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Phanerozoic biodiversity, macrotaxa and families

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ABSTRACT - Traditionally, global Phanerozoic diversity patterns of eukaryotes have been studied by analyzing the variation of the number of taxa at family or genus rank in time. The question of which global processes these diversity patterns reflect remains unanswered. We show that for understanding Phanerozoic biodiversity an ecological-taxonomic approach is preferable to a purely taxonomic approach. Consequently, an ecologically modified taxonomic unit, the macrotaxon, is introduced. This approach allows us to exploit the potential of complex diversity indices, as well as the richness and evenness components.

KEY WORDS: biodiversity, diversity indices, evenness, Phanerozoic

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INTRODUCTION

How can the ecological constraints to the global diversity of eukaryotic higher taxa be evaluated for a given moment of Earth's history? Are there any limiting trends in eco-taxonomical diversity? Here, we attempt a preliminary contribution towards the understanding of the questions above.

Traditionally, Phanerozoic diversity patterns of eukaryotes have been studied by analyzing the number of taxa at some particular rank (usually families or genera) obtained from compilations from the literature over series of time intervals (e.g., Valentine, 1969; Raup, 1972; Sepkoski, 1984, 2002; Benton, 1997, 2001; Alroy et al., 2008). These studies show the variation through time of the number of taxa at different taxonomic ranks, from species to phyla, and the levelling through time of this increase in higher taxa (i.e., orders and above). This levelling goes back in Earth history as the taxonomic level becomes more inclusive (Sepkoski, 1984, 1993a, 1993b, 1996; Signor, 1985; Benton, 1997, 2001; Lane and Benton, 2003).

Clearly, evidence on the variation in the biosphere's biomass, energy, etc., would be crucial for the understanding of the present issue, but reliable proxies for these parameters are not available for the geological past.

The use of taxonomic categories as statistically reliable tools in an ecological context is a debated issue. Taxonomic richness has been traditionally considered as a surrogate for ecological importance (Madin et al., 2006). Synoptic compilations and theoretical studies demonstrate that diversity patterns vary according to taxonomic ranks (Sepkoski and Kendrick, 1993; Sepkoski, 1998; Benton, 2001). Nevertheless, from an ecological perspective, we may assume a direct, positive relation between the number of species and the number of more inclusive taxonomic categories (e.g., families).

Obviously, the usefulness of taxonomic categories is linked to the nested classification of organisms. From species to phyla, the difference in biological content between hierarchically nested taxa varies greatly, from nil (e.g., *Symbion pandora* Funch and Kristensen, 1995, the only known species in the phylum Cycliophora) to very large numbers (e.g., in the Arthropoda). Similarly, from an ecological perspective, the number of habitats of a given supraspecific taxon may vary from one to many.

Two main objections have been made to this approach. First, it is widely acknowledged that supraspecific taxa are conventional and subjective (i.e., ontologically they are not real) and that the biological equivalence of any two taxa of the same Linnaean rank cannot be demonstrated (Stevens, 1997; Mishler, 1999; Minelli, 2000; Pleijel and Rouse, 2003). Second, some specialists maintain that ecological diversity should be computed ideally at species level (Legendre and Legendre, 1998). We believe that the use of families and higher taxa instead of species in paleobiology is justified because of the intrinsic limitations of the fossil record and because genera and families are deemed to represent reasonable proxies for the elusive fossil species record (Sepkoski, 1998). According to the paleobiological literature, the family rank is deemed to represent an acceptable compromise between recognizability and inclusiveness in respect to subordinate taxa (genera and species) at global Phanerozoic level (Benton, 2000). The latter assumption has some support by theoretical and empirical neontological studies (Gaston and Williams, 1993; Roy et al., 1996). Thus, although we are aware of the limits of this approach, we may assume here that the number of families within higher taxa can serve as a tool in biodiversity studies in particular for assessing taxonomic diversity trends.

Until now, Phanerozoic biodiversity has been analysed mostly as counts of taxa through time. In the paleobiological literature, these counts of taxa are referred to as richness or diversity. In contrast, in theoretical ecology richness refers usually to the number of different taxa from normalized samples (e.g., a standardized sampling area or volume). In

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addition, in theoretical ecology there is a long-standing tradition in considering diversity as a dual concept linked to two components (richness and evenness), analyzed by using indices combining information about both these components. Most diversity indices provide a mathematical measure of the weighted number of taxa (richness) and patterns of their relative abundance (evenness). A large number of diversity indices have been proposed, and each index has its own different conceptual quantitative meaning (Magurran, 1988; Solbrig, 1991) and weaknesses (Lande, 1996).

In the paleobiological literature there are some notable exceptions to the generalizations above. These include e.g. studies on evenness based on sampled species abundance from fossil assemblages (Powell and Kowalewski, 2002) and morphological diversity (disparity) reflecting the number of ecologic roles that are occupied by taxa through time (Foote, 1992, 1993).

Our objectives in this paper are twofold. First, we aim to start from a dataset with a reasonably unimodal distribution. The rationale of this assumption is that, when dealing with ecological patterns of taxa, it is desirable to deal with a sampling universe with homogeneous (normal) distribution. In order to achieve this we differ from authors which employ as the highest taxonomic category the phylum and we introduce a statistical correction taking into account the greater evolutionary role of some phyla through the novel concept of macrotaxon. Second, we attempt to analyze the eukaryote fossil record through different diversity indices and their components using macrotaxa as groups and families as units.

MATERIALS AND METHODS

The present analysis is based on 80 time intervals, from the Precambrian to the Holocene, and the stratigraphic distribution of about 7100 families and 118 macrotaxa, mainly after the on-line version of *The Fossil Record 2* (Benton, 1993). In our analysis, we did not attempt to distinguish between minimum and maximum occurrences, using the maximum family range distributions of this database.

