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MATTERS OF THE RECORD

Theoretical diversity of the marine biosphere

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In considering the history of biodiversity paleontologists have focused on exploratory investigations of empirical data derived from the fossil record. Starting with the pioneering work of Philips (1860), and continuing at an increasing pace through today, this inductive approach has dominated diversity research. In contrast, deductive theoretical considerations that focus on the expected history of biodiversity, and develop independently of empirical knowledge, have remained underexplored. Appreciating the need for a nomothetic paleobiology (Gould 1980), we here reconsider the history of biodiversity, using deductive models constrained by a few, self-evident parameters. This analysis centers on the marine fossil record, the primary target of most previous empirical studies on the geological history of global biodiversity (e.g., Valentine 1969; Raup 1972, 1976; Sepkoski et al. 1981; Alroy et al. 2008).

Biosphere-scale studies of the geological history of diversity have followed two general strategies: (1) analyses of global-scale literature and meta-analytical compilations of fossil ranges and occurrences (e.g., Sepkoski 1981, 1984, 1993; Sepkoski et al. 1981; Benton 1995; Alroy et al. 2001, 2008; Stanley 2007); and (2) local-scale (alpha) abundance-diversity analyses of sets of quantifiable bulk samples, preferably with broad geographic coverage (e.g., Bambach 1977; Powell and Kowalewski 2002; Bush and Bambach 2004; Kowalewski et al. 2006; Wagner et al. 2006; Alroy et al. 2008). Given this empirical focus, it is not surprising that most of the process-oriented hypotheses and theoretical models proposed over the years represent inductive strategies—a posteriori explanations of preexisting empirical patterns. The logistic growth model (e.g., Sepkoski 1981, 1984), the unconstrained exponential model (Stanley 2007; see also Bambach 1999), rock-volume/sea level effects (e.g., Raup 1972; Peters and Foote 2001; Peters 2006), and "Pull-of-the-Recent" (e.g., Jablonski et al. 2003) are just a few examples of explanations that develop from, are evaluated against, or are motivated by preexisting data. Thus, whereas deductive approaches have been used in macroevolutionary contexts (e.g., Raup 1966; McShea 1994; Holland 1995; Niklas 1997), the history of global biodiversity has been considered primarily from the inductive standpoint. Consequently, some fundamental questions remain largely unaddressed. Can we infer from first principles what the upper bound of global biodiversity is? Is it possible, given the basic physical and biological parameters of the marine biosphere, to estimate the expected biodiversity of the modern oceans? What sorts of diversity histories do we predict when we consider how these physical and biological parameters may have changed through time? Could diversity have changed by many orders of magnitude through time or is such volatility theoretically prohibited?

Here we outline a series of simple deductive models for discerning theoretical attributes of global marine biodiversity indepen-

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dent of, and largely uninformed by, empirical data from the fossil record or modern oceans. The models aim to derive constraints from first principles, rather than from empirical data (e.g., Sepkoski 1981, 1984) to provide deductive inference regarding various aspects of the global marine biodiversity including, for example, upper limits to global diversity (carrying capacity of MacArthur and Wilson 1967; Sepkoski 1981, 1984), long-term temporal volatility in diversity levels, or mathematical relations between basic macroecological parameters (such as body size distribution patterns) and the expected global diversity. And although some empirical parameterization is required, the initial model constraints are limited to basic values such as ranges of possible body sizes or an approximate ocean volume.

We hope that this admittedly simplistic deductive exercise will help to establish an initial framework for developing heuristically useful models that would complement empirical research on diversity. We refer to this concept here as "theoretical diversity." Like the Drake Equation (Drake and Sobel 1992), it represents a first explicit, if possibly misguided, step toward considering a major and complex question from a purely theoretical perspective: how many species should we expect to find in the global oceans, given only the most fundamental constraints, and how much should we expect this number to have changed throughout geological time? Our approach is intentionally naïve and somewhat tongue-in-cheek, but is intended to start a conversation that may ultimately lead to far more sophisticated and realistic models, perhaps by considering diversity from a thermodynamic perspective (e.g., Allen et al. 2002) or by marrying recently developed models for the generation and maintenance of diversity (e.g., Chow et al. 2004) to physical models simulating the distribution of energy and nutrient resources in the oceans.

Defining Theoretical Diversity Using the Simplest Model

Many forcing mechanisms have been postulated to have influenced the history of global biodiversity, including intrinsic genetic mechanisms (e.g., hox gene clusters), biotic factors (e.g., niche engineering, ecospace utilization, and ecological interaction), and extrinsic abiotic factors, including sea level changes, supercontinent cycle, ocean chemistry, climate, cosmic ray flux, bolide impacts, and many other causative drivers (e.g., Sepkoski 1984; Vermeij 1987; Benton 1995; Stanley and Hardie 1998; Peters 2006; Bambach et al. 2007; Huntley and Kowalewski 2007; Erwin 2008; Trotter et al. 2008; and numerous references therein). Various biasing factors, including variation in the type and amount of preserved sedimentary rock (Raup 1972; Peters and Foote 2001; Smith and McGowan 2007), sampling accessibility/intensity (e.g., Raup and Sheehan 1977; Alroy et al. 2001, 2008), latitudinal distribution of paleocontinents (Allison and Briggs 1993), taphonomic and time-averaging artifacts (e.g., Raup 1972; Kowalewski and Flessa 1996; Cherns and Wright 2000; Bush and Bambach 2004; Tomašových and Kidwell 2009), and sampling methodology related to lithification (e.g., Kowalewski et al. 2006; Hendy 2009; Sessa et al. 2009), have been invoked as important, if not primary mechanisms.

