

Alpha diversity of Phanerozoic marine communities positively correlates with longevity of genera

Alexander V. Markov

Abstract.—Several lines of theoretical and empirical evidence suggest that there can be a positive correlation between alpha diversity (genus richness) of marine communities (D) and average longevity of marine genera included in these communities (L). One possible reason for such a correlation is that diversity can be expected to give rise to ecosystem stability, which, in turn, may slow down the extinction of taxa. However, this hypothesis has not been verified on the global scale. The analysis of two large data sets (Sepkoski's compendium of fossil marine genera and the Paleobiology Database) shows that the correlation (1) actually exists and (2) is robust to some possible sources of errors in L and D estimation. Further analysis reveals that the correlation is not a secondary pattern caused by any of the following factors: (1) encounter probability of taxa, which is greatly influenced by differential incompleteness of the fossil record; (2) degree of sediment lithification, which is one of the major factors affecting the preservation of fossils; (3) onshore-offshore gradient; (4) parallel growth of both L and D through the Phanerozoic; (5) paleolatitudinal gradient. Although there may be other factors that influence both L and D in a similar way, the results generally confirm the hypothesis that higher alpha diversity enhances longevity of genera.

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Introduction

The relationship between diversity and stability of ecosystems has been extensively discussed by ecologists for more than half a century. Classic studies suggest that more diverse communities enhance ecosystem stability (MacArthur 1955; Elton 1958; May 1973). Further research introduced some controversy, known as the "diversity-stability debate" (see McCann 2000 for a review). Although experimental work on extant communities does not indicate a simple, monotonic relationship between community stability and diversity, these studies have confirmed the importance of biodiversity to the functioning of ecosystems, and it is generally agreed that higher diversity can be expected, on average, to give rise to ecosystem stability (McCann 2000; Naeem and Wright 2003).

Paleontological data indicate that alpha diversity of marine communities (average number of species or genera in a community) increased in a stepwise manner through the Phanerozoic. Pioneer studies by Bambach (1977) and Sepkoski (1988) revealed that marine alpha diversity was low during the Cambrian, increased rather abruptly at the begin-

ning of the Ordovician, and then remained almost constant until the end of the Mesozoic. The third step corresponds to the Cenozoic era, when alpha diversity once again demonstrated an abrupt increase, followed by stabilization.

Although Powell and Kowalewski (2002) argued that the observed increase in alpha diversity might be an artifact caused by several particular 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; see also Kowalewski et al. 2006).

If alpha diversity can enhance ecosystem stability, then it can be expected that stability of marine communities also increased through the Phanerozoic.

Another important indicator 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 skewed (community is over-

whelmingly dominated by a few very abundant species) (Magurran 1988). Such communities are generally more vulnerable to environmental fluctuations. Evenness of distribution of species richness in marine communities increased substantially during the Phanerozoic (Powell and Kowalewski 2002; Bush and Bambach 2004; Peters 2004; see also Wagner et al. 2006). Numerous facts indicate that there was also an increase in habitat utilization, guild structure complexity, diversity of modes of life (both within and between communities), total biomass, and rate of trophic flow in marine biota through the Phanerozoic (Vermeij 1995; Bambach 1983, 1985, 1999; Bambach et al. 2007; Powell and Kowalewski 2002). Bush and Bambach (2004) also suggested that the increase of ecospace utilization could facilitate both the growth in alpha diversity and the increase in evenness of distribution of species abundances (see also Bambach et al. 2007).

If marine communities, in general, were becoming more complex and stable through the Phanerozoic, it is reasonable to suggest that genera composing these communities were also becoming more stable and extinction resistant. Merely living in a stable community presumably can decrease the extinction risk. The stability of a complex community partially arises from 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, some factors may arise that will facilitate its recovery (e.g., there will be more food and fewer predators). Even if the species becomes extinct, its vacant niche may be occupied by another species, most probably a related one that may acquire morphological similarity to its predecessor and thus will be assigned to the same genus by taxonomists. So a complex community probably can enhance the stability (and longevity) of its components, such as niches, taxa, and morphotypes (see also Jackson and Erwin 2006).

The positive correlation between alpha diversity and longevity of taxa is also predicted by the hyperbolic model of the Phanerozoic marine diversity dynamics (Markov and Ko-

rotayev 2007). Among diverse models that were used to describe and interpret the changes in global marine biodiversity through the Phanerozoic, the exponential ($dN/dt = kN$) and logistic ($dN/dt = k \cdot (N_{\max} - N) \cdot N$) models, traditionally used in population biology, are the most popular (Sepkoski 1991b; Courtillot and Gaudemer 1996; Benton 1999; Miller 1998; Lane and Benton 2003). The correlation between exponential and logistic models and the empirical data is generally low. I have argued recently that the hyperbolic model ($dN/dt = kN^2$) describes the entire Phanerozoic history of marine biodiversity at genus level better than the exponential model (Markov and Korotayev 2007). The hyperbolic model is widely used in macrosociology and demography. The hyperbolic pattern of the world population growth (von Foerster et al. 1960; Kremer 1993) arises from a second-order positive feedback between the population size and the rate of technological growth: more people \rightarrow more potential inventors \rightarrow faster technological growth \rightarrow the carrying capacity of the earth grows faster \rightarrow faster population growth \rightarrow more people \rightarrow more potential inventors, and so on (Korotayev et al. 2006). We proposed that the hyperbolic character of biodiversity growth could be similarly accounted for by a feedback between the diversity and community structure: more genera \rightarrow higher alpha diversity \rightarrow the communities become more stable and "buffered" \rightarrow average life span of genera grows; extinction rate decreases \rightarrow faster diversity growth \rightarrow more genera \rightarrow higher alpha diversity, and so on. There is also another possible positive feedback loop, because higher alpha diversity appears to generate opportunities for more speciation (Emerson and Kolm 2005; Erwin 2005; Benton and Emerson 2007). Thus, our model predicts a positive correlation between alpha diversity and longevity of genera (Markov and Korotayev 2007).

In agreement with this prediction, both alpha diversity and average longevity of marine genera were growing through the Phanerozoic. The observed growth of marine diversity through the Phanerozoic was to a large extent due to the increase of average longevity of genera and gradual accumulation of long-

lived genera in the biota (Sepkoski 1991a). This pattern reveals itself in the decrease of extinction rate (Raup and Sepkoski 1982). The longevity of newly arising genera was growing in a stepwise manner. Cambrian taxa tended to have the shortest durations; longer-lived genera appeared in the Ordovician to Permian; the next two stages correspond to the Mesozoic and Cenozoic (Markov 2002). It is not well understood, however, whether this parallel growth of alpha diversity and longevity arises from causal relationship between the two values or whether it is due to other factors (e.g., differential incompleteness of the fossil record or some natural factors that changed gradually through the Phanerozoic and influenced both values in a similar way).

Generally, although several lines of theoretical and empirical evidence suggest that there can be a positive correlation between alpha diversity and longevity (resistance to extinction) of genera, no large-scale verification of this hypothesis has been undertaken. Here I demonstrate that complex analysis of two global-scale paleontological databases (Sepkoski's compendium and the Paleobiology Database) reveals a highly significant correlation between alpha diversity of marine communities and longevity of genera, and that this correlation is independent of such factors as geologic time, lithification, onshore-offshore gradient, geographic latitude, and occurrence rate.

Materials and Methods

Two global-scale paleontological databases were used:

1. Sepkoski's database (SDB), which includes stratigraphic intervals for more than 35,000 fossil marine genera (<http://strata.ummp.lsa.umich.edu/jack/>). I used absolute datings of stratigraphic boundaries from Gradstein et al. (2004).

2. The Paleobiology Database (PBDB), comprising extensive data on about 75,000 paleontological collections from all over the world (<http://paleodb.org/>; Alroy et al. 2001). Generally, each "collection" in PBDB represents fossils from a single age and a single locality and contains several "occurrences" (= list of taxa). Each occurrence is linked to a particular

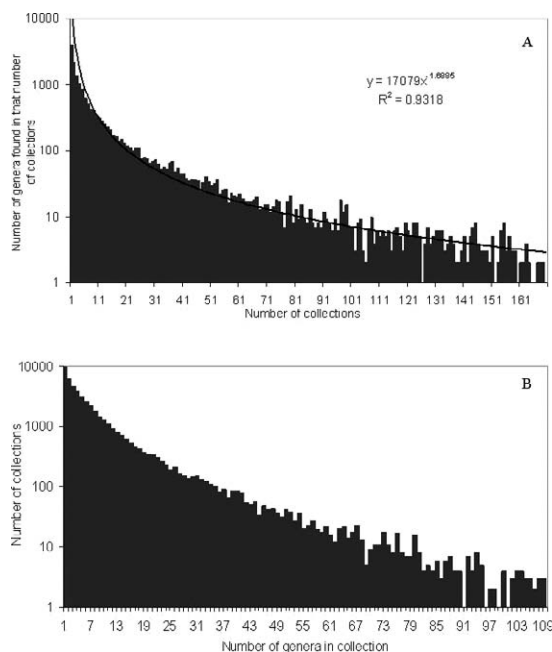


FIGURE 1. Data set statistics. A, Distribution of genera across the collections. x-axis, number of collections containing a genus; y-axis, number of genera found in that number of collections. Scale is semilogarithmic. Power trend is shown for schematic purposes only. B, Distribution of collection size. x-axis, number of genera in a collection; y-axis, number of collections with that number of genera.

taxon (usually genus or species). Despite its impressive volume, PBDB is definitely incomplete, and its spatial and temporal coverage is highly uneven (e.g., the Mesozoic data are less complete than the Cenozoic data; there are many more collections from the United States than from Russia; etc.). Data used herein were downloaded from the PBDB server on 9 October 2007.

