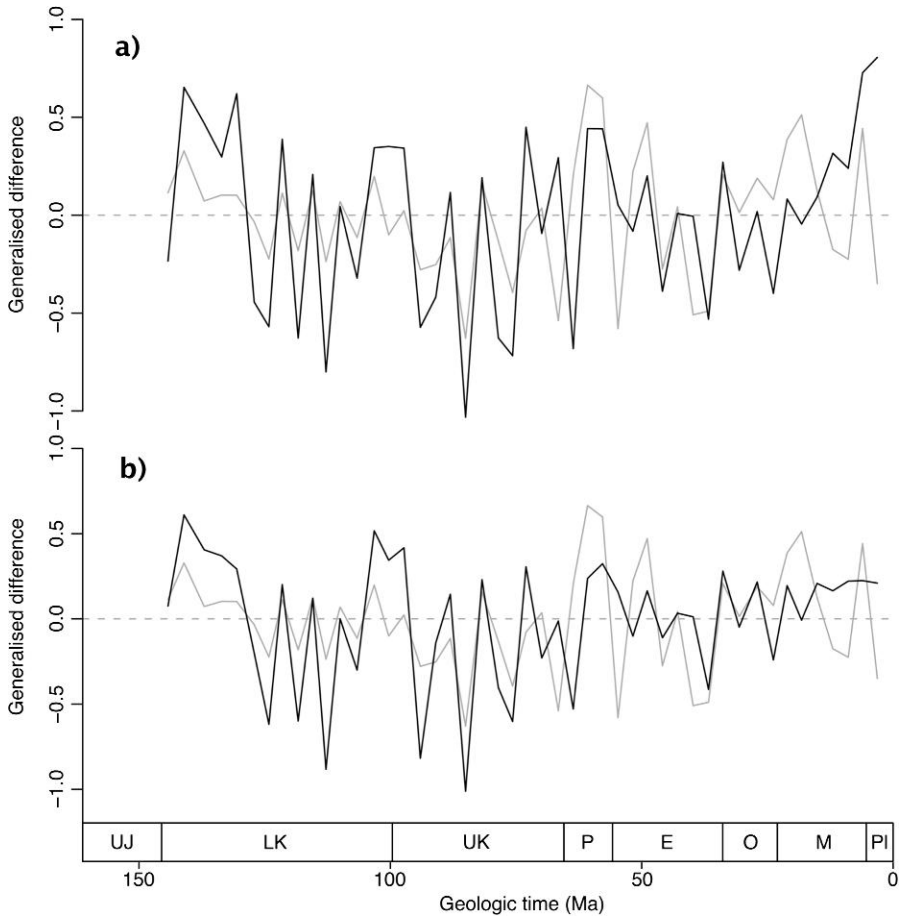

FIGURE 4. a) Plot of generalized differences (McKinney 1990) for the time series species-to-genus ratio (gray) overlaid with the generalized differences for the number of DSDP/ODP sites with recorded coccolithophorid microfloras (black). b) Plot of generalized differences for the time series species-to-genus ratio (gray) overlaid with the generalized differences for number of individual authors publishing on the taxonomy of coccolithophorids from these sites (black). Geologic epoch abbreviations are as in Figure 2.

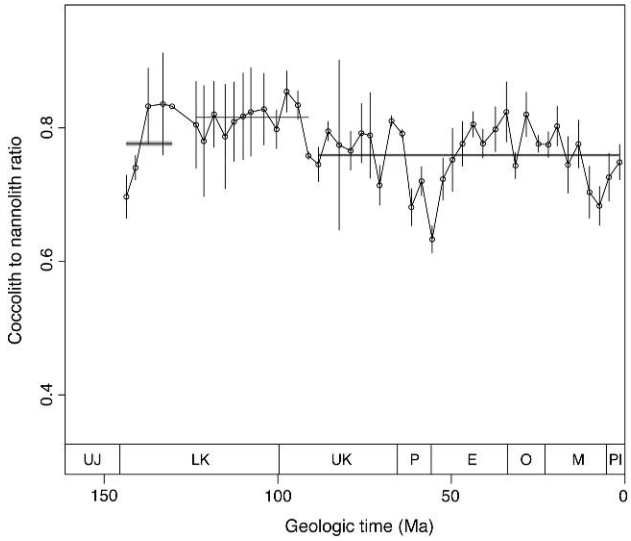

FIGURE 5. Plot of the ratio of nannolith to coccolith genera through time with the two-step model (Table S4). Points indicate mean values and vertical lines 1.96 standard deviations indicating uncertainty over dating. Horizontal lines indicate the values of θ for each step and the gray bars $\theta \pm \omega$ (Hunt 2008). Geologic epoch abbreviations are as in Figure 2.