Although the number of credible forcing and biasing factors is not overwhelming, they are complexly linked and interdependent in a way that makes it difficult to translate them into numerical parameters applicable from a theoretical standpoint. For example, despite the correlation between mean temperature (a putative energy proxy [see Clarke and Gaston 2006]) and diversity in the modern oceans (e.g., Roy et al. 2000; Allen et al. 2002) and in the fossil record (e.g., Stanley and Powell 2003; Hunt et al. 2005; Powell 2007; Trotter et al. 2008), it is impossible to predict by how much we should expect global diversity to change following, for example, a 2°C global cooling over a period of 1.2 Myr. Moreover, any such estimate would at present have to be derived from empirical data provided by the fossil record.

We will not offer a solution to this problem here, but hope to start the long process of working toward a realistic deductive model of global biodiversity by beginning with the most fundamental question: what is geometrically possible when populating marine ecosystems with taxa? That is, rather than asking how causative forces can shape biodiversity, we can ask how many species could, theoretically, be packed into the three-dimensional space defined by the oceans? In the simplest rendering of this question, global marine diversity (B), expressed as the total number of marine species (species richness), is a function of four parameters: (1) volume of potentially inhabitable space (E_V) that can be physically occupied by organisms, expressed here in m^3; (2) the proportion of that inhabitable space (E_V) that is actually occupied by organisms (E_O), expressed as a percentage of E_V; (3) the average population size of a species (A_{PS}), expressed as mean number of specimens per species; and (4) the average body volume represented by an average specimen size within a given species (A_{BS}), expressed in m^3. The generalized formula for maximum global marine biodiversity is then as follows:

$$B = \frac{E_V E_O}{A_{PS} A_{BS}} \tag{1}$$

That is, B increases linearly in relation to the size of the occupied ecosystem volume and is inversely proportional to the average biovolume occupied by all individuals representing a given species (a product of A_{BS} and A_{PS}). A somewhat refined variant of this crude formula is used below to model theoretical diversity, while making the following a priori assumptions and parameterizations:

1. In this initial parameterization, the present-day ocean volume of ~1.3*10^{18}m^3 (Garrison 2005) is taken as a constant, so the parameter E_V is a fixed coefficient. Note that in reality E_V is a parameter, and not a fixed coefficient (its behavior is explored in detail below). The fixed coefficient is used initially because even though ocean volume varied through the Phanerozoic, this variation is trivial compared with other modeled parameters. A sea level drop of 100 m in an ocean that has a footprint of 360 million km^2 reflects a volumetric change of ~3%; by comparison E_O, A_{PS}, and A_{BS} can all vary potentially by many orders of magnitude. Obviously, the area occupied by shelf and epeiric seaways may be an underappreciated variable here because of their volatile response to sea level changes, so the impact of sea level changes on diversity should not be dismissed (e.g., Schopf 1974; Peters 2006). Likewise, only certain zones in the ocean may be conducive to the presence of abundant life (e.g., photic zone, mid-oceanic ridges, sediment-water interface) and the potentially habitable volume can change through time dramatically for various reasons (e.g., a shift from anaerobic deep oceans in the Precambrian to aerobic oceans of today may have affected the value of E_V, making it a volatile parameter and not a static coefficient). These issues will be explored in more detail below, but, initially, to keep our analysis as straightforward as possible, we assume a constant volume of inhabitable space.
2. Average individual body size is expressed below as diameter (D) reported in meters. This is a more intuitive depiction of body size than the volumetric measure A_{BS} used in equation (1) above. Body diameter is then converted into occupied biovolume A_{BS} by using the following formula:

$$A_{BS} = 1.35 \frac{4}{3} \pi \left(\frac{D}{2}\right)^3 \tag{2}$$

where biovolume is computed for a perfectly spherical organism of diameter D, and 1.35 is a constant that corrects for hexagonal or cubic packing of spherical organisms in three-dimensional space. This formula assumes that organisms are packed into the oceans like oranges at the supermarket, with maximal geometric efficiency. This is clearly a gross distortion given both inter- and intraspecific variation in size and shape. However, equation (2) is certainly adequate for this exercise where accuracy and precision within an order of magnitude are sufficient.
3. The biovolume occupied by the average species is a product of A_{BS} and A_{PS}. Consequently, equation (1) is applicable

only when population sizes (number of individuals per species) are constant across all species (i.e., a biosphere with perfect evenness) and all species have the same body size. These are self-evidently false premises. For example if dominant taxa tend to be small bodied and rare taxa tend to be large bodied (not an unreasonable expectation; see below), averaging body sizes without weighting them by the population sizes of respective species would severely overestimate the total biovolume of marine biosphere. Any serious empirical attempt to estimate the total biovolume of the marine biosphere requires either computation of the average body size of each species weighted by its population size (a purely inductive proposition with unrealistic data requirements) or integration of these two parameters as a function of mathematically related variables (a more feasible and less inductive approach, which we explore below). However, as is always the case with theoretical models, it is instructive to start with the simplest case.