Data from the two sources were combined via "genus name" field and checked for consistency. After removing a few hundred doubtful relationships, the final list of 16,952 Phanerozoic marine genera was obtained with reliable data from both SDB and PBDB. All higher taxa found were included.

I used data only on those PBDB collections that contain genera from this list (47,398 collections). Figure 1A shows the quantitative distribution of genera across the collections. Predominance of genera found in only one or two collections indicates incomplete sampling (otherwise the pattern is expected to be more

TABLE 1. Data set statistics (only genera found in both PBDB and SDB are included).

Type of collection	No. of collections	Total no. of genus occurrences	Total no. of genera
Paleozoic	21,995	148,628	8769
Mesozoic	17,813	108,073	5401
Cenozoic	7590	71,231	4069
Lithified	21,082	137,256	11,421
Poorly lithified	2265	20,231	3182
Unlithified	1334	22,620	2063
Undefined	22,717	147,825	11,762
Offshore	7480	59,294	6821
Onshore	8753	63,487	7795
Undefined	31,165	205,151	14,466
Total	47,398	327,932	16,952

similar to log-normal distribution). Collections containing only one or two genera constitute about one-third of the data set (15891 collections out of 47,398; Fig. 1B). General statistics of the data set are summarized in Table 1.

I used the following numerical measures:

1. *L* (longevity), Myr, was calculated as the length of time between the moments of first and last occurrences of the genus, according to SDB. Time of the first (last) occurrence in SDB is represented by a stratigraphic interval; I used a random time point within the interval as an approximation of origination (extinction) time. For extant genera, the calculation of "expected" longevity was based on the assumption that the observed median Cenozoic extinction rate (about 0.7% genera per Myr for marine genera that have crossed at least one stratigraphic boundary) would persist in the future. For each extant genus found in the pre-Holocene deposits, its future "existence" was modeled with extinction probability of 0.007 at each 1-Myr step. Using the mean Cenozoic extinction rate (about 1.0% genera per Myr) instead of the median rate does not alter the results significantly (Markov 2000, 2001, 2002). In this study, *L* was used as a proxy of stability (resistance to extinction) of genera. This is why the complete stratigraphic ranges of genera were used to calculate *L* in all instances, including situations when some particular time interval was considered, during which some genera were only partially through their range.

2. *D* (average number of genera in collections containing the genus) was used as a proxy of the degree of adaptation of the genus to complex (or simple) biotic environment (or to living in communities with high or low alpha diversity). Genera with high value of *D* are found predominantly in diverse collections, whereas genera with low *D* tend to be found in collections with a low level of diversity. This estimate is based on the assumption that the underlying alpha diversity of paleo-communities is an important factor affecting the taxonomic diversity of paleontological collections (along with other factors such as preservation, sampling effort, collection purpose, and methods). The facts that confirm this assumption are discussed below. *D* was calculated for all 16,952 genera found in both PBDB and SDB; calculation was based on the original full lists of genera for each PBDB collection rather than on the restricted lists that contain only genera with matching records in SDB.

3. *A* is an estimation of "abundance," "occupancy" (Foote et al. 2007), occurrence rate, or encounter probability. $A = N_1/N_2$, where N_1 is the number of collections containing the genus, and N_2 is the total number of collections (according to PBDB) within the stratigraphic interval of the genus (according to SDB).

Other factors included in the analysis are paleogeographic latitude, degree of sediment lithification, and onshore-offshore gradient (according to PBDB).

Results

Correlation between L and D.—Figure 2 shows the positive correlation between *L* and *D* for genera found in ten or more PBDB collections ($N = 5569$). Generally, the relationship between *L* and *D* is best described by a power function; therefore it is convenient to use natural logarithms of the two values so that the relationship becomes linear. The correlation remains highly significant if all 16,952 genera are included in the sample ($R = 0.299$, $p \ll 0.00001$).

Comparatively low values of Pearson's correlation coefficient indicate that correlation between *L* and *D* is weak, although highly sig-

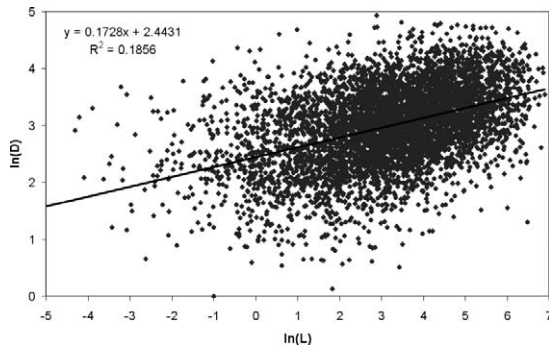


FIGURE 2. Relationship between $\ln(L)$ and $\ln(D)$ for genera found in ten or more PBDB collections ($N = 5569$). Linear regression parameters: $R = 0.431$, $p \ll 0.00001$.

nificant. Weakness of the correlation is expected for two reasons.

First, both values (L and D) are very rough and imprecise approximations of the underlying natural characteristics of genera. Under such circumstances, strong correlation would most probably indicate an artifact. Second, longevity of a genus cannot depend solely on its confinement to complex or simple communities. Obviously, L depends upon many factors, including random ones (Jablonski 2007; see “Discussion”). Therefore, weak correlation is exactly what should be expected on the basis of the initial hypothesis that higher alpha diversity enhances resistance to extinction.

The results are robust to possible errors in L estimation. Such errors arise predominantly from two categories of genera: (1) singletons, or genera known from a single stratigraphic interval (their L was calculated as a random number between 0 and the duration of the interval); and (2) extant genera (“expected” L was calculated from the observed Cenozoic extinction rates). However, the correlation remains statistically significant if either or both groups of genera are excluded from the analysis (for genera found in ten or more PBDB collections, singletons and extant genera excluded: $N = 3957$, $R = 0.267$, $p \ll 0.00001$).

It is noteworthy that when both extant genera and singletons are excluded from the analysis, the total variation of L becomes greatly diminished, because the most short lived and the most long lived genera are excluded at the

same time. Therefore, the preservation of statistical significance in this case is a strong argument in favor of the robustness of correlation to the effect of outliers.

It can be argued that the stratigraphic ranges of genera from Sepkoski’s compendium may be not precise enough for meaningful biological interpretations. It can be demonstrated, however, that the level of precision of stratigraphic ranges does not matter much in this particular case. If we estimate stratigraphic ranges of genera using data from PBDB rather than SDB, that is, if we use an unrelated data set to calculate L , the results remain essentially the same. Importantly, PBDB is definitely incomplete, and it makes no attempt to cover the complete stratigraphic ranges of genera. However, PBDB-based estimations of L appear to be almost as fit for the purposes of the current study as SDB-based ones. As expected, the former correlate positively with the latter. The correlation is not very strong, although it is highly significant. For genera found in ten or more PBDB collections, singletons and extant genera excluded ($N = 3957$), the relationship can be approximated by the equation $L_{\text{PBDB}} = 0.507 \cdot L_{\text{SDB}} + 10.2$; $R = 0.633$; $p \ll 0.00001$. For the same sample, the correlation between L_{PBDB} and D ($R = 0.206$; $p \ll 0.00001$; regression slope 0.147 ± 0.022 [95% confidence intervals]) is almost indistinguishable from the correlation between L_{SDB} and D ($R = 0.267$; $p \ll 0.00001$; regression slope 0.139 ± 0.016). These results imply that, for the purposes of the current study, the estimations of L do not need to be very precise.

Positive correlation between L and D can be explained either by causal relationship (direct or indirect) between the two values or by some additional factor (or factors) that affect both values in a similar way. Below I discuss five factors that theoretically can produce such an effect.

