BOOK REVIEW

Diversity Curves Revisited

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The analysis of taxonomic diversity dynamics in the geological past is one of the principal methods of studying the rates and nature of evolutionary changes. For this purpose, most paleontologists have plotted numbers of taxa (families, genera, or species) known from successive geological intervals. This will be referred to below as the traditional approach. Such plots are usually interpreted as reflecting changes of taxonomic diversity in the course of time. Such an interpretation is incorrect and distorts the actual picture of historical dynamics. Plotting numbers of taxa known from successive geological intervals would make sense only if the taxa appeared and disappeared exclusively at the boundaries of these intervals. Clearly, the continuous background extinction makes this assumption completely unrealistic. At every point of time within a given interval, the actual diversity was lower than the plotted value. Consider an extreme case. During one interval, a total of ten taxa replaced one another successively, while, during another, ten taxa coexisted throughout its length. The same value will be plotted for both intervals, although, during the first one, the actual diversity was ten times lower. Now consider a different situation. Imagine that, for a long period of time, actual diversity remained at a constant level of ten taxa. It means that the rates of origination and extinction were equal to each other (say, two taxa per 1 Ma). However, if we divide the period in question into three intervals, which lasted for 5, 12, and 3 Ma, the total number of taxa will be 20 for the first interval, 34 for the second, and 16 for the third. The traditional interpretation will hold that the second period was characterized by "a peak of diversity" and the third by "a mass extinction."

The recently published data on the dynamics of the Donaciinae beetle fauna of Japan during the Quaternary (Hayashi, 2004) can be used for a realistic example. Seven species are known from the Pliocene and 12 from the Pleistocene, six of which survived to the Holocene. The traditional approach will discover a twofold increase in diversity in the Pleistocene and a severe extinction at the boundary with the Holocene, while, in reality, at no given time did the fauna comprise more than six species, and the diversity remained constant despite the origination and extinction of taxa.

The number of taxa known from a particular age is strongly affected by the availability of Lagerstätten (localities with unusually high diversity of fossils) or any particularly intensively studied localities of that age. If such localities are known for one horizon but not for the next one, the plot will show a peak of diversity followed by an extinction. Lagerstätten can particularly strongly biased estimates of diversity for insect localities, because diversity of fossil insect assemblages depends primarily on the amount of collecting effort. For example, large-scale excavations in search of unique fossil vertebrates have quickly made the insect assemblages of the Chinese localities Daohugou and Yixian the most diverse. For a long time the Baltic amber remained better studied than any other fossil insect fauna, and many taxa have been thought to enter the record during the corresponding period of time. However, recent studies of the Cretaceous amber have demonstrated that many such taxa were in fact considerably older.

These shortcomings of the traditional approach to describing diversity dynamics prompted one of us to develop an alternative method (Dmitriev, 1978), which was extensively used in a later book on the evolution of taxonomic diversity (Alekseev et al., 2001). It was suggested to plot the number of taxa crossing the boundary between two periods, i.e., the taxa known prior and after that boundary. This number can be tied to a particular point in time, which allows an actual curve to be built. The corresponding book chapter was therefore titled "The curves of diversity." Relevant results on fossil insects have also been published in English (Rasnitsyn and Quicke, 2002). We know of only two studies published in our country that discuss the proposed method. Both argue for sticking to the traditional approach. Because some of the arguments in those publications appear erroneous and some are based on misunderstanding, we found it prudent to publish the present reply.

The first publication is the afterword written by Aleksandr Rasnitsyn in 2004 for a new edition of his collected works on the dynamics of biological diversity (Rasnitsyn, 2005). While acknowledging that the proposed method is mathematically sound, he nevertheless

believes that it yields a distorted picture of diversity dynamics. This is because the method ignores the taxa not crossing any interval boundaries (singletons in Foote, 2000), while, conversely, counting the "passing" taxa not recorded from the given interval together with the taxa actually recorded from it. However, the reasons for extrapolating singletons onto larger time intervals are as few as for doing it to the taxa known from a preceding interval and almost certainly crossing into the current one. Apparently, taxa disappear from the geological record more often due to changes in the taphonomic window or landscape changes than due to a decrease in their abundance. The statement that the method of instant diversity "ignores the ecological dependence of the fossil record" does not seem fair. Both this and the traditional method take this dependence into account, yet each in a different way. Shortcomings of the traditional method can be clearly seen using the example of a series of papers on the evolution of vertebrate diversity, one of which (Kalandanze and Rautian, 1993) Rasnitsyn considers an accomplishment. The idea of the "Jurassic crisis" in that study can be accounted for by time intervals analyzed being too long. Summation of all the taxa found within each interval has inevitably led to a picture of drastic changes in diversity. As an alternative to this method, Rasnitsyn suggested comparison of the diversity of local faunas. Indeed, local faunas can be considered instantaneous on the geological scale and, therefore, such data can be used to study diversity dynamics. Yet, even more than the traditional method, such data are affected by chance factors, particularly by the sample size. Although analyzing local faunas is absolutely necessary, it has to be considered as nothing more than analysis of local faunas.