Given this set of assumptions and simplifications, global marine biodiversity (B) can be represented by the following three-parameter function:

$$B = \frac{1.3 \cdot 10^{18} E_O}{A_{PS} A_{BS}} \tag{3}$$

A SAS/IML code developed from equation (3) and used to generate Figure 1 is included as Appendix 1 here. Obviously, this equation is thermodynamically indefensible because the diversity of the oceans cannot be regulated by the availability of space per se. Rather, in addition to the spatial packing limitation discussed above, any serious deductive model should also, at the very least, account for the limits imposed by the availability of nutrients and energy (with which to build and power bodies), oxidants to fuel metabolism, and substrates, all of which are dependent on body size distributions. Although our model does not incorporate these limitations explicitly, it does express them crudely via the parameter E_O, which constrains the ecospace occupancy rate. Thus, by decreasing the value of E_O, the model explicitly corrects for the fact that not all available ocean volume can be occupied for all the obvious reasons listed above. By varying the parameter E_O over a wide range of percentage values, the potential quantitative impact of resource constraints on the modeled diversity levels can be explored. Empirical constraints on E_O will be also considered below.

Parameterization of the Simplest Theoretical Diversity Model

The theoretical maximum diversity of the oceans can be calculated by assuming that (1) all diversity is represented by the smallest functional taxa that are capable of opportunistic metabolism (e.g., not restricted to a given spatially limited resource such as the photic zone); (2) resource acquisition is independent from population density (e.g., no shading of sunlight by other photosynthetic organisms); (3) each species is represented by just one specimen ($A_{PS} = 1$); and (4) ecospace occupancy is 100%. That is, the oceans are completely packed with taxonomically unique specimens all representing the smallest possible species. The recently reported prokaryotic organism *Nanoarchaeum equitans* (Huber et al. 2002) has a diameter of ~0.4 μm but is an obligatory symbiont. However, comparably small, or even smaller, self-sustaining ultramicrobacteria exist (Torrella and Morita 1981). A bacterium with a diameter of 0.4 μm has a body volume of $\sim 3.3 * 10^{-20}$ m^3, which translates into an occupied space (eq. 2) or A_{BS} of $4.51 * 10^{-20}$ m^3. Plugging this value of A_{BS} into equation (3) (and constraining other parameters with the four assumptions listed at the start of this paragraph) yields a ludicrously high upper bound for the marine biosphere of $2.9 * 10^{37}$ species, which exceeds by ~30 orders of magnitude the high-end estimates for global marine biodiversity today (Sala and Knowlton 2006 and references therein; but see Lambshead 1993; Bouchet et al. 2002), and almost certainly exceeds the number of individual organisms alive in the oceans at any instant.

Even when more reasonable upper-bound values are chosen, absurdly high diversity estimates result. For example, if we assume the minimum size of preservable (biomineralized) organisms at $A_{BS} = 8.8{*}10^{-14}$ m^3 (which corresponds to a coccolithophore with a diameter of 25 μm), and a respectable minimum viable population size ($A_{PS} = 10^6$ individuals), and allow for only a small fraction of ocean volume to be occupied by biomass ($E_O = 0.5\%$), the resulting diversity value of ~$6{*}10^{23}$ species approximates Avogadro's number and exceeds high-end estimates of marine biodiversity by ~16 orders of magnitude.

If we limit the estimate to metazoan animals (to make it most relevant to the existing empirical data), we still arrive at an unreasonably high upper bound. A biosphere populated by minute metazoans (e.g., ostracodes, roundworms) with an average diameter of ~1 mm, a viable population size of 10^6 individuals, and 0.5% ecospace occupancy would still contain nearly 10^{19} species. Even if we assume an extremely low ecospace occupancy of 0.0001%—a proposition more than feasible thermodynamically—such a biosphere would still include more than 10^{15} species.

The above estimates assume that E_V (the inhabitable ecospace volume) is a fixed, maximized value, where the entire volume of the ocean is habitable. Realistic constraints on E_V need to be considered when evaluating the maximum feasible biodiversity. Let us therefore consider an aggressive parameterization that imposes stringent limits on E_V. If the habitable zone is restricted to a mere 10-m-thick layer of ocean water—this restriction assumes an unrealistically thin photic zone, a two-dimensional benthic habitat (no infaunal organisms), and the total absence of bioproductivity outside photic zones (e.g., zones of upwelling, mid-ocean hydrothermal systems)—the value of E_V would be reduced to a still respectable value of $3.6{*}10^{15}$. Even if we assume 0.01% ecospace occupancy in this restricted habitable space, we still end up with an upper bound of global biodiversity of over 10^{14} species.