1. *Occurrence rate (A).*—Differential incompleteness of the fossil record is the main source of uncertainty and biases in the quantitative analysis of the paleontological data. Occurrence rate of genera is highly sensitive to the incompleteness of the record. Thus we can, to some extent, evaluate the effects of in-

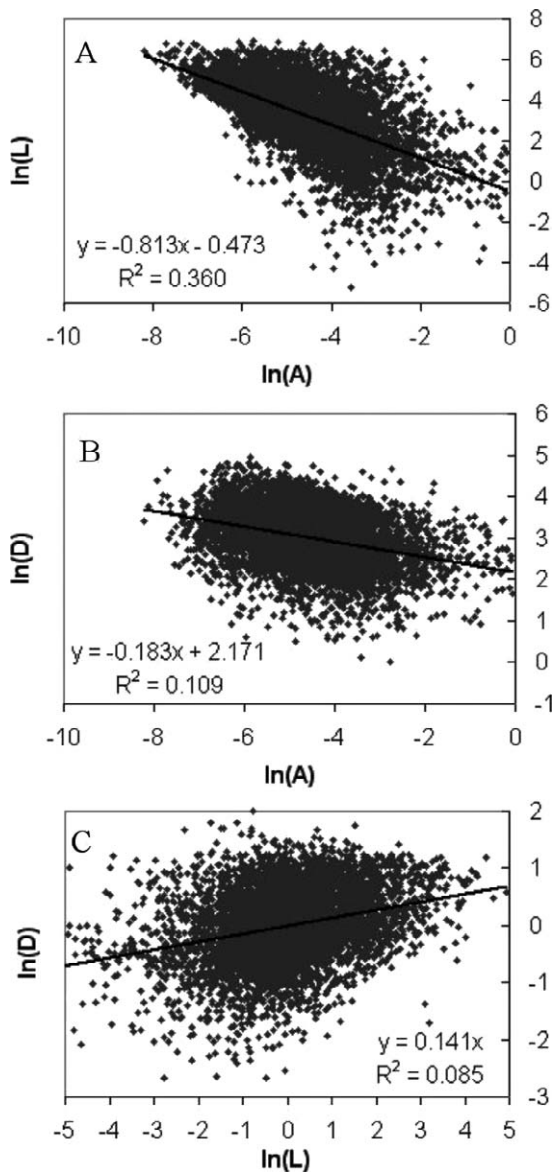


FIGURE 3. Relationships between $\ln(L)$ and $\ln(A)$ (A), $\ln(D)$ and $\ln(A)$ (B), and $\ln(D)$ and $\ln(L)$ after extracting the linear trends shown in A and B (C). Genera found in ten or more PBDB collections are included ($N = 5569$).

completeness on L and D (and on their correlation) by comparing these values with A .

Regression analysis reveals significant negative correlation between A and L and between A and D (Fig. 3A,B). For all genera, $R = -0.409$ (A versus L); $R = -0.161$ (A versus D); for genera found in ten or more collections, $R = -0.600$ (A versus L); $R = -0.331$ (A versus D); $p \ll 0.00001$ for all cases. Note that A correlates more strongly with L than with D .

Both negative correlations (between A and L and between A and D) most probably arise from differential incompleteness of the fossil record, although alternative explanations are possible (see "Discussion").

Considering that both L and D depend upon A in a similar way, it seems reasonable to suggest that this relationship provides explanation for the positive correlation between L and D . In other words, we can suggest that long-lived genera have higher D simply because they have lower A (due to incomplete sampling), given that genera with low A generally have high D (also due to incomplete sampling). Confirming this suggestion would mean that the observed relationship between L and D is an artifact of incomplete sampling.

However, the data do not confirm this suggestion. After introducing appropriate corrections (that is, when the linear trends depicting the influence of $\ln(A)$ on $\ln(L)$ and $\ln(D)$ are subtracted from corresponding values), the positive correlation between L and D still remains highly significant (Fig. 3C). The relationship between the corrected values can be approximated by the equation $\ln(D)_{\text{corrected}} = 0.141 \cdot \ln(L)_{\text{corrected}}$ ($R = 0.292$, $p \ll 0.00001$). Therefore, the relationships between A and L and between A and D cannot provide sufficient explanation of the observed positive correlation between L and D .

2. *Lithification.*—Degree of sediment lithification has a major effect on the completeness of the fossil record and the diversity of paleontological collections. On average, more fossils can be extracted from unlithified or poorly lithified rocks, all other conditions being equal (Powell and Kowalewski 2002; Bush and Bambach 2004). This is evident from the comparison of mean genus diversity of PBDB collections originating from localities with different degrees of lithification. There are, on average, 7.521 genera per collection in "lithified" collections ($N = 21082$) and 14.739 genera in "unlithified" or "poorly lithified" collections ($N = 3599$) ($p \ll 0.00001$, two-tailed t -test).

Genera found in lithified collections only (a), in collections of both types (b), and in unlithified or poorly lithified collections only (c) have different mean values of L and D . How-

ever, the relationship is different for the two values (Fig. 4). D grows continuously from (a) to (b) to (c). This trend most probably mirrors the impact of lithification on sampling effectiveness. Collections derived from unlithified rocks have higher genus diversity, and this is why genera confined to unlithified rocks have higher D . On the contrary, L is the highest in group (b), although difference between (b) and (c) is below the level of statistical significance. This is expected because group (b) obviously comprises the most eurytopic genera, and it is generally accepted that such environmentally tolerant genera are less extinction prone (different factors affecting the duration of taxa are discussed below).

The differences between groups (a) and (c) are similar for both L and D : genera restricted to unlithified collections have higher values of L and D compared to genera confined to lithified rocks. Thus, lithification theoretically can provide an explanation for the correlation between L and D . This is not the case, however, because the correlation remains significant within the samples of genera found in lithified (or unlithified) collections only.

For all genera found in lithified collections only ($N = 8674$) a linear relationship between $\ln(D)$ and $\ln(L)$ can be described by the equation $\ln(D) = 0.107 \cdot \ln(L) + 2.567$ ($R = 0.232$, $p \ll 0.00001$). After introducing corrections for the influence of A (see previous section), the relationship can be approximated as following: $\ln(D)_{\text{corrected}} = 0.089 \cdot \ln(L)_{\text{corrected}} - 0.108$ ($R = 0.171$, $p \ll 0.00001$). The correlation is stronger for genera found in ten or more collections ($N = 2885$): $R = 0.323$, $p \ll 0.00001$ without corrections; $R = 0.203$, $p \ll 0.00001$ after correcting for the influence of A (Fig. 4C).

For genera found in unlithified or poorly lithified collections only ($N = 1238$), and in at least ten collections in total, $R = 0.190$, $p \ll 0.00001$ (uncorrected), or $R = 0.132$, $p = 0.000003$ (corrected for A).

The results demonstrate that two major factors related to differential incompleteness of the fossil record, namely encounter probability (A) and lithification, when considered either separately or together, cannot provide sufficient explanation for the positive correlation between L and D , despite the fact that

both L and D do depend upon them to some extent. Thus it seems reasonable to suggest that this correlation is not merely an artifact of incomplete sampling and that it may bear some biological signal. In the latter case, the relationship can be either "primary" (causal) or "secondary" (caused by another natural factor(s) that influence both L and D in a similar way).

3. *Onshore-offshore gradient.*—Among PBDB collections that contain genera from SDB, 8753 collections can be assigned to "onshore" environments, according to data presented in PBDB, and 7480 collections can be regarded as "offshore." Mean number of genera in the two groups of collections is 8.237 and 8.905, respectively ($p = 0.0003$, two-tailed t -test). Thus, offshore collections are slightly more diverse, in accordance with previous findings (Sepkoski 1988, 1991a).

The onshore-offshore gradient affects L and D in different ways (Fig. 5). Genera found in both types of environments have the highest L . As in the situation discussed in the previous section, this is probably because eurytopic genera (e.g., capable of living at different depths) can withstand environmental fluctuations better and are thus generally less extinction prone.

Mean L is higher in genera found only in onshore collections than in those confined to offshore collections. On the contrary, mean D is somewhat higher in genera confined to offshore collections. This is probably because the offshore communities are generally more diverse, and this pattern is adequately reproduced by the collection sizes.

Given that onshore-offshore gradient affects L and D differently, this factor cannot explain the observed correlation between L and D . In fact, the correlation exists despite this factor rather than because of it. Possible theoretical implications of the results presented in this section are discussed below.