Minor amendments to the on-line version of this database concern:

(a) Discrepancies between the published database and the on-line files. In all such cases, we amended the on-line files according to the printed version of Benton (1993).

(b) Higher taxonomic groups lacking family classification in Benton (1993). This problem affects notably some algal and protist groups. For family numbers and distributions in these missing groups, we followed recent major revisions, respectively Berger and Kaever (1992) for dasyclads, and Fensome et al. (2000) for dinophytes. Acritarchs, an important, mainly mixotroph phytoplankton grouping, had to be culled from our analysis, because no consistent family classification is given for them in Benton (1993) or is generally agreed upon.

(c) Brachiopod and mollusk families were assigned to classes according to the classifications proposed in the *Treatise on Invertebrate Paleontology*.

(d) A number of formal families or informal monotypic families based on described genera. These taxa, which include mainly Proterozoic-early Paleozoic *problematica* and *incertae sedis* such as the Vendobionta, were excluded from our analysis, because of uncertainty in taxonomic assignment, subjectivity in systematic ranks, and uneven or missing suprageneric classifications.

(e) Whenever necessary (stratigraphic gaps in the distribution of families within macrotaxa), we added ghost range families.

The number of taxonomic groups and their size distributions are known to affect the recovery of diversity information (Robeck et al., 2000). Ideally, any analysis in biodiversity should be based on a homogeneous dataset; this should, although not necessarily, coincide with a unimodal distribution. The rationale for this is the observation that when sampling together several diverse present-day communities, the species-abundance distributions are usually lognormal (May, 1975, Pielou, 1975). Lognormality is a statistical model based on the assumption that relative taxic abundances are determined by a large number of independent factors (Signor, 1985), a circumstance which can be postulated reasonably for the fossil record of eukaryotes in the last 600 Ma. Data normality is a logical requisite for many diversity measures (e.g., Magurran, 1988). Here, our purpose is to recover a unimodal grouping of higher taxa/families distributions which may reflect their ecological impact. In contrast, as shown below, an analysis based on a families vs. phyla dataset does not fulfil this requisite. However, we wish to stress here that this should be considered as a preliminary approach to assess the complex issue of the relationship betweeen systematics and ecology.

After logarithmic scale transformation because of the large range of the values encountered, the family abundance distribution of the fossilizable eukaryote heterotroph phyla shows a bimodal distribution, corresponding to a negative binomial ($\bar{x} = 1.55$; $\sigma^2 = 1.83$) (Fig. 1).

The bimodality of the abundance distribution of Fig. 1 reflects the difference between a majority of heterotroph phyla (left in Fig. 1) and a remainder of larger phyla (to the right, showing a peak and an outlier). This right peak includes Porifera, Brachiopoda, Bryozoa, Coelenterata, Echinodermata, and Protozoa; the rightmost class corresponds to Arthropoda, Mollusca and Chordata. It is noteworthy that these few oversized phyla, with a disproportionately large number of families, played a major

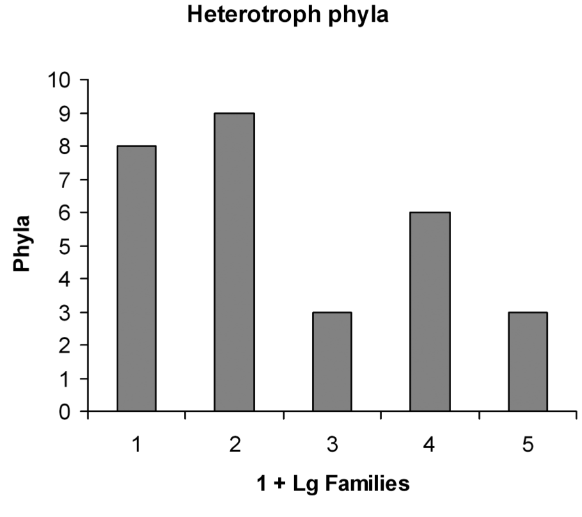

Fig. 1 - Logarithmic abundance distribution of the number of families within fossilizable heterotroph phyla (n = 29). The right peak corresponds to the following phyla: Brachiopoda, Bryozoa, Coelenterata, Echinodermata, Porifera, and Protozoa; the right tail outliers are Arthropoda, Chordata and Mollusca.

ecological role at least since the Cambrian. Indeed, most of the Phanerozoic family diversity lies in this tail, which includes a large set of taxa that are both functionally important and abundant in fossil assemblages. Thus, the grouping of families into phyla does not fulfil the unimodality requisite.

In order to obtain a reasonably unimodal distribution, the 9 oversized phyla were split into Linnaean classes, thus leading to family distributions for two distinct taxonomic levels (phyla or classes). The resulting units (n = 118, including 20 phyla and 98 classes belonging to the oversized phyla) are here referred to as *macrotaxa*. We are however aware that this term has been used already by Levchenko (1997), with a different, broader meaning.

The ensuing distribution of heterotrophs approaches an unimodal positive binomial distribution ($\bar{x} = 1.42$; $\sigma^2 = 0.87$) (Fig. 2). In contrast, the autotroph phyla are few and their distribution is very scattered; their classes (n = 18) show a nearly unimodal family distribution ($\bar{x} = 1.103$; $\sigma^2 = 0.713$). Thus, for the purposes of this study, autotroph classes were directly considered as macrotaxa (Fig. 3).

The family distributions outlined above are suitable for analytic testing at several, more or less inclusive levels. On the one hand, a logical choice is an analysis on the whole biosphere through time. On the other hand, both the marked isolation of terrestrial and aquatic environments, and the trophic differences existing between heterotrophs and autotrophs are intuitive. In this perspective, we subdivide the eukaryotic fossil record into four biota, which roughly correspond to ecofunctional groupings: marine autotrophs (MA), marine heterotrophs (MH), continental autotrophs (CA) and continental heterotrophs (CH). Macrotaxa which could not be assigned to a single biota were split accordingly (e.g., the families of Aves and Mammalia were assigned to either CH or MH).