have each used species-to-genus ratios as evidence for differences in speciation history driven by life history traits, biogeographical traits, or ecological traits. Species-to-genus ratios are also widely used in paleontological research. They have been used as a measure of specialization (Aberhan and Fursich 2000), of how oversplit dinosaur taxonomy is (Benton 2010), to infer species-level dynamics (Stanley 2009), and to investigate randomness of extinction (Janevski and Baumiller 2009). Finally, conservationists such as Balmford et al. (1996) have also advocated the use of higher taxa as a proxy for estimating species level diversity with respect to establishing conservation priorities.

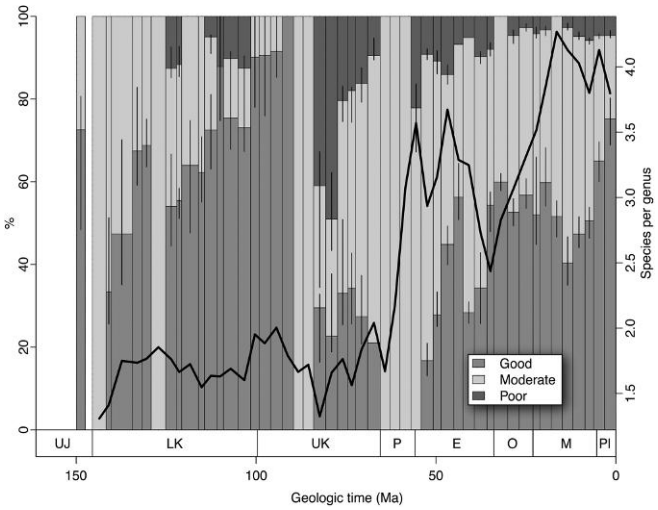

FIGURE 6. Shifts in the relative proportions of preservation quality over the last 150 myr using the DSDP/ODP classifications of "good," "moderate," and "poor." Values are assigned based on the best sample in the unit with vertical lines indicate 95% confidence interval based on dating uncertainty. The mean species-to-genus (black line) is overlain for comparison. Geologic epoch abbreviations are as in Figure 2.

However, despite the extensive use of species-to-genus ratios, few have considered the inherent dangers. Adrain (2006) noted that species-to-genus ratios changed in trilobites over time but in a relatively small way and concluded that genera are good direct proxies for sampled species diversity in the geological record. Much more damning criticism, however, has come from Gotelli and Colwell (2000). In their wide-ranging review of the problems of calculating species richness, Gotelli and Colwell (2000) point out that the species-to-genus ratio is strongly affected by sample size, and that its use without correcting for sampling will lead to spurious results. Our findings reinforce this and suggest that there are important nonbiological factors (number of workers as well as number of sites, not to mention taxonomic arbitrariness, Patterson and Smith 1989) that can distort the species-to-genus ratio and make this a very unreliable measure.

Although the sampling issues have been known since Simberloff (1970), that the number of workers can shape how speciose higher taxa become has not been treated quantitatively elsewhere. It is noteworthy that in this example, the two steps more or less coincide with the Mesozoic–Paleogene and Paleogene–Neogene boundaries, traditional divides among taxonomic workers who tend to specialize in geological time intervals. Focus on high-resolution biostratigraphy in the Neogene may, for example, have had the effect of encouraging taxonomists to recognize smaller and more numerous subdivisions within genera. Furthermore, as the number of sites with rocks of a particular age increases towards the Recent, so too do the numbers of taxonomists recording the microflora, resulting in a more heterogeneous taxonomy. The more workers describing microflora of a time interval, the more diverse taxonomic opinions become, and the more likely varieties are to be formally named.