4. *Parallel growth of L and D .*—The Phanerozoic growth of average longevity of marine genera (L) was nearly linear, interrupted by local fluctuations (Fig. 6) (Markov 2000; Markov and Korotayev 2007), whereas the growth of D was distinctly nonlinear, with three prominent "steps" similar to those found in

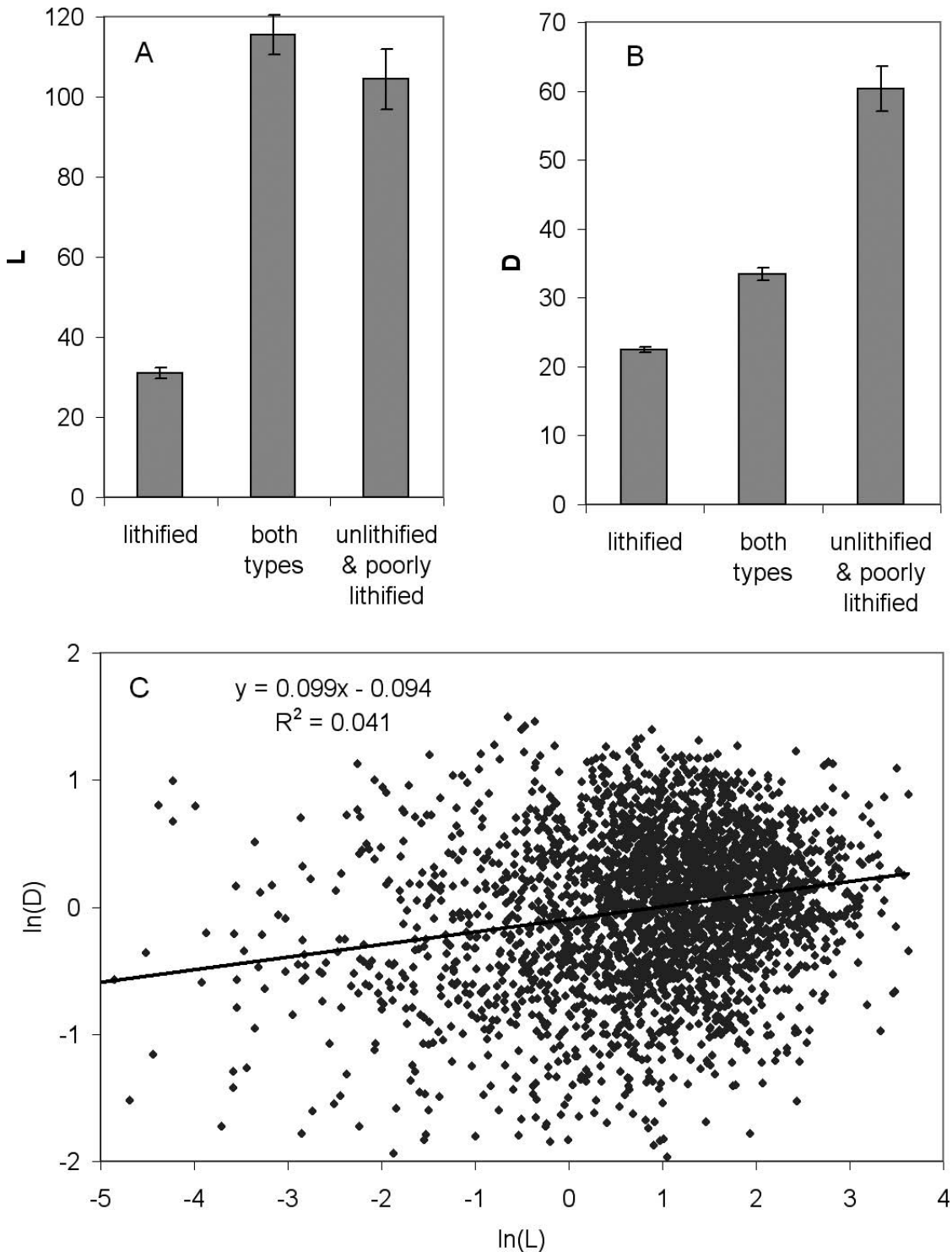


FIGURE 4. Relationship between L , D , and lithification. A, Mean longevity (L) of genera found in "lithified" collections only (8674 genera), in both types of collections (2747 genera), and in "unlithified" or "poorly lithified" collections only (1238 genera). B, Mean value of D in the same three groups of genera. Bars show 95% confidence intervals. C, Relationship between L and D for genera found in "lithified" collections only, and in ten or more collections (2885 genera), after introducing corrections for the influence of occurrence rate (A). The statistical significance of the correlation between L and D ($p \ll 0.00001$) in case illustrated in C implies that the correlation cannot be sufficiently explained by the combined effect of two factors related to incomplete sampling (lithification and A).

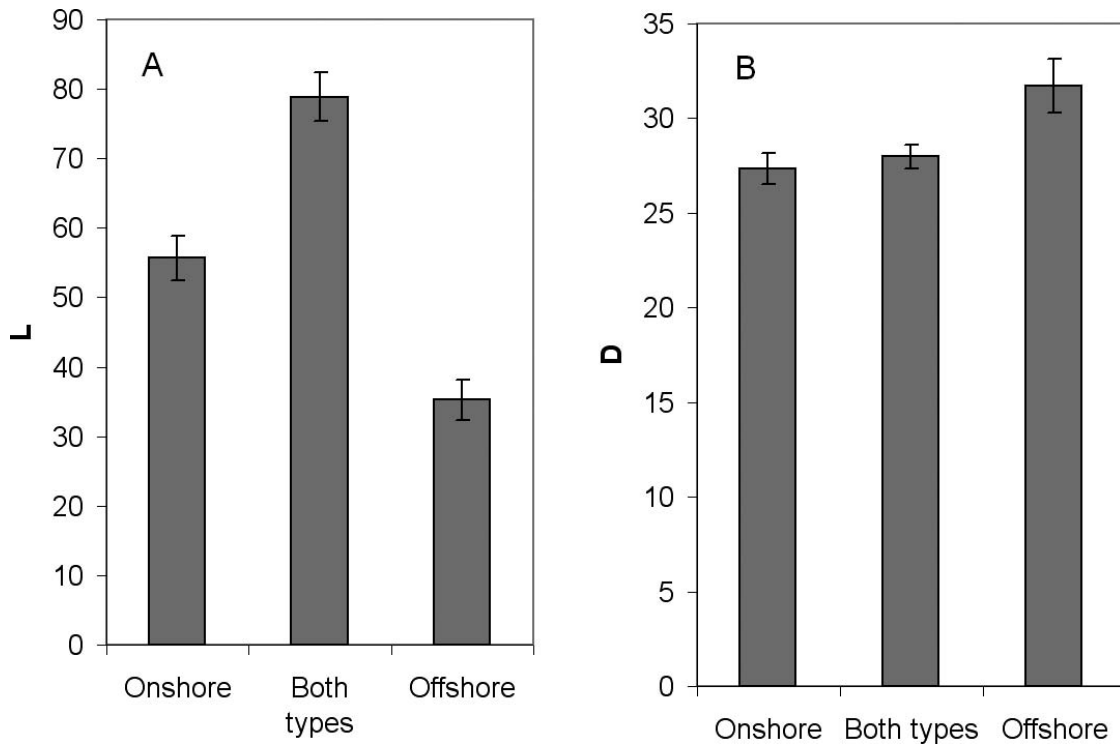


FIGURE 5. Onshore-offshore gradient affects L and D in different ways. A, Mean L of genera found in onshore collections only (3725 genera), in both types of collections (3980 genera), and in offshore collections only (2742 genera). B, Mean D in the same three groups of genera. Bars show 95% confidence intervals.

alpha-diversity dynamics (Fig. 7A) (Bambach 1977; Sepkoski 1988). This stepwise growth pattern of D supports the assumption that D can be used as a rough estimation of alpha diversity (see "Discussion"). The fact that growth patterns of L and D are so strikingly

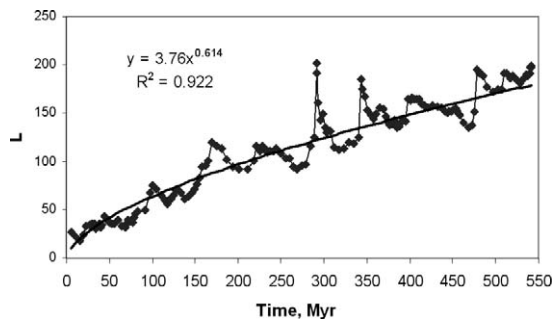


FIGURE 6. Dynamics of average longevity of marine genera (L) through the Phanerozoic. x-axis, time from the beginning of the Cambrian, Myr. y-axis, mean L of genera that existed during the geochronological interval according to SDB. All genera present both in SDB and PBDB, dated with substage or stage-level precision, are included (15,503 genera). Power trend is shown for schematic purposes only.

different does not support the suggestion that the observed growth of the two values is due solely to sampling bias (e.g., because the completeness of the fossil record decreases with age). It is possible that the Phanerozoic growth of L is partially due to random factors (the more elapsed time from the Cambrian, the higher L can potentially be); however, randomization experiments imply that the observed growth is much more rapid than expected if driven by random chance alone (Markov 2000). Notably, the growth of L is accelerated by selective extinction of younger genera and gradual accumulation of extinction-resistant genera in the biota (Sepkoski 1991a; Markov and Korotayev 2007).