It is clear that the theoretical physical carrying capacity of the oceans massively exceeds empirical estimates of biodiversity in the oceans, even when reasonable parameter values are assumed. However, the graphic visualization of equation (3) (Fig. 1) suggests that we can easily shift down from these ludicrous diversity levels by varying the relevant parameters within a realistic range of values. Theoretically, anything is possible: from a monospecific biosphere (with just one species occupying all available ecospace) to an absurdly diverse one, where more than a mole of species share the oceans at the same time. Empirically estimated diversity levels of 10^6–10^7 species for present-day marine ecosystems (e.g., Sala and Knowlton 2006; but see Lambshead 1993) can be arrived at for a very wide range of parameter values, with average per-species population size ranging over many orders of magnitude, average body size varying from coccolith-sized species (D = 25 μm) to giant-ammonite-sized species (D = 1 m), and occupancy of only an infinitesimal fraction of ocean volume (as obvious from the graph, ecosystem occupancy levels that are multiple orders of magnitude smaller than 0.01% used on the plot can also produce present-day levels of diversity within an intuitively realistic range of values for the other two parameters).

The theoretical diversity space remains vast even when the assumed Ecospace Volume is constrained to a 10-m-thick layer of ocean water (Fig. 1B). This constraint merely shifts all curves down along the y-axis by less than three orders of magnitude (compare Fig. 1A and Fig. 1B)—a trivial change in theoretical biodiversity, when considering its potential range of 30+ orders of magnitude. Unsurprising, theoretical diversity is extremely volatile when modeled in this barely constrained fashion. A more sophisticated theoretical model is needed to acknowledge and explore intuitively obvious interdependencies that must exist among the parameters that constrain theoretical biodiversity.

Toward (Slightly) More Realistic Theoretical Biodiversity Models

The most obvious set of interdependencies concerns the relationships among body size, population density, and diversity. A simple

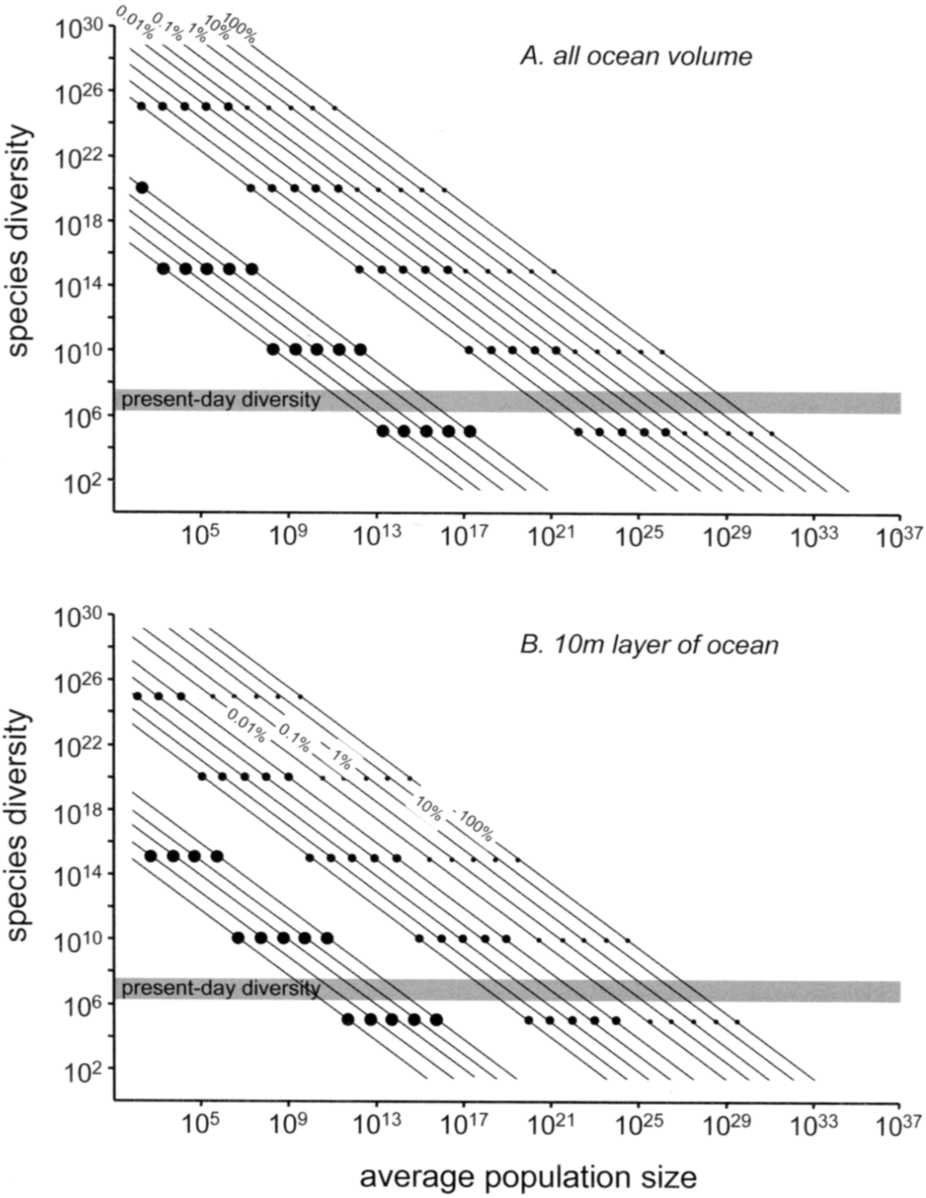

FIGURE 1. Visual representation of equation (3) showing diversity (y-axis) as a function of average population size (A_{PS}) for 25 different combinations of ecospace occupancy (E_O = 0.01, 0.1, 1, 10 and 100%) and average body size (A_{BS}) (body diameter D = 25 μm [smallest solid dots], 1 mm [intermediate-size solid dots], and 1 m [largest solid dots]). The two panels represent two sets of models for two different ecospace volume (E_V) values: E_V assumed to represent the entire ocean volume (A), and E_V assumed to represent a 10-m-deep layer of ocean water (B). Estimates for likely levels of the present-day-marine biodiversity shown as a gray zone.

