

Research paper

Phanerozoic marine biodiversity follows a hyperbolic trend

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Abstract

Changes in marine biodiversity through the Phanerozoic correlate much better with hyperbolic model (widely used in demography and macrosociology) than with exponential and logistic models (traditionally used in population biology and extensively applied to fossil biodiversity as well). The latter models imply that changes in diversity are guided by a first-order positive feedback (more ancestors, more descendants) and/or a negative feedback arising from resource limitation. Hyperbolic model implies a second-order positive feedback. The hyperbolic pattern of the world population growth arises from a second-order positive feedback between the population size and the rate of technological growth. The hyperbolic character of biodiversity growth can be similarly accounted for by a feedback between the diversity and community structure complexity. The similarity between the curves of biodiversity and human population probably comes from the fact that both are derived from the interference of the hyperbolic trend with cyclical and stochastic dynamics.

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1. Introduction: mathematical modeling of biodiversity dynamics

Mathematical modeling of fossil biodiversity dynamics is essential for understanding general trends of biotic evolution. Among diverse models that were used to describe and interpret the changes in global marine biodiversity through the Phanerozoic, the exponential and logistic models and their combinations are the most popular (Sepkoski, 1991a; Benton, 1999). The exponential, or expansionist, model implies simple positive feedback between the diversity (N) and its growth rate (more ancestors produce more descendants): $dN/dt = kN$.

Diversity growth is constrained only by the ability of taxa to occupy new niches, or ecospace (Benton, 1995). The logistic model adds a negative feedback (diversity growth is constrained by the limited volume of available ecospace): $dN/dt = k(N_{\max} - N)N$, where N_{\max} is a constant (Sepkoski, 1991a, 1992; Benton, 1995). Both models imply that interactions between contemporary taxa, except for their competition for ecospace, do not influence the pattern of diversification and extinction, so that the biota grows much like a population of amoebas in a tank of water, either constrained by resource limitation (logistic model) or not (exponential model). The advantages and drawbacks of these two models are extensively discussed, while other potentially useful models (e.g., hyperbolic) received little or no attention (Benton, 1995; Miller, 1998; Lane and Benton, 2003). The correlation between exponential and logistic models and the empirical data is generally low. It can be improved, however,

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by dividing the Phanerozoic into several segments and calculating parameters of exponential or logistic model for each segment separately (Sepkoski, 1991a, 1992; Miller, 1998; Benton, 1999). Apparently, such technique would fit any possible pattern, given that the number of segments is big enough. Apart from these models that are designed to capture directional trends, there is evidence that some aspects of biodiversity dynamics are stochastic (Raup et al., 1973; Sepkoski, 1994; Markov, 2001a; Cornette and Lieberman, 2004), while others are periodic (Raup and Sepkoski, 1984; Rohde and Muller, 2005). In this paper, we demonstrate that hyperbolic model ($dN/dt = kN^2$) describes the entire Phanerozoic history of marine biodiversity at genus level better than exponential model. The main difference between the hyperbolic and exponential growth is that the former requires a more complex positive feedback between the diversity and its growth rate. We suggest that this feedback was accomplished via the progressive changes in marine community structure.

2. Materials and methods

We used Sepkoski's compendium of fossil marine animal genera (available online at <http://strata.ummpp.lsa.umich.edu/jack/>). We considered only genera dated with substage or stage-level precision. We used absolute datings from Gradstein et al. (2004). In order to estimate how the changes in absolute geochronology can influence the results, we also applied an older scale for comparison (Harland et al., 1982). The results were practically the same (data not shown). The best-fit parameters for the discussed models have been identified with the least squares method with the use of SPSS14.0 software.

3. Results

Exponential model describes Phanerozoic marine biodiversity better than linear model; however, simple hyperbolic model ($dN/dt = kN^2$) fits much better to empirical data than exponential model (Fig. 1a–c). The latter explains only 46–54% of total macrovariation, while the former explains 85.4%. Notably, it is not necessary to divide the Phanerozoic into segments in order to achieve good correlation; the whole Phanerozoic history of biodiversity fits well to a single hyperbolic trend.