However, it is reasonable to ask if the positive correlation between L and D can arise from the fact that both values were growing through time. One possible way to address this question is to consider the relationship between L and D within a subset of genera confined to some particular time interval when no

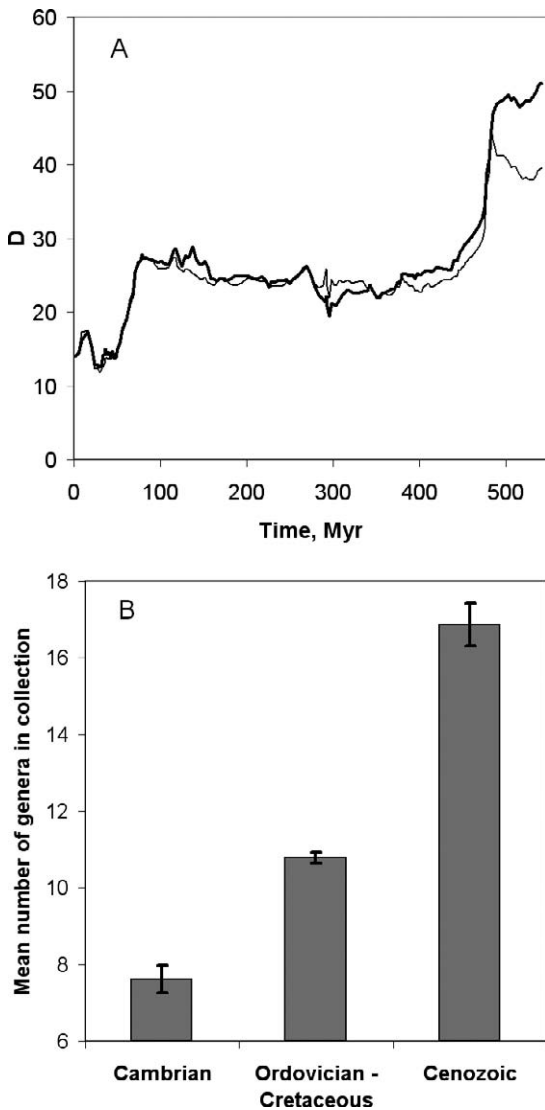


FIGURE 7. Mean genus diversity of PBDB collections grows through time. A, Changes of mean D of genera through the Phanerozoic. x-axis, time from the beginning of the Cambrian, Myr. y-axis: average D of genera in each stratigraphic interval. Thick line, all genera with stage or substage-level precision of dating of the first and last occurrences in SDB, $N = 15,503$; thin line, genera found in lithified collections only, $N = 8674$. B, Mean number of genera in the Cambrian, Ordovician—Cretaceous, and Cenozoic collections. Bars show 95% confidence intervals.

significant growth of the two values is observed. If positive correlation is still present in such a sample, then it can be concluded that this correlation is not derived from the parallel growth of L and D .

The longest interval with no significant

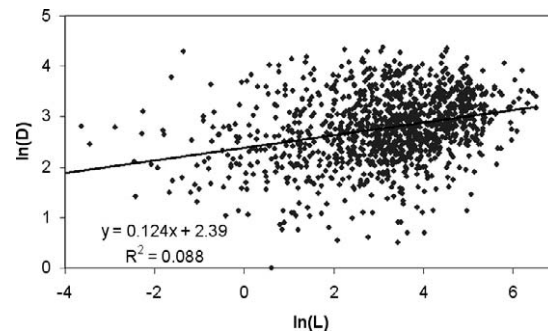


FIGURE 8. Relationship between L and D for genera found in five or more PBDB collections within the time interval from the beginning of the Late Devonian to the end of the Early Permian (1184 genera). The values of D are based on the collections from this time interval only.

growth of either L or D ranges from the beginning of the Late Devonian to the end of the Early Permian (ca. 385–271 Ma). For genera found in five or more PBDB collections from this time interval ($N = 1184$), L correlates positively with D when the latter value is based only on collections from the interval: $\ln(D) = 0.124 \cdot \ln(L) + 2.389$; $R = 0.297$, $p \ll 0.00001$ (Fig. 8). The result remains essentially the same if D is based on all collections where the genus is found, irrespective of their age: $\ln(D) = 0.134 \cdot \ln(L) + 2.400$; $R = 0.337$, $p \ll 0.00001$. The correlation remains significant when only genera from lithified collections are considered ($N = 575$), and the values of $\ln(L)$ and $\ln(D)$ are corrected for the influence of A (see section 1): $\ln(D)_{\text{corrected}} = 0.145 \cdot \ln(L)_{\text{corrected}} - 0.201$; $R = 0.279$, $p \ll 0.00001$.

Positive correlation between L and D also remains significant within shorter time intervals (10-Myr bins as described in Alroy et al. 2001). Statistical significance of correlation decreases in the Cenozoic (data not shown). This is expected because the majority of the Cenozoic marine genera are extant. The “expected” values of L were calculated for all extant genera in the same way, regardless of their ecology, taxonomic affinity, and other features. Thus there can be no correlation between the “expected” longevity and D (or any other “natural” characteristics of genera). The “expected” value of L is supposed to predict only the mean longevity of all extant marine genera, in order to make their comparison with extinct genera possible.

Therefore, the parallel growth of L and D during the Phanerozoic (considered either alone or together with other factors such as A and lithification) cannot provide sufficient explanation for the positive correlation. The correlation remains significant when no growth is observed, as was the case during the Late Paleozoic. It can be concluded that the correlation contains a time-independent component that cannot be derived from the factors related to incomplete sampling, such as lithification and encounter probability.

5. *Paleolatitude*.—Figure 9A shows the quantitative distribution of PBDB collections containing SDB genera across nine absolute paleolatitudinal zones (e.g., the second zone, 10° – 20° , comprises data on paleolatitudes from 10° to 20° S and from 10° to 20° N). The fourth zone (30° – 40°) contains the largest number of collections. Mean genus diversity of collections varies slightly with paleolatitude. On average, the most diverse collections come from midlatitudes (Fig. 9B).

In order to analyze the latitudinal distribution of genus diversity, L , and D , each genus was assigned to a single zone that corresponds to the mean absolute paleolatitude of all collections that contain the genus. The highest genus diversity in PBDB is confined to zones between 10° and 40° (Fig. 9C). It should be noted that the method used here is expected to overestimate genus diversity in higher latitudes, because the genus composition of collections tends to become increasingly different away from the equator. So genus compositions of the 10° – 20° bins on either side will be more similar than those of the 30° – 40° bins. Combining the latter bins from the south and the north inflates perceived diversity there relative to the 10° – 20° bins. However, for the purposes of the current study, it turned out to be impractical to consider northern and southern bins separately, because in this case the graphs become much more complicated and difficult to interpret, and some patterns become obscure, most probably because of sampling problems. The Southern Hemisphere appears to have been sampled in a more uneven way, both because it had much less land in intermediate latitudes, especially during the recent geological epochs, and because it is generally

less studied paleontologically (data not shown).

The latitudinal distributions of L and D are similar: both values reach their maximum at midlatitudes (30° – 60°) and gradually decline toward the equator and the poles (Fig. 9D,E). The latitudinal distribution of PBDB collections is influenced by the unevenness of spatial distribution of paleontological data presented in PBDB. 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. This is why numerous and diverse Cenozoic collections are mostly from midlatitudes, whereas the Paleozoic collections, generally less diverse, are mostly from low latitudes. The most long lived Mesozoic and Cenozoic genera are confined to midlatitudes for the same reason.

However, the latitudinal distribution of L and D may partially reflect some natural patterns. For instance, the accumulation of long-lived taxa in midlatitudes may be promoted by the fact that during major climatic changes the inhabitants of midlatitudes always have a place to retreat: they can move toward the poles in the case of global warming, or toward the equator in the case of global cooling, in contrast to species confined to either the warmest or the coldest latitudinal zones. The detailed analysis of such patterns is beyond the scope of this study.