theoretical model that acknowledges these relationships can be developed by considering some general scaling principles that relate numbers of individuals and species to body size. Spectral analyses of the distribution of marine biomass among $\log_{10}$ size classes typically indicate that total biomass is roughly invariant across size classes or may decrease slightly going from smaller to larger size classes—a slope of −0.05 in log-log space is typical (Kerr and Dickie 2001). The number of individuals per unit biomass scales as the direct inverse of body size (−1.0), and hence the distribution of individuals among size classes is given by a line with a slope of ∼−1.05. The total number of individuals, N, in all $\log_{10}$ size classes combined would then be given by

$$N = \sum_{i=\log_{10}\min}^{\log_{10}\max} aM_i^{-1.05} \qquad (4)$$

where *min* is the volume of the smallest individual, *max* is the volume of the largest individual, M_i is the average body size of an individual in the i^{th} $\log_{10}$ size class, and a is an empirical coefficient (see below). In order to estimate diversity from the number of individuals, it is also necessary to account for the allometric scaling of species population density with body size. This relationship appears to have a slope of ∼−0.75 for terrestrial mammals (Damuth 1981, 1987). Evidence is mixed as to whether a similar exponent describes the scaling of population density in marine ecosystems (Belgrano et al. 2002; Damuth 1987; Dugan et al. 1995; Marquet et al. 1990), but here it is assumed as a starting point.

Population density can be used as a proxy for total global population size only if there is no association between body size and geographic range size. This is certainly not the case in reality. However, the relationship between body size and geographic range size across the full size spectrum of marine organisms is largely unknown and likely complex, so this relation is difficult to parameterize directly. If we assume that not just population density but also total population size scales with body size to the abovementioned −0.75 power, a scaling coefficient of 0.75 for the average species/individual ratio can be applied. The predicted global marine biodiversity (B) based on size range is then given by

$$B = \sum_{i=\log_{10}\min}^{\log_{10}\max} \left(aM_i^{C}\right)\left(bM_i^{D}\right) \qquad (5)$$

where c is a scaling parameter for defining number of individuals in a given size classes ($c = -1.05$ is assumed here); d defines the scaling relations between body size and species-to-individual ratio ($d = 0.75$ is assumed here); and a and b are coefficients describing the intercepts of the slopes relating total individuals and total species, respectively, to $\log_{10}$ body size class. We define *min* as $3.3 * 10^{-20}$ m^3 (the volume of the smallest functional bacteria) and *max* as 172 m^3 (the volume of a large blue whale). A SAS/IML code developed from equation (5) and used to generate Figures 2 and 3 is included as Appendix 2 here. There is no obvious way to parameterize a and b because true biodiversity is not known in most size classes. We will consider here briefly two indirect ways of constraining these two parameters: "whale parameterization" and "occupancy parameterization."

1. *Whale Parameterization.*—It is well established empirically that very few species occupy the largest $\log_{10}$ size class—a few rorqual species, with a combined population of perhaps 100,000 (though this low number may, in part, be a legacy of human predation in the recent past). For the c and d values assumed above, we can iteratively determine the value of a at which a total population of 100,000 individuals occupies the largest size class ($a = 2.22488 * 10^7$). Given that value of a, the number of whale-sized species documented for present-day oceans (specifically three species at >20 m in length) occurs when $b = 0.632 * 10^{-6}$. This "whale parameterization," which produces a biosphere with realistic values for diversity and population size of whales, yields a total biodiversity across all size classes of ∼70 million species (Fig. 2), a reasonable number when compared with empirical estimates of the global biodiversity in the oceans today (e.g., Sala and Knowlton 2006). However, only ∼56,000 of these species are in size classes greater than 1 mm in diameter (Fig. 2)—by any standard, a gross underestimate of the true diversity of multicellular eukaryotes (nematodes alone can include up to 10^8 million species [Lambshead 1993], small deep-sea macrofauna may on its own account for 10^7 species [Grassle and Maciolek 1992], and careful surveys suggest that individual groups of mollusks in single regions may by themselves contribute many thousands of species to global diversity [Bouchet et al. 2002, 2009]).