4. Discussion

4.1. Reliability of the fossil record

The fossil record provides important insights into the quantitative patterns of evolution, although the degree of reliability and adequacy of this source of data is

disputable. The skeptics mention, for instance, differential incompleteness of various parts of the record and 'the pull of the recent' effect (Raup, 1979). By the end of the 20th century, however, most authors had agreed that the paleontological record is representative and robust enough to adequately reveal the main quantitative patterns of evolution (Raup, 1987; Sepkoski, 1993; Benton, 1999; Foote and Sepkoski, 1999; Benton et al., 2000). Launching of the large international project entitled 'The Paleobiology Database' (<http://paleodb.org/>) (Schiermeier, 2003) initiated a new step in this discussion. New analytical approaches are being developed in order to clarify real evolutionary patterns by means of correcting various biases (e.g., different sampling intensity) that presumably distort the original paleontological data. The first results appeared discouraging as they suggested that almost all Meso-Cenozoic growth of marine biodiversity was possibly an artifact (Alroy et al., 2001). It was pointed out, though, that these conclusions were not final, because a number of factors still had to be taken into account. For instance, the majority of collections come from the paleontologically well-studied regions such as Western Europe and North America, which were near the equator during the Paleozoic but shifted to temperate latitudes by the Cenozoic. As far as diversity typically increases from the poles to the equator, this continental drift may bias the 'corrected' evolutionary pattern against the recognition of a diversity increase through the Phanerozoic (Allison and Briggs, 1993; Jackson and Johnson, 2001).

It has been shown recently that the effects of different biases can largely cancel out. Moreover, the increase in Phanerozoic marine biodiversity may be underestimated, rather than overestimated, by the 'raw data' (Bush and Bambach, 2004). Until the correction procedures become sufficiently well developed and comprehensive, it is still plausible to analyze fossil biodiversity as it is, which is indeed the case in the vast majority of publications on the subject.

4.2. Positive feedback between the demographic growth and technological development results in the hyperbolic growth of the World System

To interpret the hyperbolic pattern of biodiversity growth, we used data on another natural system that follows similar hyperbolic trend, namely the humanity, or the World System (von Foerster et al., 1960; Kremer, 1993; Cohen, 1995; Korotayev et al., 2006a,b). The dynamics of marine biodiversity is strikingly similar to the population dynamics in China, the country with the best-known demographical history (Fig. 1d). The simi-