Given that both L and D have similar latitudinal distributions (Fig. 9D,E), it is reasonable to ask if this similarity can provide explanation for the positive correlation discussed here, either on its own or together with other factors. I used the sample of 575 genera discussed in the previous section to verify this suggestion. Each genus in the sample is found (1) in five or more collections from the time interval between the beginning of the Late Devonian and the end of the Early Permian, and (2) in "lithified" collections only. Most of genera in this sample are confined to low paleolatitudes, as is the case for the majority of the Paleozoic PBDB collections (see above). Within this sample, genera from three different paleolatitudinal zones were considered sepa-

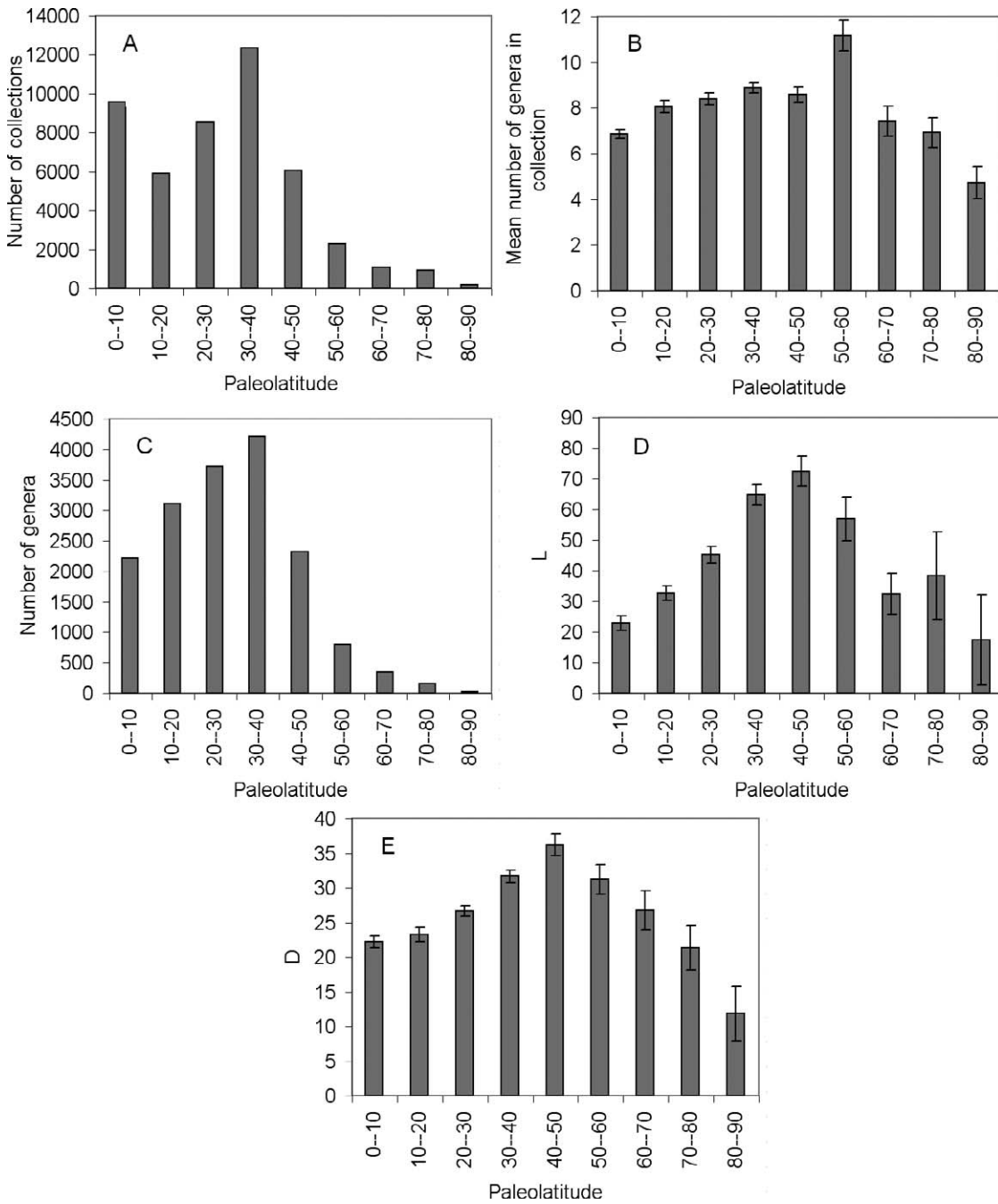


FIGURE 9. Distribution of *L*, *D*, number of PBDB collections, mean number of genera per collection, and total genus diversity across paleolatitudinal zones. x-axis, absolute values of paleolatitude (distance from paleoequator). 95% confidence intervals are shown for mean values. A, Number of collections. B, Mean number of genera per collection. C, Total number of genera. D, Mean *L* of genera. E, Mean *D* of genera. In C-E, each genus is assigned to a single paleolatitudinal zone that corresponds to the mean absolute paleolatitude of all collections that contain the genus.

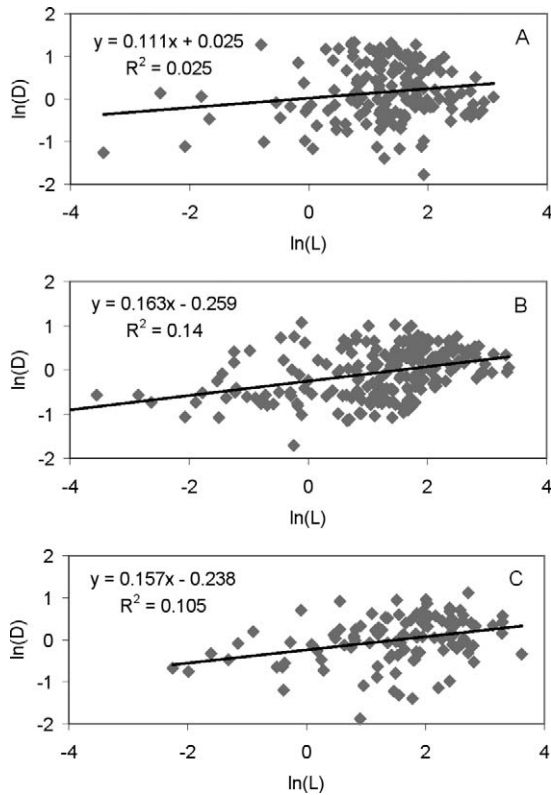


FIGURE 10. Correlation between L and D after eliminating the effects of occurrence rate, lithification, geologic time, and paleolatitude. Included are genera found in five or more collections from the time interval between the beginning of the Late Devonian and the end of the Early Permian, in "lithified" collections only. A, Genera confined to the first paleolatitudinal zone, 0° – 10° N and S (167 genera). B, 10° – 20° (220 genera). C, 20° – 30° (113 genera).

rately: 0° – 10° (167 genera), 10° – 20° (220 genera), 20° – 30° (113 genera). In all the three groups, the positive correlation between L and D (after statistically controlling for the influence of A) is significant despite the small sample size (Fig. 10): (1) $\ln(D) = 0.111 \cdot \ln(L) + 0.025$, $R = 0.159$, $p = 0.04$; (2) $\ln(D) = 0.163 \cdot \ln(L) - 0.258$, $R = 0.374$, $p = 0.00000001$; (3) $\ln(D) = 0.157 \cdot \ln(L) - 0.238$, $R = 0.324$, $p = 0.0005$.

Consequently, the correlation remains significant even after the effects of the four factors (occurrence rate, lithification, parallel growth of L and D through time, and paleolatitude) have been eliminated.

I acknowledge that the methods used in this section are too simple and imperfect to pro-

vide deep insights into paleobiogeographical problems. However, the aim of this section was not to find real paleobiogeographical patterns, but rather to explore the way in which the relationships between paleolatitude and L and D in the raw data can influence the correlation between L and D . Many intriguing questions concerning the paleobiogeographical implications of the relationship between L and D (e.g., the effects of geographic ranges of genera, migrations) remain to be elucidated.

Randomization experiments.—I used a resampling based test that builds random communities in order to demonstrate that the assemblages sampled by the PBDB collections are essentially nonrandom. The randomization test was performed as following. Occurrences of genera within each time interval (10-Myr bin) were randomly assigned to collections from the same interval, so that the number of collections within the interval remained unchanged, as well as the number of occurrences (genera) within each "collection" and the total number of genus occurrences within the interval. Thus, real collections were replaced by random assemblages of genera, while the quantitative distribution of collections and occurrences within each interval remained exactly the same. The procedure was intended not to affect stratigraphic distribution of genera significantly, so that it would be possible to use the old ("real") values of L and A for comparison with the new ("randomized") values of D . Calculations of new D values were based on the randomized data set.

Randomization produced a dramatic effect on the relationship between L and D . The positive correlation between L and D became generally weaker in large samples, and almost (or completely) disappeared in smaller samples, e.g., in samples confined to limited stratigraphic intervals and/or latitudinal zones.

For instance, in the large sample used in Figure 3 (genera found in ten or more collections, $N = 5569$), the correlation between L and D can be approximated by the equation $\ln(D) = 0.173 \cdot \ln(L) + 2.44$; the regression slope equals 0.173 ± 0.010 (95% confidence intervals). After randomization, the regression slope went down to 0.094 ± 0.006 . Pearson's

correlation coefficient and the p -value also decreased.

In medium-sized samples, like the one used in Figure 8 (genera found in five or more PBDB collections within the time interval from the beginning of the Late Devonian to the end of the Early Permian, $N = 1184$), the effect of randomization was even more prominent. The regression slope decreased from 0.134 ± 0.021 to 0.035 ± 0.012 ; Pearson's correlation coefficient (R) decreased from 0.337 to 0.167; p from $7 \cdot 10^{-23}$ to $7 \cdot 10^{-9}$.