Although these ecological groupings are not monophyletic, the number of families in a macrotaxon - albeit a crude indication - can be considered to reflect its quantitative impact on the biosphere for a given geological interval.

The present analysis is based on the 80 time intervals of Benton (1993, ed.), from the Precambrian (Riphean, Sturtian, Vendian) to the Holocene. The numerical ages of the Phanerozoic chronostratigraphic boundaries follow Gradstein and Ogg (1996), the International Stratigraphic Chart of the International Commission on Stratigraphy (Remane, 2000), and other sources. In consequence, the duration of the time intervals as employed here differs from those of Harland et al. (1990), used e.g. by Sepkoski (1984, 1998) and Benton (1993, 2000). For each time interval, we calculated the midpoint age and referred its family record arbitrarily to this age (different solutions have been suggested, e.g.: Ruban and van Loon, 2008; Ponomarenko and Dmitriev, 2009). In consequence, the Vendian and Phanerozoic time intervals are of very unequal length, ranging from >20 million years (Ma) to 0.01 Ma (mean length 7.0 Ma; n = 77). In Benton's (1993) timescale, the Cambrian is subdivided into three long-ranging time intervals. Thus, considering only the Ordovician-Pleistocene timespan, the average length of the 74 time intervals is slightly shorter (6.6 Ma). In some of the analyses, the Precambrian and the Holocene, which are respectively of extremely long and short duration, were omitted.

In this respect, we recall that the boundaries between time intervals are mainly historically derived from discontinuities in fossil biota, and not according to any statistical sampling criterion. This implies that the length of the time intervals reflects a methodologic constraint, which negatively affects the statistical treatment of the data – of course, a subdivision of the whole investigated time span into periods of equal duration would be preferable. Various methods to reduce the variance in the duration of time intervals have been employed. Hewzulla et al. (1999) used a 7 Ma sampling period, Sepkoski (1998) a ca. 5 Ma sampling period, and Madin et al. (2006) time bins with an average duration of 11.1 Ma. A means to minimize this dispersion is subdividing and cumulating adjacent periods (e.g., Sepkoski, 1998). We decided not to employ time-standardization methods, because these methods cannot solve the issue of the historical subjectivity in the choice of the chronostratigraphic boundaries and may introduce further uncertainties in the duration of the taxa.

There are many ways to calculate diversity and its components and many indices have been proposed. Our analysis focuses mainly on the Shannon (1948) information function, H, for occurrences of families through time:

$$H = -\Sigma\, p_i \ln p_i$$

where the frequence p_i is the number of families of the ith macrotaxon (n_i) divided by the total number of families (n) of

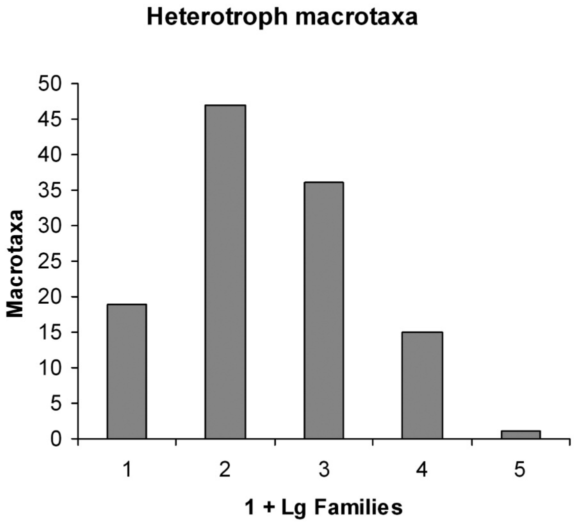

Fig. 2 - Logarithmic abundance distribution of the number of families within autotroph classes (macrotaxa).

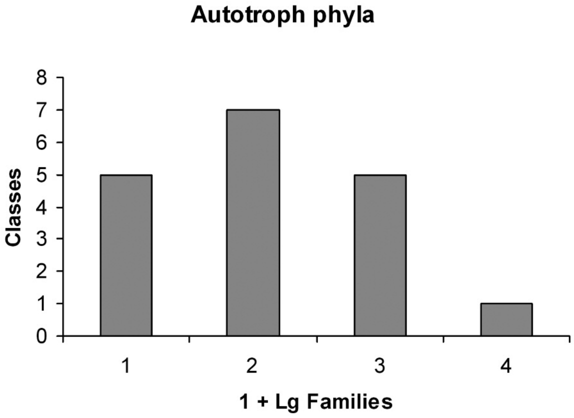

Fig. 3 - Logarithmic abundance distribution of the number of families within heterotroph macrotaxa.

all macrotaxa (Fig. 4). This index, which should be referred to as the Shannon (1948)–Wiener (1948) index (Contoli, 2001; Spellerberg and Fedor, 2003), is considered as a good compromise between richness and evenness, as reflected by its intermediate position in the range of the series of Rényi (1961), Hill (1973), and Patil and Taillie (1976). Once H is computed, an evenness measure equitability (*J*), was calculated, as the Shannon–Wiener diversity index divided by the natural logarithm of the number of macrotaxa.

Because many diversity indices and their richness and evenness components are generally hypothesized to be strongly cross-correlated (May, 1975; Giavelli et al., 1986; Smith and Wilson, 1996; Stirling and Wilsey, 2001), calculating a plethora of indices is not very meaningful. Nevertheless, we computed several other traditional diversity indices (Gini-Simpson, Parker-Berger, Mehnininck) and diversity components (Margalef's richness, Pielou's evenness) (Fig. 5), using PAST for Windows, ver. 1.97 (Hammer et al., 2001). Statistical analyses were performed using Microsoft Excel 2001 for Macintosh and SPSS for Windows, ver. 10. Two-tailed test statistics were used. The distribution of data was inspected for normality by Kolmogorov–Smirnov one-sample tests. Regression lines were drawn according to the best fit between linear and exponential models.