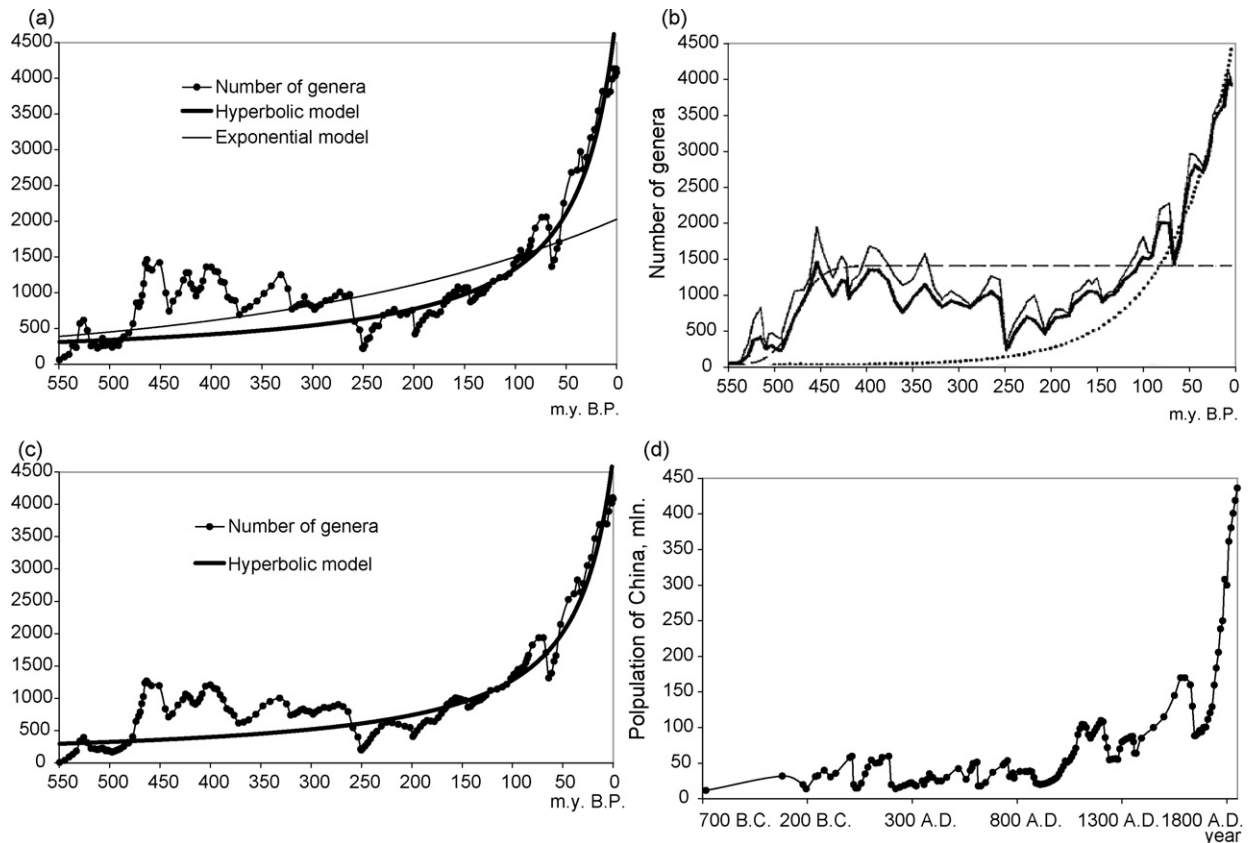


Fig. 1. (a) Global change in marine biodiversity (number of genera, N) through the Phanerozoic fits hyperbolic model ($N_t = 183,320/(37 - t)$; $R^2 = 0.854$) better than exponential model ($N_t = 2029 e^{0.003t}$; $R^2 = 0.463$). (b) Exponential model of Lane and Benton (2003) produces a better fit (dotted line) with the data they used ($R^2 = 0.54$), due to the fact that they excluded genera known from only a single geological interval (singletons) and used stage-level rather than substage-level resolution (from Lane and Benton, 2003). (c) Excluding singletons also improves correlation with hyperbolic model ($N_t = 175,777/(37 - t)$; $R^2 = 0.876$). Note that equations of type $X_t = C/(t_0 - t)$ are solutions to differential equations of type $dX/dt = kX^2$ (where $k = 1/C$) that describe nonlinear second-order positive feedbacks; the exponential equations are solutions of differential equations of type $dX/dt = kX$ and describe first-order linear feedbacks (see, e.g., Korotayev et al., 2006a, pp. 118–123). (d) Population growth of China (million people), based on estimates in Korotayev et al. (2006b, pp. 47–88). Note that the hyperbolic trend of Chinese population growth continued till the 1970s when it started to level off in direct connection with the demographic transition process (Chesnaïs, 1992).

larity probably comes from the fact that both curves are produced by the interference of three different components (general hyperbolic trend, as well as cyclical and stochastic dynamics).