In various small samples the correlation disappeared altogether. For instance, in the sample of 312 genera (found in five or more PBDB collections within the time interval from the beginning of the Late Devonian to the end of the Early Permian, assigned to the "equatorial" paleolatitudinal zone), the regression slope dropped from 0.085 ± 0.050 to -0.008 ± 0.026 ; Pearson's correlation coefficient from 0.185 to 0.032; p from 0.001 to 0.568.

Randomization also resulted in a dramatic decrease in variation of D , although the mean values of D remained almost unchanged. For the sample used in Figure 4 (genera found in ten or more PBDB collections, $N = 5569$), mean values of D before and after randomization are very similar (24.88 and 24.99 respectively), whereas standard deviation dropped from 17.05 to 11.14. These results imply that random factors alone cannot explain why some genera have very high D , whereas others have very low D . However, the negative correlation between A and D persisted after randomization and became only slightly weaker. This fact indicates that negative correlation between A and D probably arises from random factors and may bear no significant biological signal. In the randomized data set, the correlation is apparently due to the fact that rare genera tend to be found in large assemblages just because they are large, the probability for each generic occurrence to be found in a given assemblage being proportional to the size of the latter.

The results of the randomization test may be difficult to interpret in detail, because the randomization procedure affected different variables and distributions in different ways. Generally, the results indicate that PBDB col-

lections are quite different from random assemblages, as far as the values of D are concerned.

It is not at all unexpected that the positive correlation between L and D did not disappear completely in all samples after randomization. It is evident from the previous sections that the correlation is affected by several different factors, including those that were not affected by the randomization procedure (e.g., the simultaneous growth of mean L and D through the Phanerozoic, and the effects of A). Therefore randomization was expected to remove the correlation between L and D only partially, or to make it weaker.

Discussion

Reliability of the Fossil Record and the Data Sets Used.—It is widely acknowledged that various sampling biases may distort the macroevolutionary patterns observed in the fossil record. It is also recognized that both data sets used in this study, the Paleobiology Database and Sepkoski's classic compendium, may be replete with biases (Alroy et al. 2001; Peters and Foote 2001; Peters 2005; Smith 2007). For instance, the stratigraphic ranges of many taxa are expected to be truncated because of incomplete sampling (Foote 2007). Several possible sources of artifacts are taken into account in this study (see "Results"). However, there is evidence that the paleontological record is representative and robust enough to adequately reveal many important quantitative patterns of evolution (Raup 1987; Sepkoski 1993; Benton 1999; Foote and Sepkoski 1999; Benton et al. 2000; Miller 2002; Bush and Bambach 2004; Bambach et al. 2007). For instance, although the observed stratigraphic ranges of genera may be truncated, it is obvious that actual longevity of genera is, on average, a very important factor that affects their "observed" longevity.

Several different correction techniques and sampling standardization procedures have been developed, but they are generally not regarded as adequate and comprehensive enough to be universally accepted and applied (Alroy et al. 2001; Bush et al. 2004). Importantly, some of them may even make things worse than they are, compared to the

“raw” data sets. For instance, the increase in average collection size through the Phanerozoic, a very prominent trend observed in the raw PBDB data, is affected by several different biases that may largely cancel out each other’s effects (Bush and Bambach 2004).

Alroy et al. (2001) suggested that this trend was due to the fact that younger strata were being better sampled, partially because of a higher proportion of collections coming from unlithified rocks, and applied sampling standardization procedures to correct for this bias.

Results of the present study contradict the hypothesis that the observed increase in alpha diversity through the Phanerozoic is an artifact of lithification. Stepwise growth of mean D through time (Fig. 7A) apparently arises from the increase in alpha diversity. It is noteworthy that this growth is only slightly less prominent within the subsample of genera found in lithified collections only (Fig. 7A, thin line) than in the whole sample (Fig. 7A, thick line). Mean D of genera from lithified collections is slightly lower in the Cretaceous and considerably lower in the Cenozoic, compared to the whole sample, but the general pattern is essentially the same.

Notably, plate tectonics may be the source of another bias that produces an opposite effect. As mentioned above, a second trend in the PBDB data is for collections to come predominantly from Western Europe and North America; these regions were near the equator during the Paleozoic but shifted to temperate latitudes by the Cenozoic. Because tropical marine communities tend to be, on average, more diverse than temperate ones, this trend is expected to diminish the observed rate of growth in collection size. Bush and Bambach (2004) performed a comprehensive analysis of the two trends and concluded that the bias introduced by plate tectonics might be stronger than the bias of sampling intensity; the observed increase in alpha diversity, therefore, was probably underestimated rather than overestimated by the “raw” data (the positive correlation between alpha diversity and collection size is discussed below). Thus, sampling standardization procedures designed to correct for the sampling bias may actually make things worse.

Until the correction procedures that take the geological processes into account become sufficiently well developed, analyses of fossil biodiversity in its present-day state still appear credible (see Smith 2007 for the contrary view; see also Benton and Emerson 2007 for detailed discussion of the current debates concerning the incompleteness of the record).

Mean Taxonomic Diversity of Paleontological Collections.—Of course, one cannot use the number of genera in any given collection as a reliable and precise measure of underlying alpha diversity. Taxonomic diversity of paleontological collections is affected by many factors, e.g., (1) collection purpose and methods; (2) degree of sediment lithification; (3) other factors affecting the preservation of fossils and the effort needed for their extraction and identification; (4) time-averaging (Kidwell 1998); and (5) evenness of distribution of genus abundances (Powell and Kowalewski 2002).

However, actual alpha diversity of the paleocommunity (-ies) sampled by the collection is also an important factor affecting its taxonomic diversity. Thus a positive correlation between average alpha diversity and average taxonomic diversity of collections (in large samples of collections) is expected.

This assumption can be verified by comparing the general pattern of alpha diversity changes through the Phanerozoic as revealed by special research (Bambach 1977; Sepkoski 1988; Bush and Bambach 2004) with the temporal dynamics of collection size in PBDB. The similarity of the two patterns would support our assumption.

Marine alpha diversity was growing in a stepwise manner. The three steps correspond to (1) Cambrian, (2) Ordovician—Cretaceous, and (3) Cenozoic (see “Introduction”). In accordance with this pattern, average genus diversity of collections in PBDB also increase through time (Fig. 7B). There are, on average, 7.614 genera in each Cambrian collection ($N = 1163$), 10.792 genera in each Ordovician—Cretaceous collection ($N = 24,963$), and 16.864 genera in each Cenozoic collection ($N = 5381$). All differences are significant ($p \ll 0.00001$, two-tailed t -test) (collections with fewer than three genera were excluded from this calculation). Overall growth of genus diversity of

PBDB collections through time can be approximated by the linear function $y = 0.011 \cdot t + 8.332$, where y is the number of genera in a collection, t is time from the beginning of the Cambrian, in Myr ($R = 0.137$, $p \ll 0.00001$). The stepwise growth of alpha diversity is perfectly reproduced by the stepwise growth of average D of genera (Fig. 7A), the three steps being essentially the same as those discovered by Bambach (1977) and Sepkoski (1988).

These results indicate that it is admissible to use genus diversity of PBDB collections as a very rough estimation of alpha diversity in large samples. Correspondingly, D can be used as a proxy of tendency of a genus to live in complex (or simple) communities.

It can be argued that only multi-taxic collections can be used for alpha diversity studies. In this study, however, all collections were included in the analysis, regardless of their taxonomic diversity. This approach was based on the assumption that genera adapted to simple biotic environments are expected to be found in collections with very low taxonomic diversity more frequently than genera adapted to complex biotic environments, and therefore data on such collections are not likely to be meaningless in the context of the study. It should be acknowledged that a genus may have low D due to various taphonomic and sampling reasons rather than ecological ones. However, the results remain essentially the same if the least diverse collections are excluded from the analysis, because small collections, although numerous, appear to affect the calculated values of D only very slightly. For instance, collections with only one or two genera constitute about one-third of the total number of collections in the data set (see "Materials and Methods"), but they contain only about one-sixteenth (20,592 out of 327,932) of the total number of genus occurrences. Thus the values of D based on all collections (D_{all}) are identical or almost identical to those based on collections with three or more genera ($D_{>2}$) for the majority of genera. Correlation between D_{all} and $D_{>2}$ is strictly linear and very strong; the regression slope is very close to 1 ($D_{>2} = 0.996 \cdot D_{\text{all}} + 0.791$; $R = 0.995$; $p \ll 0.00001$). These facts indicate that collections

with the lowest taxonomic diversity do not affect the resulting values of D significantly.