RESULTS

The shape of macrotaxa distribution and the hidden macrotaxa

Starting with the seminal contribution of Preston (1948), there is consensus among ecologists that in universes consisting of large numbers of taxa (generally, species) and individuals, the frequence-abundance distributions follow log-normal patterns, either because of the large number of implied ecological factors (Whittaker, 1972), or for purely mathematical reasons (May, 1975).

On the basis of Figs. 2 and 3, and if (and only if) the distribution obtained is considered to be log-normal and the relevant ordinate as "veil line" (Preston, 1948) limiting a hidden tail of the distribution, it may be possible to predict heuristically the amount of yet unknown macrotaxa, when additional data become available. The present figure that seems to correspond approximately to the lower tail of both distributions and could amount to about one order of magnitude less than our present knowledge is merely indicative.

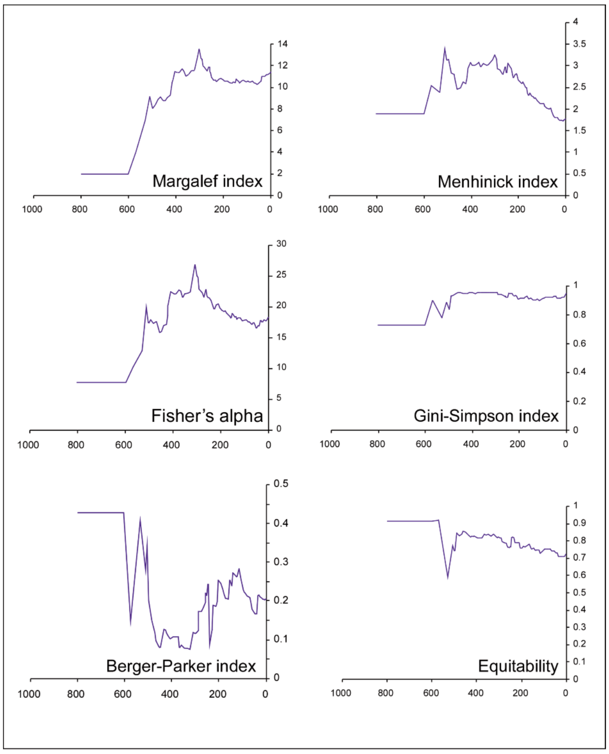

Fig. 5 - Additional diversity measures for all macrotaxa; horizontal axis indicates age in Ma (million years ago).

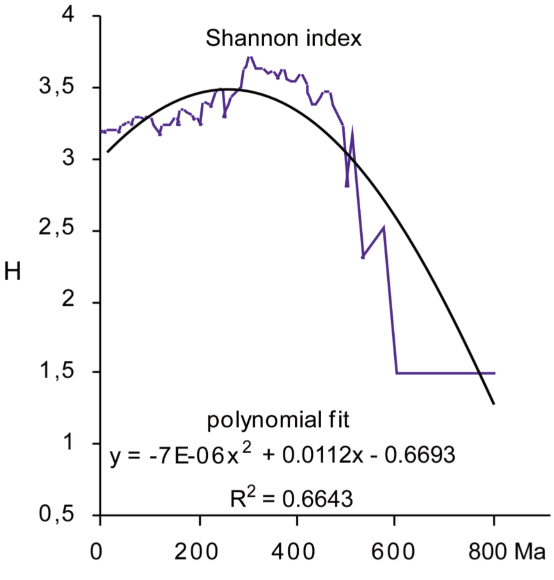

Fig. 4 - Shannon index for all macrotaxa.

In this perspective, the high value of the leftmost class, near the ordinate axis, could be in part linked to macrotaxa which may eventually be reassigned to other more inclusive macrotaxa, e.g. because of improvements due to modern taxonomic tools. On the other hand, at least in part the hidden tail could be explained by the "Problematica" sensu Benton (1993) and other groups for which as yet there is no satisfactory suprageneric classification (e.g., acritarchs).

Diversity analysis: evenness vs. richness

Diversity indices can be split into a number of conceptual and numerical components. A graph for our data relating two of the most widely used components in ecology, richness and evenness (Fig. 6), enables us to clarify the differences among universes and their respective diversities (see e.g., Contoli, 1986). The total ranges of these two components calculated for each of the four biota under study, show some distinctive features:

- a completely isolated position of MH, due to their extraordinary richness (possibly due to the relatively high number of different trophic levels and the generalized trophic specialization within macrotaxa); the difference with MA is particularly striking, in contrast with the largely overlapping ranges for CA and CH;
consistently high values of evenness in MA and MH, linked to the absence of dominant macrotaxa;
- a very similar vpattern for CA and CH, showing a markedly low richness (also due to the large number of

families and to the sharing of various trophic levels by many macrotaxa) and a very wide variation in evenness, perhaps in relation to the dominance of few taxa during early stages of land colonization (highest values) and the P/T-extinction rebound;

- the lack of records in the high-richness-and-low-evenness range, which is occupied, albeit in other ecological and temporal contexts and scales, by immature or ephemeral ecosystems.

The trend of diversity over time

In our data, Shannon-Wiener's and Gini-Simpson's indices show strong variations over time, but these indexes, as well as Margalef's richness component, are strongly correlated (Tab. 1). Therefore, for the following discussion, we take into account mainly Shannon's H index. An exception is Pielou's evenness, which strongly depends from sample size; sample size in turn is affected by the length of each time interval.

For all eukaryotes, H shows a significant trend even with a binomial model in time (Fig. 4). However, the observed data show a more complex pattern, with a slow final decrease.