It has been shown that the hyperbolic pattern of the world population growth arises from a non-linear second-order positive feedback between the demographic growth and technological development (more people – more potential inventors – faster technological growth – the carrying capacity of the Earth grows faster – faster population growth – more people – more potential inventors, and so on). It has been also shown (see Korotayev et al., 2006a, b) that non-linear second-order positive feedback between the demographic growth and technological development led to the hyperbolic growth of literacy and urbanization in the long-term perspective

(until the 1970s), as well as to the quadratic-hyperbolic growth of the world GDP, the number of literate people and urban-dwellers, and the population of the largest settlement of the World System. As has been shown by Naroll and Divale (1976) for pre-agrarian, agrarian, and early industrial societies, the population of the largest settlement is an effective indicator of the general level of sociocultural complexity of the respective system, which suggests that the overall sociocultural complexity of the World System was also growing in a quadratic-hyperbolic way during the “blow-up epoch”.

Hyperbolic growth of any variable implies that its value will become infinite in a finite moment of time, known as “critical time” (t_0). Calculations indicate that critical times for most of the hyperbolically growing World System development indicators fall within the

first half of the 21st century (Korotayev et al., 2006b, pp. 8–30). This implies that if the hyperbolic development of the World System continued, its main indicators would become infinite in the nearest future. Of course, in no way can this serve as a ground for any “eschatological expectations”, though such conclusions from the hyperbolic models are still sometimes made (see, e.g., Johansen and Sornette, 2001), because, since the 1970s we observe the systematic withdrawal of the World System from the blow-up regime. For a three differential equation model describing both the hyperbolic growth of the World System and its withdrawal from the blow-up regime, see Korotayev et al. (2006a, pp. 67–80).

4.3. *Evolution of marine communities can account for the hyperbolic growth of marine biodiversity*

We suggest that the hyperbolic character of biodiversity growth is similarly explained by a non-linear second-order positive feedback that exists between the diversity and community structure (more genera – higher alpha diversity – the communities become more stable and ‘buffered’ – average life span of genera grows; extinction rate decreases – faster diversity growth – more genera – higher alpha diversity, and so on).

The growth of genus richness through the Phanerozoic was mainly due to the increase of average longevity of genera and gradual accumulation of long-lived (stable) genera in the biota. This pattern reveals itself in the decrease of extinction rate. Interestingly, in both marine biota and humanity, growth was facilitated by the decrease in mortality rather than by the increase in birth rate. The longevity of newly arising genera was growing in a stepwise manner. The most short-lived genera appeared during the Cambrian; more long-lived genera appeared in Ordovician to Permian; the next two stages correspond to the Mesozoic and Cenozoic (Markov, 2001a, 2002). We suggest that diversity growth can facilitate the increase in genus longevity via the progressive stepwise changes in the structure of marine communities.

Most authors agree that there were three major biotic changes that resulted in fundamental reorganization of marine community structure during the Phanerozoic: Ordovician radiation, end-Permian extinction, and end-Cretaceous extinction (Bambach, 1977; Sepkoski et al., 1981; Sepkoski, 1988, 1992; Markov, 2001a,b; Bambach et al., 2002). Generally, after each major crisis the communities became more complex, diverse and stable. The stepwise increase of marine alpha diversity (average number of species or genera in a community) through the Phanerozoic was demonstrated by Bambach (1977) and Sepkoski (1988). Although Powell and Kowalewski

(2002) argued that the observed increase in alpha diversity might be an artifact caused by several specific biases that influenced the taxonomic richness of different parts of the fossil record, there is evidence that these biases largely compensated each other, so that the observed increase in alpha diversity was probably underestimated rather than overestimated (Bush and Bambach, 2004).

Another important symptom of progressive development of marine communities is the increase in evenness of distribution of species (or genus) abundances. In the primitive, pioneer or suppressed communities, this distribution is strongly uneven (community is overwhelmingly dominated by a few very abundant species). In more advanced, climax or flourishing communities, this distribution is more even (Magurran, 1988). The former type of community is generally more vulnerable. Evenness of distribution of species richness in marine communities increased substantially during the Phanerozoic (Powell and Kowalewski, 2002; Bush and Bambach, 2004). Most probably there was also an increase in habitat utilization, total biomass and rate of trophic flow in marine biota through the Phanerozoic (Powell and Kowalewski, 2002).