Negative Correlation of A with L and D.—Negative correlations between A and L and between A and D may seem unexpected and intriguing. It can be argued that negative correlation between A and L arises from the incompleteness of the fossil record in general and of PBDB in particular. This suggestion is based on the following facts. Remember that $A = N_1/N_2$, where N_1 is the number of collections where the genus is found, and N_2 is the total number of PBDB collections within the stratigraphic interval of the genus. There is a strong positive correlation between L and N_2 ($R = 0.697$, $p \ll 0.00001$), because the number of PBDB collections that fall within the time interval automatically increases when the interval becomes longer. There is also a positive correlation between L and N_1 , but this is much weaker ($R = 0.190$, $p \ll 0.00001$), largely because of incomplete and uneven sampling. For instance, many long-lived genera are found only in one or two PBDB collections, although short-lived genera are rarely found in many collections (data not shown). Therefore, increasing L generally promotes strong increase of N_2 and only feeble increase of N_1 ; hence the negative correlation between L and A .

Negative correlation between A and D is probably also due to incomplete sampling. The proportion of genera with low probability of fossil preservation is apparently higher among genera with a low occurrence rate. Such genera are more likely to be collected by paleontologists either if the locality is characterized by exceptionally good preservation of fossils or if the sampling effort is extremely high. In either situation high genus diversity of the collection is expected.

Alternative explanations are possible. It has been suggested that many marine animal species are capable of surviving for long periods of time with little or no evolutionary change by habitat tracking, that is, moving in and out of particular area as the environmental gradients change through time (Bonuso et al. 2002; Brett et al. 2007). Thus they can also move in and out of sampling windows determined by sequence stratigraphy and rock availability, so that their observed stratigraphic

ic ranges may become, on average, more truncated. If habitat tracking is more typical of abundant taxa than of rare ones, then this pattern could induce the observed negative correlation between A and L . This is probably not the case, however, because habitat tracking is typical of stenotopic species rather than of eurytopic ones (Brett et al. 2007). Eurytopic species, on average, tend to have wider geographic distributions, and therefore they are expected to have higher A than stenotopic species. More research is needed to address intriguing questions concerning possible relationships between the geographic ranges of taxa and their A , D , and L .

It can be argued that A is sensitive to the fact that SDB is focused entirely on range endpoints, whereas PBDB makes no attempt to recover the full range of a genus. It is possible, then, that a genus will be well sampled throughout its range in PBDB, but will have a much wider range in Sepkoski's data set and will therefore have a depressed A . In order to check if the two data sets can be combined in this way, I recalculated A for each genus using its stratigraphic range from PBDB instead of SDB. The results were essentially the same: both negative correlations (between A and L and between A and D) were still present and highly significant (for genera found in ten or more PBDB collections, $R = -0.303$ for the former correlation, -0.321 for the latter; $p \ll 0.00001$ in both cases, $N = 5569$). These results indicate that the correlations are robust to the way in which stratigraphic ranges and longevities of genera are estimated. The same is true for the positive correlation between L and D (see "Results").

Onshore-Offshore Trends.—As shown in Figure 5, mean longevity is somewhat higher in genera found in onshore collections than in those confined to offshore collections. This fact may seem to contradict the widely acknowledged notion that taxonomic turnover rate tends to increase onshore because nearshore environments are generally less stable. However, even though genera within individual taxonomic classes do tend to have their highest extinction onshore, whole communities exhibit increasing extinction offshore (Jablonski et al. 1983; Sepkoski 1987). The off-

shore trend at the community level results from a concentration of genera in classes with low characteristic extinction rates in nearshore environments (Sepkoski 1987). Notably, the variance in extinction rates among environmental zones is less than the variance among taxonomic orders and classes (Sepkoski 1987, 1991a). The model suggested by Sepkoski (1991a) predicts that, if extinction intensity is highest in nearshore habitats, extinction-resistance clades will expand preferentially in the onshore direction, build up diversity there, and then diversify outward toward the offshore. In general, lower environmental stability near shore leads to gradual accumulation of extinction-resistant (and eurytopic) taxa in the onshore habitats. These considerations appear to provide sufficient explanation for higher L in onshore collections. Additionally, the fossil record of the onshore habitats is generally more complete, and therefore the observed stratigraphic ranges of taxa may be less truncated by incomplete sampling.

In accordance with previous findings (Sepkoski 1988, 1991a), the results of this study show that offshore collections are slightly more diverse than onshore collections. Given that the offshore communities tend to have higher alpha diversity, genera that are found only in offshore collections are expected to have higher D than those restricted to onshore collections. This is indeed the case (Fig. 5B).

Interestingly, the global positive correlation between L and D is not reproduced by an interzonal comparison (although it is present within each individual zone). Whereas L tends to increase onshore, D appears to increase offshore. However, this does not mean that alpha diversity is not promoting genus longevity throughout the shelf. Generally, the results presented in this study demonstrate that L and D depend on many different factors. Some of them (e.g., negative relationships between A and D and between A and L , lithification bias, simultaneous growth of L and D through time, as well as the suggested causal relationship between alpha diversity, stability of communities, and longevity of genera) tend to strengthen the global positive correlation between L and D , whereas others, like onshore-offshore patterns, appear to work in the

opposite direction, making the correlation weaker. The net outcome of the competing trends is that the latter group of factors is overridden by the former.

A detailed analysis of distribution and temporal dynamics of L and D within individual clades may provide additional insights into the nature of the global correlation between the two variables, but this is beyond the scope of the present study.

Alternative Explanations of the Observed Correlation between L and D .—The results of this study generally confirm the prediction that higher alpha diversity may facilitate stability of taxa and improve their ability to resist extinction. One possible explanation of the observed correlation between L and D is that diverse communities are more stable and “buffered,” and therefore genera confined to such communities are less likely to become extinct compared to genera that live in less diverse and more vulnerable communities (see “Introduction”). Alternative explanations are also possible. It can be argued that the causal relationship between alpha diversity and longevity of genera may work in opposite directions: high alpha diversity may result from the fact that genera within the community are long-lived and extinction-resistant. It is difficult to distinguish between the two possibilities, and the problem is further complicated by the fact that extinction-resistant clades are expected to accumulate in unstable environments (e.g., onshore), where the extinction risk is generally higher, whereas extinction-prone clades retreat to more stable environments (e.g., offshore) (Sepkoski 1991a). This pattern appears to work against the positive correlation between alpha diversity and longevity (e.g., onshore communities are less diverse and at the same time they contain genera with higher average longevity), but it is apparently overridden by other factors and relationships.

Longevity of genera can be influenced by different factors, including random ones. Notably, geographic range of genera is known to correlate positively with geologic duration (Jablonski and Hunt 2006; Jablonski 2007; see also Russell and Lindberg 1988 for discussion of biases that may affect this correlation). An-

other important factor that can enhance longevity of a genus is species richness. This may be one reason why several post-Paleozoic mass extinction recovery cohorts were significantly longer lived than other cohorts (Miller and Foote 2003).

The volume of ecological space occupied by (or potentially available to) a genus is arguably the most important factor that moderates its longevity, geographic range, and species richness. Because eurytopic genera tend to be less extinction-prone than stenotopic genera, they are more likely to have longer durations. They are also expected to be found in varying environments and to have wide geographic ranges. It can be also argued that eurytopic genera may be more easily adaptable to complex biotic environments, and therefore more likely to be found in diverse communities, where the resources are plentiful but competition is high. Another possibility is that a complex biotic environment may facilitate the development of multipurpose adaptations (e.g., complex nervous system, flexible behavior and ability to learn), and this, in turn, may make genera less extinction prone. More research is needed to evaluate relative probabilities of these and other possible explanations. Generally, the observed correlation between L and D supports (although does not definitively prove) the idea that there may be a positive feedback between diversity and its rate of growth, as implied by the hyperbolic character of diversity growth in the Phanerozoic (Markov and Korotayev 2007), and that this feedback may be mediated by some kind of causal relationship between alpha diversity and extinction rate.

Conclusions

The results obtained in this study imply that positive correlation between L (an approximate measure of genus longevity) and D (a very rough estimate of alpha diversity) (1) is possibly not an artifact and may bear a natural biological signal; and (2) may represent a direct or indirect causal relationship between alpha diversity of communities and longevity of taxa. The results support the hypothesis suggested to explain the hyperbolic character of the growth of marine biodiversity in the

Phanerozoic (Markov and Korotayev 2007). I have argued that higher alpha diversity probably could facilitate longevity of genera because diverse communities are more stable, and because ecosystems with high level of genus or species diversity may develop negative feedback loops and other homeostatic mechanisms. It is also possible that living in a diverse community may, by facilitating the development of multifunctional adaptations, enhance the adaptability of taxa so that they become more “buffered” and extinction-resistant. I acknowledge that there may be other possible explanations for the pattern observed, and that there may be other factors that can theoretically act as a “common cause” of coordinated changes of *L* and *D*. Further research should draw more light on the relationship between alpha diversity and longevity of taxa.

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