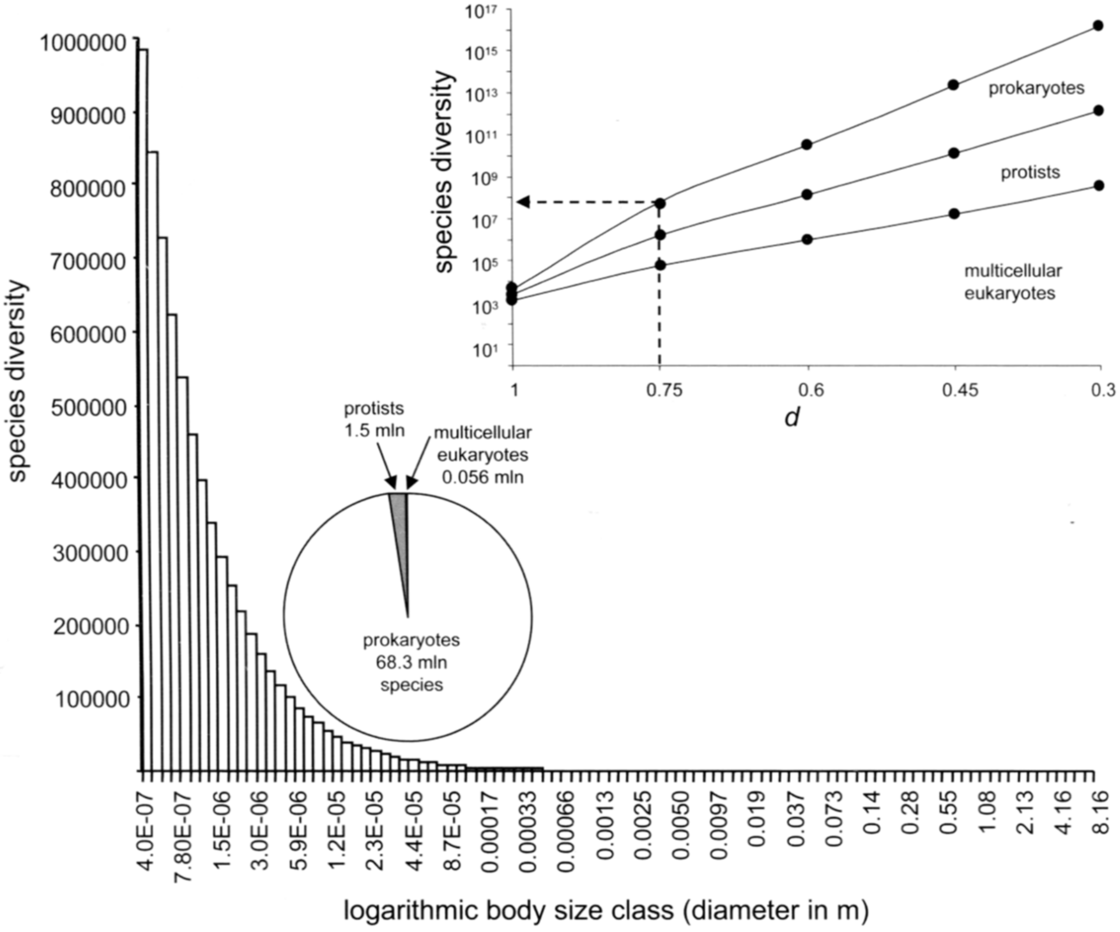

FIGURE 2. Distributions of diversity across log-binned size classes using equation (5) with the empirical parameterization discussed in text (''whale parameterization''). The inset pie-chart illustrates relative contributions of prokaryotes, protists, and multicellular eukaryotes to global diversity. The inset plot shows the effect of d on diversity, including changes in partitioning across major grades of organisms. The curves are cumulative (i.e., the highest line marks the total diversity of all life at given d, whereas the spaces between the lines represents contributions to diversity of major grades of life as labeled on the plot). Given that the y-axis of the inset plot is logarithmic, the plot shows that the diversity is overwhelmingly dominated by the prokaryotic grade of life. Note that the pie-chart is a non-logarithmic representation of the same data as shown on the inset plot for $d = 0.75$. The position of the specific model of global biodiversity based on the ''whale parameterization'' is indicated by the dashed line.

Two possible explanations can be offered to explain the failure of this parameterization. First, the largest size class may be an outlier (as often is the case for extreme endpoints of distributions) that drastically departs from the $d = 0.75$ model. Thus, the population size and diversity of the largest size class, though easy to estimate empirically, may not be useful for the parameterization of a and b. Second, the true exponent relating *average* species population size to body size is likely much shallower than -0.75, because this exponent describes the relationship between body size and maximum, rather than mean, population density (Belgrano et al. 2002). Decreasing the value of d quickly leads to more reasonable estimates. Already at $d = 0.60$, the model yields a reasonable estimate for multicellular eukaryotes (nearly a million species) and predicts a total biodiversity of $\sim 40*10^9$, which is well above the range of actual estimates for the modern biosphere. As is clear from the inset (Fig. 2), changes in d can have a great effect both on overall biodiversity and on its partitioning across major grades of life.