Although the stepped pattern we have observed in the species-to-genus ratio is most likely an artifact of changing taxonomic practice and better sampling, some genuine biological signal exists in our data. Analysis of generalized differences demonstrates that the correlation between species-to-genus ratios and sampling is strongest where sampling is at its poorest and weakens as sampling improves. So, although the species-to-genus ratio, not unexpectedly, responds very closely to changes in sampling intensity in the Cretaceous, we find this relationship breaks down for extended periods in the Paleogene and Neogene. Changes in the sampling of rock or number of authors follow the species-to-genus curves closely up to around 45 Ma (Fig. 4) after which the species-to-genus ratio drops markedly to reach a minimum at 33 Ma before starting to rise again. This contrasts with a constant (sites) or slightly rising (authors) trend in the other two time series over the same period (Fig. 2). Furthermore, the species-to-genus ratio has declined over the last 12 myr,

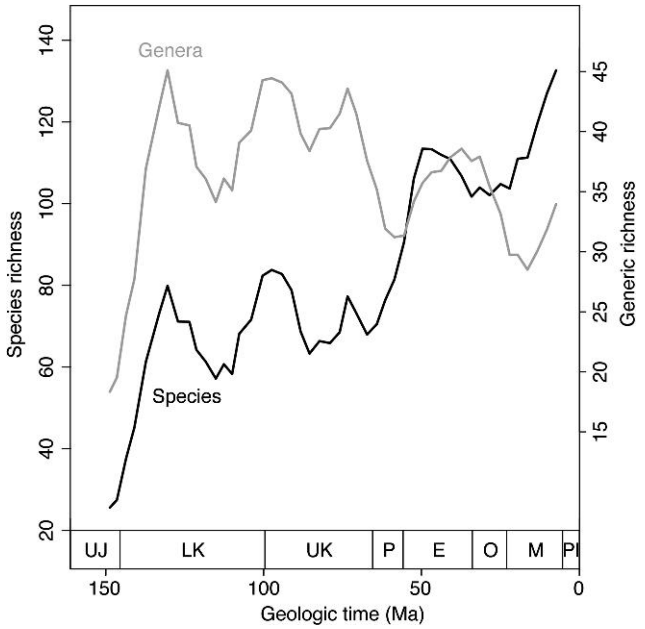

FIGURE 7. Plot of mean sampled-in-bin generic and species richness over the last 150 myr based on a five-bin moving average. Geologic epoch abbreviations are as in Figure 2.

despite rising numbers of authors and sampled sites. In both cases, neither sampling nor taxonomic practice can explain the drops in species-to-genus ratio, and the most likely explanation is that they record an extinction signature. As genera on average include multiple species, random extinction of species will lower the species-to-genus ratio. Our data suggest that, both in the run-up to the end-Eocene extinction and to the present day, species numbers were in decline across most nannofossil genera over an extended period (Fig. 7). An intriguing contrast can be drawn between the end-Cretaceous extinction, which did not affect the species-to-genus ratios, and the later end-Eocene and Miocene–Pleistocene extinctions, which clearly did.

CONCLUSIONS

We have shown that species-to-genus ratios of nannofossils have changed by almost a factor of three over the last 150 myr. Furthermore, these changes coincide in time with major geological boundaries that have been traditionally recognized and correlate strongly with changes in both the number of deep-sea sites yielding coccolithophorids that have been studied and with the number of taxonomists who have published on those sections. Although some biological signature of major extinction events can be teased out of these data, much of the pattern, including the obvious step-like rises, appears to reflect taxonomic practice and sampling. Counts of genera, or indeed any higher taxon, as a proxy for species-level diversity are likely to be strongly affected by both the quality of the fossil record and by the numbers of taxonomists interested in the faunas and floras of different time periods.

SUPPLEMENTARY MATERIAL

Supplementary material, including data files and/or online-only appendices, can be found at http://www.sysbio.oxfordjournals.org/.

FUNDING

This work was supported by a grant from the Natural Environment Research Council [NE/F016905/1 to A.B.S. and J.R.Y.]

ACKNOWLEDGMENTS

The authors would like to thank Gene Hunt for help with the paleoTS library, Manabu Sakamoto for help with the variance partitioning analyses, and Shanan Peters for providing the R (http://cran.r-project.org/) function used in adding the geologic time scale to the -axis in Figures 2 and 4–7. The manuscript was greatly improved by suggestions from Ronald DeBry, Wolfgang Kiessling, and an anonymous reviewer.

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