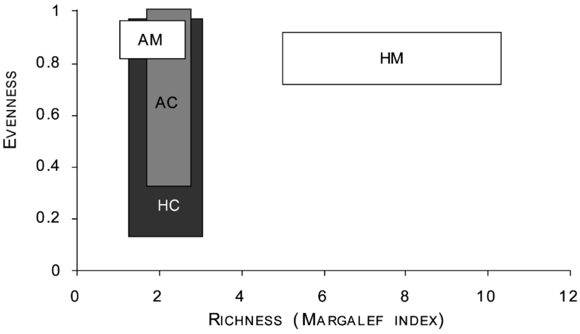

Fig. 6 - Relation between richness and evenness based on the Phanerozoic database for each ecofunctional compartment.

Each biota shows some differences in diversity trends (Fig. 7): namely, MH, an early and sharp rise followed by a long and slow decrease, one of the more intriguing results in the present study; MA, a very long timespan of low values followed by a sharp increase and, then, a long and slow increase until recent periods; CA, a sharp increase followed by a plateau and later a net decrease; CH, a sharp increase, a decrease and a new increase.

The values ot the Shannon index calculated for each biota are significatively correlated to each other, with $p < .001$ (2-t) for CA/MH, CH/CA, MH/MA, and $p = .016$ (2-t) for CA/MA; two are positively correlated (CA/MH, CA/MA), and two negatively (CH/CA, MH/MA).

The simultaneous increase of MA and that of continental organisms, instead of that of MH, is a striking feature which cannot be easily explained. It may reflect a global impact of continental biota, which affects selectively MA by changing e.g. continental runoff, or, alternatively, it may in part represent an artifact of the incompleteness of the database (which does not include acritarchs).

Another prominent feature is the opposing trends in continental organisms from the Early Carboniferous: although the correlation between CH and CA is always significative, this correlation is reversed from positive to negative.

DISCUSSION AND CONCLUSIONS

A methodologic approach

Despite three decades of active research, controversies still rage in global Phanerozoic diversity studies (Stanley, 2007; Benton, 2009). Clearly, and by definition, global diversity does not account for variations among clades, habitats and regions; also, it reflects biases related to a range of sampling, study effort and preservational artefacts, points which have been discussed extensively elsewhere (for a recent summary, see Smith, 2003) and that are not addressed

	Pearson	Shannon	Margalef	Evenness	Simpson	Families	Macrotaxa
Kendall							
Shannon	Corr. coeff.	1	.693(**)	.545(**)	.894(**)	-.193	.419(**)
	Signif. (2-t)	.	.000	.000	.000	.090	.000
Margalef	Corr. coeff.	.252(**)	1	-.148	.464(**)	.295(**)	.883(**)
	Signif. (2-t)	.001	.	.195	.000	.009	.000
Evenness	Corr. coeff.	.648(**)	-.024	1	.668(**)	-.705(**)	-.467(**)
	Signif. (2-t)	.000	.759	.	.000	.000	.000
Simpson	Corr. coeff.	.727(**)	.224(**)	.523(**)	1	-.095	.289(*)
	Signif. (2-t)	.000	.004	.000	.	.410	.010
Families	Corr. coeff.	-.367(**)	.167(*)	-.690(**)	-.235(**)	1	.695(**)
	Signif. (2-t)	.000	.031	.000	.002	.	.000
Macrotaxa	Corr. coeff.	-.113	.497(**)	-.475(**)	-.008	.700(**)	1
	Signif. (2-t)	.152	.000	.000	.921	.000	.

Tab. 1 - Summary of test statistics of cross-correlations among diversity indices and number of families and macrotaxa for the last 650 Ma (78 time intervals). Correlations are significant (2-tailed) (**) at the 0.01 level, (*) at the 0.05 level.

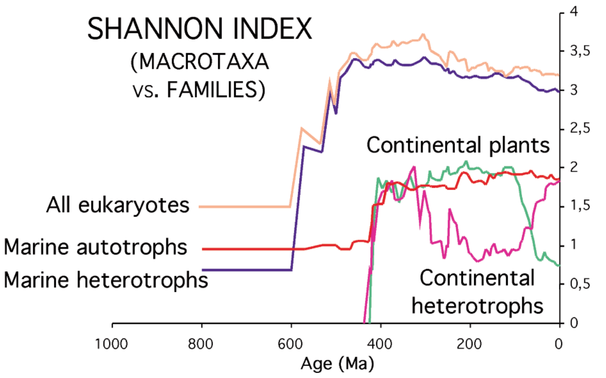

Fig. 7 - Shannon index for the four ecofunctional compartments and for all eukaryotes.

here. Some critics argue against the possibility to estimate taxonomic biodiversity to some degree of accuracy because of the intrinsic limitations of the fossil record. Other critics go even further and maintain that global taxonomic diversity is "an ecologically and evolutionarily meaningless concept" (Vermeij and Leighton, 2003), favouring bottom-up approaches on multiple lines of evidence.

Taking into account these considerations, our position is that this contrast can be solved through a novel methodology and that diversity is biologically meaningful at many different scales, provided that the results are not unjustifiably extrapolated across scales (Badgley, 2003). Our diversity analysis for the Phanerozoic yields coherent results and seems a rather effective instrument at its appropriate scale. Conversely, there is "safety in numbers": if, in spite of the numerous factors producing them, the patterns extracted are non-random, it seems reasonable to infer that these patterns *are* meaningful. However, the question *how* global diversity patterns reflect *which* global processes remains unanswered.

We believe that an ecological-taxonomic approach is preferable to a purely taxonomic approach for the understanding of this kind of diversity. Consequently, an ecologically modified taxonomic unit, the macrotaxon, is introduced, in order to manage more easily the fossil record, in the light of its limits and biases. The results enable us to suggest a workable solution for normalizing the macrotaxa-families distribution. Moreover, this approach allows us to exploit the potential of complex diversity indices, such as Shannon's index, as well as the richness and evenness components.