The more complex is the community, the more stable it is due to the development of effective interspecies interactions and homeostatic mechanisms based on the negative feedback principle. In a complex community, when the abundance of a species decreases, many factors arise that facilitate its recovery (e.g., there will be more food and fewer predators). Even if the species becomes extinct, its vacant niche may ‘recruit’ another species, most probably a related one that may acquire morphological similarity with its predecessor and thus will be assigned to the same genus by the taxonomists. So a complex community can facilitate the stability (and longevity) of its components, such as niches, taxa and morphotypes. This effect reveals itself in the phenomenon of ‘coordinated stasis’: the fossil record shows many examples of persistence of particular communities for many million years while the rates of extinction and taxonomic turnover are minimized (Brett et al., 1996).

Selective extinction leads to accumulation of ‘extinction-tolerant’ taxa in the biota (Sepkoski, 1991b). Although there is evidence that mass extinctions can be nonselective in some aspects (Jablonski, 2005), they are obviously highly selective with respect to the ability of taxa to endure unpredictable environmental changes. This can be seen, for instance, from the selectivity of the end-Cretaceous mass extinction with respect to the time of the first occurrence of genera. In younger cohorts the extinction level was higher compared to the

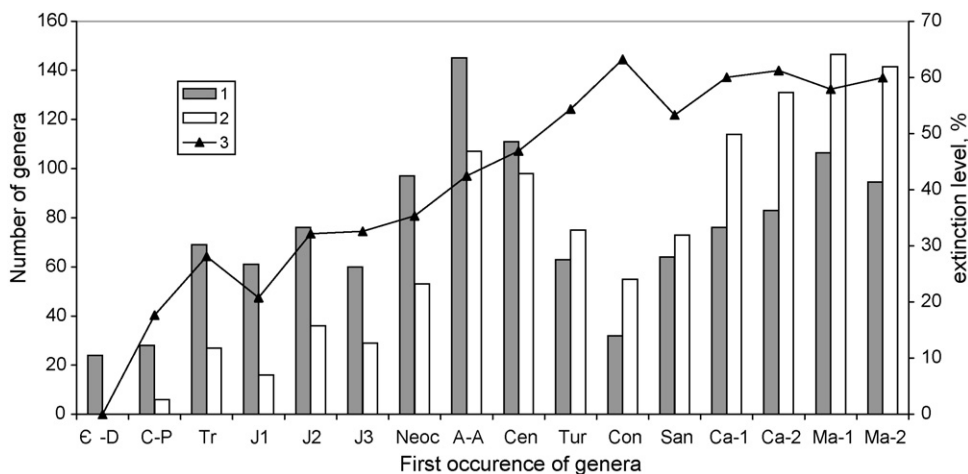


Fig. 2. Selectivity of the end-Cretaceous mass extinction with respect to the time of the first occurrence of genera: extinction level is higher in younger cohorts. Horizontal axis: time of the first occurrence of genera. (1) Number of genera that originated at the time shown on the horizontal axis and survived the end-Cretaceous extinction; (2) number of genera that originated at the time shown on the horizontal axis and became extinct at the Cretaceous/Tertiary boundary; (3) extinction rate at the Cretaceous/Tertiary boundary in the cohort (%). Neoc: Neocomian; A-A: Aptian–Albian; Cen: Cenomanian; Tur: Turonian; Con: Coniacian; San: Santonian; Ca-1: early Campanian; Ca-2: late Campanian; Ma-1: early Maastrichtian; Ma-2: late Maastrichtian.

older cohorts (Fig. 2). The same pattern can be observed during the periods of ‘background’ extinction as well (Markov, 2000). This means that genera differ in their ability to survive extinction events, and that extinction-tolerant genera accumulate in each cohort in the course of time.

Thus, taxa generally become more stable and long-lived in the course of evolution, apart from the effects of communities. The communities composed of more stable taxa would be, in turn, more stable themselves, thus creating a positive feedback.