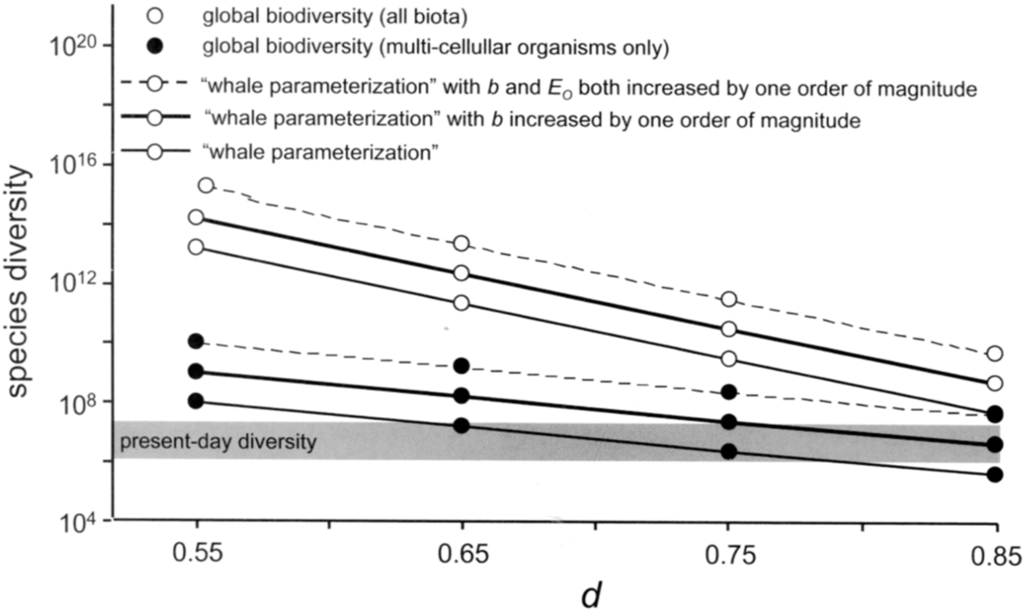

FIGURE 3. An occupancy-constrained model of the theoretical diversity based on equation (5), where the exponent c is assumed as a constant, the coefficient a is calculated to achieve $E_O = 0.01\%$, E_V is restricted to the uppermost 10 m of ocean waters only, and the initial coefficient b is derived from the "whale parameterization" discussed above. See text for more details.

The theoretical diversity model based on equation (5), as parameterized above, is not aimed at estimating the maximum possible diversity, but rather attempts to approximate the modern biosphere. Using equation (5) we can estimate the total biovolume occupied by this theoretical biosphere at $7.7*10^9 m^3$. If we define the available ecospace (ecospace volume) as the total volume of the oceans, the proportion of available habitat utilized is exceedingly low: $5.6*10^{-9}$. Even if we restrict available habitat to the upper 10 m of the oceans, the proportion of habitat utilized is still a mere 0.0002%. Because the models generated by equation (5) allow post hoc computation of the average per-species population size and average per-species body size, we can estimate corresponding biodiversity by using the more simplistic biodiversity estimate (eq. 3), which ignores interdependencies discussed here. Interestingly, for ecospace occupancy of 0.0002%, ecospace volume of 10 m, and average body size and population size derived post hoc from the whale-parameterized model, the theoretical biodiversity estimated by equation (3) is $1.2*10^{34}$ (a value of diversity more than 20 orders of magnitude higher than the 70 million species estimated by equation 5).

2. *Occupancy Parameterization.*—The other way to constrain the model is by solving for the expected ecospace occupancy rate (E_O). For example, we can assume conservatively (as in Fig. 1B) that only 0.01% of the uppermost 10 m of the ocean is occupied by organisms. Given this constraint, what type of diversity levels can we achieve by varying iteratively the parameters of equation (5)? In other words, what is the carrying capacity of the oceans (given a certain proportional occupancy), if we acknowledge the obvious dependencies between body size, population size, population density, and the resulting global diversity?

Although equation (5) is a four-parameter function, it is reasonable to parameterize three variables only (a, b, d). This is because c is likely to be roughly -1 (the number of individuals per unit of biomass should scale approximately as the direct inverse of body size). Moreover, because the parameter b defines the scaling of the species-to-individuals ratios within size classes, it has no effect on the total biovolume of the biosphere, and therefore, on the ecospace occupancy rate (E_O) used in equation (3). The parameter *d* also does not affect E_O, being a scaling parameter relating species-to-individuals ratios as a function of body size. This means that for any given E_O and *c*, there is only one specific value of the parameter *a*, which defines specimen abundance in a given size class. For the occupancy model used here ($c = -1.05$, $E_V = 10$ m layer of ocean water), the conservative occupancy rate of $E_O = 0.01\%$ is achieved when $a = 1.036*10^9$. In other words, to achieve 0.01% occupancy (when $c = -1.05$)—for the minuscule fraction of the ocean volume that is deemed most habitable—we need population size to be a function of body size with its intercept coefficient of $a = 1.036*10^9$. This model is used here as an initial occupancy model (Fig. 3). As shown in Figure 3, although *b* and *d* have no effect on ecospace occupancy, they do influence global biodiversity notably. In other words, *a* and *c* determine ecospace occupancy, but the resulting biodiversity estimate also depends on *b* and *d*, which determine how species are distributed across and within individual size classes.

If the coefficient *b* is based on the "whale parameterization" discussed above and *d* is varied around -0.75, diversity estimates yielded by this conservative occupancy model exceed the empirical estimates of global biodiversity by many orders of magnitude, and do so even if *b* is changed by an order of magnitude. Even when data are restricted to size classes corresponding to multicellular organisms only, the theoretical estimates meet or exceed the empirical values suggested for the modern biosphere.

Regardless of which values are chosen for parameterization, the model with built-in interdependencies still suggests that the total diversity could be quite volatile. Small changes in parameters relating body size, biomass, population density, and population size produce changes in global diversity that can be measured in orders of magnitude.