Completeness of the fossil record

Since Agassiz (1854) and Darwin (1859), the debate on the reliability of the fossil record is a long-standing issue.

One of the corollaries of this study is a potential means to estimate the amount of macrotaxa escaping our knowledge (Preston, 1948). Actually, this gap appears limited: a number of present-day heterotroph small-sized phyla, represented by one or few families, may eventually be re-assigned to other larger phyla by molecular-based analyses. This would imply a lowering of the leftmost class in the families-macrotaxa graphs (Fig. 2) and thus a reduction of the hidden tail of distribution.

On the other hand, the results of evenness-richness analysis (richness-evenness) do not show particular contrasts in respect to the features of the investigated system.

Evenness vs. richness

The analysis of diversity decoupled from time allows us a synoptic comparison among the studied ecofunctional compartments, as well as a post-hoc test to justify the splitting of the record into the four compartments.

The richness-evenness graph (Fig. 6) concurs in pointing out the stability of compartments and their relative sampling universes, as can be expected in the light of the long timespans and the wide geographical, chronological and taxonomical range of the data.

This seems to support to our choice of splitting the fossil record into ecofunctional compartments (biota), a procedure which may prove useful also in other works.

The complex diversity approach

Diversity is more than numbers of groups (Solbrig, 1991). Thus, unless mutually integrated, the partially contrasting patterns of levelling of number of macrotaxa and the exponential increase of the number of families over time, do not provide an exhaustive picture of diversity. Namely, the reliability of numbers of families does not seem higher than that of more inclusive taxa (e.g., phyla or classes); therefore, the apparent discrepancy above should be explained in a synthetic way.

On the other hand, based on macrotaxa as groups and families as units, we may calculate diversity indices which are more reliable and provide more information, because they reflect different components of diversity; so, the interactive roles of trophism and environment emerge, in relation to the history of biome formation. In this perspective, the broad levelling trend holds only as a general background, on which are superimposed particular patterns for each ecofunctional biota.

The difference in Shannon diversity trends among continental biota (Fig. 7, Fig. 8) seems particularly striking in the second half of the Phanerozoic (Carboniferous to Pleistocene). The pattern of autotrophs seems linked to the origin and the successive bloom of angiosperms; the pattern of heterotrophs, on the other hand, clearly reflects the radiation of arthropods (particularly, insects) and, later, a similar albeit not equivalent expansion of birds and mammals, possibly in relation to the conquest of niches at higher latitudes.

In this context, it is useful to recall that taxonomic diversity

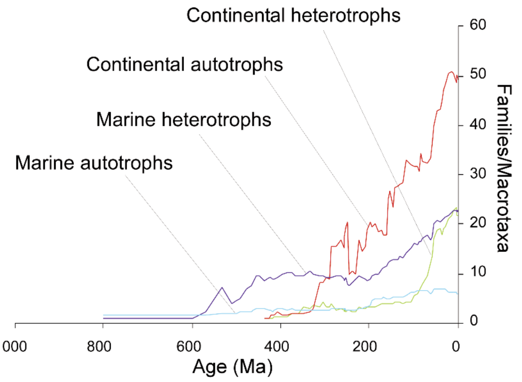

Fig. 8 - Plots of macrotaxa/families as a function of time for each ecofunctional compartment.

should be conceived only as a far from complete expression of the functional diversification, which has possibly a physical (thermodynamic) significance. In the perspective above, it is possible that the functional relations among organisms may change (generally, increase) over time, even without a growth in taxonomic richness, but at the expense of one or few rapidly expanding taxa. This may be reflected expecially by the decrease in evenness (Fig. 5). This is particularly clear in CA, where the bloom of angiosperms seems linked to their broad spectrum of ecological interactions with major heterotroph groups such as insects and mites (Labandeira and Eble, 2002). When the trophic role of a higher plant complicates, it leads to a number of trophic species (Williams and Martinez, 2000) in the same systematic taxon, owing to the complex trophic channels linking e.g. pronubes and flowers, carpophages and fruits, nitrobacteria or fungi and roots, and so on. Thus, the trends of functional and taxonomic diversity may be decoupled and diverge over time.

In the marine domain, where the number of trophic levels is generally higher, a similar, albeit less important, phenomenon could be due to, e.g., increasing complexity in life cycles and ecological niches, possibly mediated by expanding life span and body size; thus, stages in life cycles could take the ecological place of an array of different taxa.

Ecological vs. evolutionary patterns: matter of time scale?

The results of our analysis suggest a self-limiting pattern. On the whole, the overall shape of diversity curves is differs from that of classical paleontological “number of taxa through time” diagrams. In particular, the effects of the mass extinctions are much less evident. In this respect, it must be stressed that there is an important scale difference between evolutionary factors, influencing the number and the turnover of taxa, and ecological factors, acting on community structure and its expressions, among which is diversity. The taxonomic effects of some extinction events are much more prolonged in time, and may thus be recorded at a geological time scale. Conversely, the ecological effects of the same events could be overcome in a much shorter time, within the same period, whithout producing a detectable diversity variation at the temporal scale of the present analysis.

Is a synthesis possible among contrasting trends at different taxonomic levels ?

The long observed differences of trends in time from phyla and classes (early leveling off) to families, genera and species (near exponential growth) need not necessarily be explained as artifacts in the more comprehensive categories: a synthetic interpretation is possible, based e.g. on a progressive reduction of the amount of free niche space available for organisms. It is conceivable that, at first, when empty resource space is available, the different morpho-functional models corresponding to phyla or macrotaxa were expanding without facing competition and other limiting factors. But neither abiotic resources nor the potential niche space of organisms are unlimited (Wilson et al., 1987). Therefore, when large empty resource spaces became unavailable, the existing macrotaxa filled the remnant ecospace by subdividing into further taxa of intermediate level, at least up to family level. Thus, the progressively limited resources were increasingly exploited, through successive series of subtaxa of pre-existing taxa, even more specialized on ever smaller niches. This could be in agreement with the overall increase of number of taxa in time, nearly exclusively linked to progressively less inclusive taxa, when the number of higher taxa remains nearly constant.