The other response to our results was a large paper recently published by Shcherbakov (2008), where the author, among other things, criticizes our approach. According to him, the main drawback of our method is underestimation of the actual diversity. In particular, the taxa that survived to the interval in question are counted only at the preceding boundary, the taxa emerging during the interval are only counted at the subsequent boundary, and singletons are completely ignored. It is, however, a deliberate choice, which is unavoidable if one's goal is to correlate a real diversity with a particular moment in time. A series of such estimates provides a fairly well-substantiated idea of the main trends of diversity dynamics. Shcherbakov refers to this metric as "momentary" diversity. He encloses the adjective in quotation marks, although our technique indeed measures the diversity that is momentary on the geological scale. The traditional approach operates with nonexistent quantities and cannot tie them to any actual time points. Of course, nobody suggests ignoring additional data on the diversity within intervals and especially treating singletons as noise (Shcherbakov, 2008, p. 18). On the contrary, this is undoubtedly the vital source of information. It is the diversity of Lagerstätten that gives us a more or less accurate picture of the actually existing diversity. Yet one should not plot a series of such values against time. Unfortunately, Lagerstätten not only distort diversity dynamics, but also hamper correlation. Diversity of Lagerstätten is made up not so much of real singletons (i.e., the taxa, which existed exclusively in this region at the time when the locality was formed), but rather of rare taxa not preserved in common fossil deposits. Some of those rare taxa were more abundant in other areas or before or after the time when the Lagerstätt was formed. Usually the high diversity of a Lagerstätt is far from being exhaustively described. In the best studied cases, only hundreds of species were described from the thousands collected, and descriptions of additional new species continue to be published. Since only selected taxa are described, authors can focus on those with predominantly early or predominantly late distribution. For example, among insects of the well known Mongolian locality Bon-Tsagan, usually considered Aptian, one can select and describe groups with predominantly Jurassic (for example, Psilidae) or predominantly Late Cretaceous (many hymenopteran groups) distribution. The respective conclusions about the stratigraphic placement of the locality will be different. Therefore, correlating Lagerstätten with the localities where rare forms are absent from the fossil assemblage, or simply have not yet been discovered, turns out to be complicated.

It is hard to understand why our paleontologists stick so stubbornly to the traditional approach. Already in the 6th grade of the secondary schoolchildren are being taught how to build a body weight curve or a temperature curve using a technique invented by Descartes some 400 years ago. In high school, the concept of a momentary value of a function is introduced, which forms the basis of function analysis (e.g., Mordkovich and Smirnova, 2007). In our case, the function being examined is the number of taxa, which should be tied to a particular point of geological time (= momentary diversity, referred to in English literature as "standing diversity").

On the geochronological scale, the time points are boundaries of stratigraphic units. This is easy to see on any geochronological table, where the dates (in Ma) are shown, naturally, at the boundaries. In practice, as never-ending discussions about correlation of various deposits vividly demonstrate, stratigraphic boundaries cannot be considered perfectly isochronous. Yet there exists no other way to associate numbers of taxa with particular points in time. Thus, we can only hope that further research will gradually correct inaccuracies of stratigraphic correlation.

Therefore, only the plot where the ages of boundaries between geological intervals are plotted against the number of taxa at those boundaries (referred to in English papers as "boundary crossers") displays diversity dynamics based on a correct theory.

How data are represented on the traditional plots is based on tradition rather than theory. Each diversity value (= number of taxa) is there associated not with a time point, but with a time interval. This number is the sum of the number of taxa known at the interval's lower boundary plus the number of taxa first appearing during the interval. The first summation term is the number of taxa in a time point (the momentary number of taxa), while the second term is unnecessary and serves a source of errors.