The stepwise change of dominant taxa plays a major role in biotic evolution. This pattern is maintained not only by the selectivity of extinction (discussed above), but also by the selectivity of the recovery after crises (Bambach et al., 2002). The taxonomic structure of the Phanerozoic marine biota was changing in a stepwise way, as demonstrated by the concept of three sequential ‘evolutionary faunas’ (Sepkoski, 1992). There were also stepwise changes in the proportion of major groups of animals with different ecological and physiological parameters. There was a stepwise growth in proportion of motile genera compared to non-motile; ‘physiologically buffered’ genera compared to ‘unbuffered’, and predators compared to prey (Bambach et al., 2002). All these trends should have facilitated the stability of marine communities (e.g., diversification of predators implies that they become more specialized; a specialized predator regulates its prey’s abundance more effectively than a non-specialized predator).

There is also another possible mechanism of the second-order positive feedback between the diversity and its growth rate. Recent research has demonstrated a shift in typical relative-abundance distributions in marine paleocommunities after the Paleozoic (Wagner et al., 2006). One possible interpretation of this shift is that the community structure and the interactions between species in the communities became more complex. In the post-Paleozoic communities, new species probably increase ecospace more efficiently, either by facilitating opportunities for additional species or by niche construction (Wagner et al., 2006; Solé et al., 2002; Laland et al., 1999). This possibility makes the mechanisms underlying the hyperbolic growth of marine diversity and human population even more similar, because the total ecospace of the marine biota is analogous to the “carrying capacity of the Earth” in demography. As far as new species can increase ecospace and facilitate opportunities for additional species entering the community, they are analogous to the “inventors” of the demographic models whose inventions increase the carrying capacity of the Earth.

4.4. Origination and extinction rates

Exponential and logistic models of biodiversity imply several possible ways in which the rates of origination and extinction may change through time (Sepkoski, 1991a). For instance, exponential growth can be derived from constant per-taxon extinction and origination rates,