The resulting picture suggests increasing, progressively self-limiting diversity in time.

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REFERENCES

Agassiz L. 1854. The primitive diversity and number of animals in geological times. American Journal of Science and Arts: (2), 17, 1-16.

Alroy J., Aberhan M., Bottjer D.J., Foote M., Fürsich F.T., Harries P.J., Hendy A.J.W., Holland S.M., Ivany L.C., Kiessling W., Kosnik M.A., Marshall C.R., McGowan A.J., Miller A.I., Olszewski T.D., Patzkowsky M.E., Peters S.E., Viller L., Wagner P.J., Bonuso N., Borkow P.S., Brenneis B., Clapham M.E., Fall L.M., Ferguson C.A., Hanson V.L., Krug A.Z., Layou K.M., Leckey E.H., Nürnberg S., Powers C.M., Sessa J.A., Simpson C., Tomašových A., Visaggi C.C. 2008. Phanerozoic trends in the global diversity of marine invertebrates. Science: 321, 97-100.

Badgley C. 2003. The multiple scales of biological diversity. Paleobiology: 29, 11-13.

Benton M.J. 1993 (ed.). The Fossil Record 2. Chapman and Hall, London, 845 pp. (http://gly.bristol.ac.uk/FR2.html)

Benton M.J. 1997. Models for the diversification of life. Trends in Ecology and Evolution: 12, 490-495.

Benton M.J. 2000. Stems, nodes, crown clades, and rank-free lists: is Linnaeus dead? Biological Reviews: 75, 633-648.

Benton M.J. 2001. Biodiversity on land and in the sea. Geological Journal: 36, 211-230.

Benton M.J. 2009. The Red Queen and the Court Jester: species diversity and the role of biotic and abiotic factors through time. Science: 323, 728-732.

Berger S., Kaever M.J. 1992. Dasycladales: An illustrated monograph of a fascinating algal order. Georg Thieme Verlag, Stuttgart, 247 pp.

Contoli L. 1986. Sulla diversità dei sistemi trofici “strigiformi-mammiferi” nel parco del Circeo e le relative valutazioni ambientali. Atti Convegno “Aspetti faunistici e problematiche zoologiche del Parco Nazionale del Circeo”, Sabaudia, 1984. Ministero dell’Agricoltura e delle Foreste-Parco Nazionale del Circeo, 169-181.

Contoli L. 1998. Biodiversità di specie: aspetti formali e funzionali. Atti Accademia Nazionale dei Lincei: 145, 113-126.

Contoli L. 2001. Biodiversità ed aree protette. Natura e montagna: 48(1), 13-21.

Darwin C. 1859. On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. John Murray, London, ix + 502 pp.

Fensome R.A., MacRae R.A., Williams G.L. 2000. Dinoflagellate evolution and diversity through time. Bedford Institute of Oceanography Review: 2000, 45-50.

Foote M. 1992. Paleozoic record of morphological diversity in blastozoan echinoderms. Proceedings of the National Academy of Sciences, USA: 89, 7325-7329.

Foote M. 1993. Discordance and concordance between morphological and taxonomic diversity. Paleobiology: 19, 185-204.

Gaston K.J., Williams P.H. 1993. Mapping the world's species. Biodiversity Letters: 1, 2-8.

Giavelli G., Rossi O., Sartore F. 1986. Comparative evaluation of four species diversity indices related to two specific ecological situations. Field Studies: 6, 429-438.

Gradstein F., Ogg J. 1996. A Phanerozoic time scale. Episodes: 19(1/2), 3-5.

Hammer Ø., Harper D.A.T., Ryan P.D. 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. Palaeontologia Electronica: 4(1). (http://palaeoelectronica.org/2001_1/past/issue1_01.htm)

Harland W.B., Armstrong R.L., Cox A.V., Craig L.E., Smith A.G., Smith D.G. 1990. A geologic time scale 1989. Cambridge University Press, 263 pp.

Hewzulla D., Boulter M.C., Benton M.J., Halley J.M. 1999. Evolutionary patterns from mass originations and mass extinctions. Philosophical Transactions of the Royal Society of London: (B), 354, 463-469.

Hill M.O. 1973. Diversity and evenness: a unifying notation and its consequences. Ecology: 54, 427-432.

Labandeira C.C., Eble G. 2002. Global diversity patterns of insects from the fossil record. Santa Fe Institute Working Paper: 121, 1-54.

Lande R. 1996. Statistics and partitioning of species diversity, and similarity among multiple communities. Oikos: 76, 5-13.

Lane A., Benton M.J. 2003. Taxonomic level as a determinant of the shape of the Phanerozoic marine biodiversity curve. American Naturalist: 162, 265-276.

Legendre P., Legendre L. 1998. Numerical Ecology. Second edition. Elsevier, Amsterdam, xv + 853 pp.

Levchenko V.F. 1997. Biosphere evolution. In: Čejchan P., Hladil J. (eds.), Abstract Book UNESCO IGCP Project 335 "Biotic Recoveries from Mass Extinctions", Final Conference "Recoveries '97", Praha, 54-56.

Madin J.S., Alroy J., Aberhan M., Fürsich F.T., Kiessling W., Kosnik M.A., Wagner P.J. 2006. Statistical independence of escalatory ecological trends in Phanerozoic marine invertebrates. Science: 312, 897-900.

Magurran A.E. 1988. Ecological diversity and its measurement. Princeton University Press, Princeton, New Jersey, 179 pp. (Reprinted 1996, Chapman & Hall, London).