Publication of this note was provoked by the above-mentioned paper by Shcherbakov (2008). In its theoretical part, the author presents an idealized synthetic picture of diversity dynamics, illustrated by superimposition of two types of plots (Shcherbakov, 2008, text-fig. 1). He believes that the momentary numbers of taxa at the boundaries estimate the minimum diversity, which, in his opinion, is typical of boundaries between stratigraphic units, while the total numbers of taxa estimate the maximum diversity, reached by the group during each interval. The result is a picture with drastic extinctions at each boundary, interspersed with equally drastic increases in diversity. Several points here are worth being discussed.

(1) A meaningful synthesis of two alternatives is only possible when both are equally sound logically. Combining a correct approach with an obviously incorrect one will never yield a useful result.

(2) Many intervals of the stratigraphic scale are currently being revised. In particular, within the Permian (the age Shcherbakov focuses on in his paper), the former Tatarian stage has been divided into three. According to Shcherbakov's beliefs, the two new boundaries within the former Tatarian stage mark their own diversity minima. So, further refinement of the scale will continuously increase the number of hypothesized extinctions, which is unlikely to have been the case.

(3) Along with refinement of the geochronological scale, data on distribution of fossil organisms also gradually become increasingly precise and detailed. For the study of the evolution of biological diversity it opens the possibility of employing increasingly smaller time intervals. If we follow the traditional assumption that new taxa originate at random time points, the shorter the intervals the smaller number of new taxa would appear during each interval. This is exactly what is observed empirically. Therefore, refinement of the scale must be accompanied by the traditional and the momentary diversity plots becoming increasingly similar. In theory, reducing time intervals to the extreme will lead to both plots becoming congruous: the traditional plot will shift downwards, while the curve of the momentary diversity will remain unchanged. The subject of discussion will then disappear, and only the momentary diversity plot will remain, which will correctly represent changes of diversity through time.

(4) One can believe that new taxa do not originate at random points of time, and that extinction is not random either (in particular, that there is no such thing as the background extinction). Speculations of this kind can be really diverse. Alcide d'Orbigny's ideas about multiple global catastrophes followed by acts of de novo creation were quite logical for his time. It appears that Shcherbakov has an a priori idea of how biological diversity evolves. Yet the only way to find out how it actually changes is the empirical one. The universal and only way to analyze empirical data using plots is the method we know from schooldays, but not the "traditional" charts employed by the majority of paleontologists.

(5) If our goal is to obtain the most accurate data on diversity dynamics, given the current state of knowledge, then we have to use plots of momentary diversity along with plots of originations and extinctions. If our goal is to characterize diversity that actually existed, then we have to study Lagerstätten. It is better not to use traditional graphs at all.

Using the term "momentary" diversity, referring to the number of taxa at a boundary between geological intervals as a metric of diversity at that time point, may seem redundant, since there are no other ways to adequately represent the process graphically. Yet we have to keep it in order to emphasize the difference from the traditional plotting approach. The inevitable abandonment of traditional graphs will make this clarification unnecessary. This is what has essentially happened in the western paleontological literature of the last decade (e.g., Foote, 2000; Alroy et al., 2001). In some American universities, educational software for building curves of momentary diversity is already in use (Tapanila, 2007). In a short while, young scientists in the West would not even realize there was a different way to build such plots.

Of interest in this context are several earlier studies. Leonov (1973) thoroughly explained differences between the two types of plots. To illustrate the evolution of large groups, he used stepped plots with two envelope lines: the lower one representing the momentary diversity and the upper one representing the traditional diversity. Unlike Shcherbakov, he did not consider his stepped plots as correctly describing diversity dynamics. Yet he has not made the ultimate step to completely abandon traditional plots. Around the same time, Harper (1975) suggested to plot the numbers of taxa at the lower boundary of each interval plus half the number of taxa newly appearing minus half the number of taxa going extinct during that interval. Earlier yet, the same metric had been employed by Webb (1969). Both authors placed their indices at the middle of each time interval. This so-called Webb-Harper's metric has only rarely been used. It equals the half-sum of the total number of taxa for the interval and thus can serve as an estimate of diversity at its middle. The method is sound but redundant if the boundary diversity metric is employed. Moreover, it can displace diversity minima, some of which are obviously associated with boundaries. Numbers of taxa at geochronological boundaries were used as momentary diversity estimates by Dmitriev (1978) and Carr and Kitchell (1980).

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