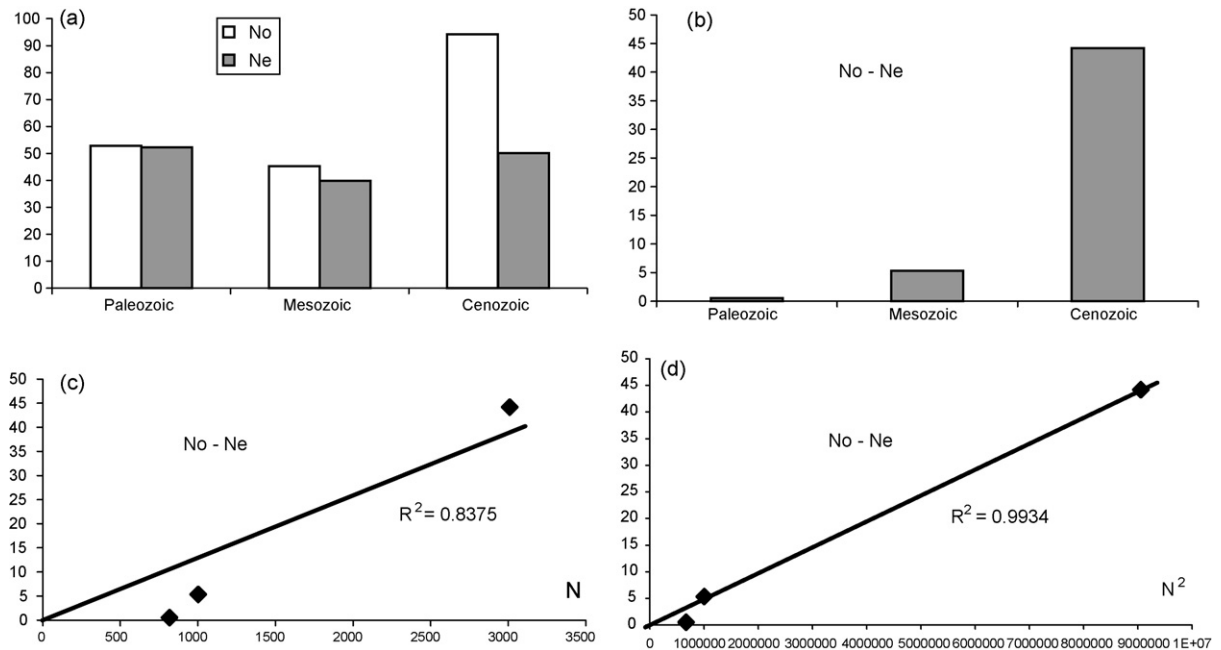


Fig. 3. Mean origination, extinction and increment rates in the Paleozoic, Mesozoic and Cenozoic. (a) N_o , mean origination rate (number of origins divided by the duration of the era, m.y.); N_e , mean extinction rate (number of extinctions per m.y.); (b) mean increment ($N_o - N_e$). (c) Mean increment (vertical axis) plotted against mean diversity level during the era (N , horizontal axis). (d) Mean increment plotted against N^2 . ($N_o - N_e$) correlates better with N^2 than with N , as predicted by the hyperbolic model.

the latter being higher than the former. However, actual paleontological data suggest that origination and extinction rates did not follow any distinct trend through the Phanerozoic, and their changes through time look very much like chaotic fluctuations (Cornette and Lieberman, 2004). Therefore it is more difficult to find a simple mathematical approximation for origination and extinction rates than for the total diversity.

In fact, the only critical requirement of the exponential model is that the difference between the origination and extinction through time should be proportional to the current diversity level: $(N_o - N_e)/\Delta t \approx kN$, where N_o and N_e are the numbers of genera with, respectively, first and last occurrences within the time interval Δt , and N is mean diversity level during the interval. The same is true for the hyperbolic model. It does not predict the exact way in which origination and extinction should change, but it does predict that their difference should be roughly proportional to the square of the current diversity level: $(N_o - N_e)/\Delta t \approx kN^2$. In demographic models discussed above, the hyperbolic growth of the world population was not decomposed into separate trends of birth and death rates. The main driving force of this growth is presumably the increase of carrying capacity of the Earth, and the way in which this capacity is realized – either by decreasing death rate, or by increasing birth rate, or

both – depends upon many factors and may vary from time to time.

The same is probably true for marine diversity. The overall shape of the diversity curve depends mostly on the differences in the mean rates of diversity growth in the Paleozoic (low), Mesozoic (moderate), and Cenozoic (high). The Mesozoic increase was mainly due to lower extinction rate (compared to the Paleozoic), while the Cenozoic increase was largely due to higher origination rate (compared to the Mesozoic) (Fig. 3a and b). This probably means that the acceleration of diversity growth during the last two eras was driven by different mechanisms of positive feedback between diversity and its growth rate. Generally, the increment rate $((N_o - N_e)/\Delta t)$ was changing in a more regular way than the origination rate $N_o/\Delta t$ and extinction rate $N_e/\Delta t$. The large-scale changes in the increment rate correlate better with N^2 than with N (Fig. 3c and d), thus supporting the hyperbolic rather than the exponential model.

5. Conclusions

Generally, the paleontological data confirm the idea that there was an increase in the complexity and stability of marine communities throughout the Phanerozoic. These changes can be accounted for through the exis-

tence of the second-order positive feedback in the course of biodiversity growth that reveals itself in the hyperbolic character of the latter. Biodiversity growth facilitated the increase in the communities' complexity and stability, and this, in turn, resulted in the increasing stability and decreasing probability of extinction of genera. Furthermore, in the complex communities new species probably increase ecospace more efficiently, either by facilitating opportunities for additional species or by niche construction; this may result in higher origination rate. Lower extinction rate and/or higher origination rate resulted in further biodiversity growth.

The similarity of the Phanerozoic marine biodiversity dynamics to that of human population provides both the possibility of meaningful and informative interpretation of this pattern and the additional evidence in favor of the hypothesis that the observed fossil biodiversity is not too strongly biased.

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