May R.M. 1975. Patterns of species abundance and diversity. In: Cody M.L., Diamond J.M. (eds.), Ecology and Evolution of Communities. Belknap Press, Cambridge, Mass., 81-120.

Minelli A. 2000. The ranks and the names of species and higher taxa, or a dangerous inertia of the language of natural history. In: Ghiselin M.T., Leviton A.E. (eds.), Cultures and Institutions of Natural History. Essays in the History and Philosophy of Science. California Academy of Sciences Memoir, San Francisco, 339-351.

Mishler B.D. 1999. Getting rid of species? In: Wilson R. (ed.), Species: New Interdisciplinary Essays. MIT Press, Cambridge, Mass., 307-315.

Patil G.P., Taillie C. 1976. Ecological diversity: concepts, indices and applications. Proceedings of the 9th International Biometric Conference. The Biometric Society, Boston, Mass., 2, 383-411.

Pielou E.C. 1975. Ecological diversity. John Wiley and Sons, New York, 165 pp.

Pleijel F., Rouse G.W. 2003. Ceci n'est pas une pipe: names, clades and phylogenetic nomenclature. Journal of Zoological Systematics and Evolutionary Research: 41, 162-174.

Ponomarenko A.G., Dmitriev V.Yu. 2009. Diversity curves revisited. Paleontological Journal: 43(2), 226-229.

Powell M.G., Kowalewski M. 2002. Increase in evenness and sampled alpha diversity through the Phanerozoic: Comparison of early Paleozoic and Cenozoic marine fossil assemblages. Geology: 30, 331-334.

Preston F.W. 1948. The commonness and rarity of species. Ecology: 29, 254-283.

Raup D.M. 1972. Taxonomic diversity during the Phanerozoic. Science: 177, 1066-1071.

Remane J. 2000 (ed.). International Stratigraphic Chart, with Explanatory Note. Division of Earth Sciences, UNESCO and International Union of Geological Sciences, Geneva, 16 pp.

Rényi A. 1961. On measure of entropy and information. In: Neyman J. (ed.), Proceedings of the 4th Berkeley Symposium on Mathematical Statistics and Probability. University of California Press, Berkeley, 547-561.

Robeck H.E., Maley C.C., Donoghue M.J. 2000. Taxonomy and temporal diversity patterns. Paleobiology: 26, 171-187.

Roy K., Jablonski D., Valentine J.W. 1996. Higher taxa in biodiversity studies: patterns from eastern Pacific marine molluscs. Philosophical Transactions of the Royal Society of London: (B), 351, 1605-1613.

Ruban D.A., van Loon A.J. 2008. Possible pitfalls in the procedure for paleobiodiversity-dynamics analysis. Geologos: 14(1): 37-50.

Sepkoski J.J. Jr. 1984. A kinetic model of Phanerozoic taxonomic diversity. III. Post-Paleozoic families and mass extinctions. Paleobiology: 10, 246-267.

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

Sepkoski J.J. Jr. 1993b. Limits to randomness in paleobiologic models: the case of Phanerozoic species diversity. Acta Palaeontologica Polonica: 38, 175-198.

Sepkoski J.J. Jr. 1996. Patterns of Phanerozoic extinctions: a perspective from global databases. In: Walliser O.H. (ed.), Global events and event stratigraphy. Springer, Berlin, 35-52.

Sepkoski J.J. Jr. 1998. Rates of speciation in the fossil record. Philosophical Transactions of the Royal Society of London: (B), 353, 315-326.

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

Sepkoski J.J. Jr. Kendrick D.C. 1993. Numerical experiments with monophyletic and paraphyletic taxa. Paleobiology: 19, 168-184.

Shannon C.E. 1948. The mathematical theory of communication. Bell System Technical Journal: 27, 379-423.

Signor P.W. 1985. Real and apparent trends in species richness through time. In: Valentine J.W. (ed.), Phanerozoic Diversity Patterns: Profiles in Macroevolution. Princeton University Press, Princeton, N.J., 129-150.

Smith A.B. 2003. Getting the measure of diversity. Paleobiology: 29, 34-36.

Smith B., Wilson J.B. 1996. A consumer's guide to evenness indices. Oikos: 76, 70-82.

Solbrig O.T. 1991 (ed.). From genes to ecosystems: a research agenda for biodiversity. Report of a IUBS-SCOPE-UNESCO workshop, Harvard Forest, Petersham, Mass., USA, June 27-July 1, 1991. IUBS, Cambridge, Mass. 124 pp.

Spellerberg I.F., Fedor P.J. 2003. A tribute to Claude Shannon (1916-2001) and a plea for more rigorous use of species richness, species diversity and the 'Shannon-Wiener' Index. Global Ecology and Biogeography: 12, 177-179.

Stanley S.M. 2007. An analysis of the history of marine animal diversity. Paleobiology: 33 (Suppl.), 1-55.

Stevens P.F. 1997. Mind, memory, and history: How classifications are shaped by and through time, and some consequences. Zoologica Scripta: 26, 293-301.

Stirling G., Wilsey B. 2001. Empirical relationships between species richness, evenness, and proportional diversity. American Naturalist: 158, 286-299.

Valentine J. 1969. Patterns of taxonomic and ecological structure of the shelf benthos during Phanerozoic time. Palaeontology: 12, 684-709.

Vermeij G.J., Leighton L.R. 2003. Does global diversity mean anything? Paleobiology: 29, 3-7.

Whittaker R.J. 1972. Evolution and measurement of species diversity. Taxon: 21, 213-251.

Wiener N. 1948. Cybernetics, or control and communications in the animal and the machine. J. Wiley & Sons, N.Y.

Williams R.J., Martinez N.D. 2000. Simple rules yield complex food webs. Nature: 404, 180-183.

Wilson J.B., Gitay H., Agnew A.D.Q. 1987. Does niche limitation exist? Functional Ecology: 1, 391-397.