Conclusions

The models and parameterizations presented above consistently suggest that the theoretical diversity exceeds empirical estimates for the modern oceans by multiple orders of magnitude. Only when models are conservatively parameterized and restricted to multicellular size classes can theoretical biodiversity levels be made comparable to the higher-end empirical estimates of total diversity of present-day oceans (Fig. 3). All of the models, including those that acknowledge the stabilizing interdependence of parameters, consistently suggest that changes in global diversity by multiple orders of magnitudes are theoretically permissible. Changes in average population size, small subtle changes in exponents defining scaling relations, and changes in ecospace volume or occupancy all can produce order-of-magnitude changes in biodiversity.

Interestingly, empirical paleontological studies all agree—despite various contentious issues and the obvious limitation of the fossil record (e.g., its restriction to the preservable fraction of species only)—that global and local diversity levels have changed through the Phanerozoic by less than one order of magnitude (Table 1). Recent work on body size evolution through geological time also suggests that average body sizes within major clades and for the biosphere in general have not changed dramatically during the Phanerozoic, with an increase in maximum body size since the Ordovician of less than three orders of magnitude (Payne et al. 2009) implying a much smaller increase in mean body size.

Because they have no time dimension, the simplistic models discussed here have no direct bearing on the question of diversity trajectories and do not rule out even the exponential diversification model recently advocated by Stanley (2007). The great volatility in biodiversity that is theoretically permitted by these models does, however, raise the question of why nearly all existing estimates of the Phanerozoic trajectory of marine biodiversity (with the exception of the unconstrained exponential model) indicate such relative stability.

Finally, and perhaps most importantly, the value of deductive models should ultimately reside in identifying the type of empirical data needed to develop more rigorous models in future. It is clear that data regarding

TABLE 1. Magnitude of changes in global biodiversity through the Phanerozoic estimated by using a variety of empirical approaches focused on the geological history of global and local-scale (alpha) diversity. Diversity change (expressed as a multiplicative factor) is based on values reported by authors or is estimated approximately by visual examination of graphs (rounded to the nearest integer to avoid the false air of accuracy). When possible the early Ordovician (at the onset of the Ordovician diversification) and Neogene (for which many studies estimate maximum diversity) were compared to maximize the magnitude of diversity changes, while minimizing boundary effects and "Pull of the Recent." All numbers are positive, indicating that all studies suggest increase in diversity through time by some factor, although all those estimates also suggest that this increase was by less than one order of magnitude.

Study	Compared time intervals	Scale of study	Diversity increase factor
Valentine 1969	Early Ordovician–Neogene	Global, families	4
Sepkoski 1981	Early Ordovician–Neogene	Global, families	4
Bambach 1999	Early Ordovician–Neogene	Global, genera	9
Alroy et al. 2008	Early Ordovician–Neogene	Global, genera	2
Bambach 1977	Early Paleozoic–Neogene	Alpha, species	2
Powell and Kowalewski 2002	Early Paleozoic–Neogene	Alpha, genera	2
Bush and Bambach 2004	Early Paleozoic–Neogene	Alpha, genera	4
Sepkoski 2002	Early Ordovician-Neogene	Global, genera	6
Philips 1860	Early Ordovician–Neogene	Global, unknown	6
Seilacher 1974	Ordovician–Cenozoic	Alpha, trace fossils	2
Raup 1976	Ordovician–Cenozoic	Global, species	4

absolute population sizes, absolute diversity levels, and scaling coefficients relating population density, body size, geographic range, and taxonomic richness are needed to develop robust parameterizations of theoretical diversity. This need obviously applies to the easily accessible modern ecosystems. Even more so, it applies to the fossil record, where absolute abundance data are limited to a few stratigraphically, taxonomically, and geographically restricted estimates (e.g., Finnegan and Droser 2005; Payne et al. 2006). In our view, the main conclusion of the modeling exercises presented here is not that a credible theoretical diversity model can be provided at this time, but only that such a deductive model is realistically feasible in the foreseeable future (targeted empirical efforts toward data-rich parameterizations of the modeled coefficients are needed).

Despite their obvious naivety, theoretical diversity models offer a deductive tool that is completely independent from empirical estimates of biodiversity. Models of this sort, even when implemented in such a cartoonish way, can provide insights that are not accessible empirically. This approach can even add some amusement to our debate with Biblical literalists. For example, it can highlight the utter unfeasibility of the Noah's Ark narrative (Appendix 3). More seriously, a more complex model incorporating realistic energetic and nutrient limitations may help us to consider what the true degree of allowable volatility in biodiversity is, though necessarily at the expense of theoretical purity. It may be instructive also to consider the effect of indirect causative mechanisms (e.g., climate, predation, sea level changes, incumbency) on basic feasibility parameters such as average population size and average body size. Continuing advances in computational power make dynamic modeling of such complex systems increasingly feasible. Whereas theoretical diversity models cannot substitute for empirical data and inductive reasoning, they may potentially provide a valuable source of independent models against which to compare our empirical data, much as theoretical morphospace and ecospace models (e.g., Raup 1966; Bambach et al. 2007), or even deductive consideration of maximum human population sustainable globally (Cohen 1995), have helped to shed light on empirically observed patterns.

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Appendix 1

A SAS and SAS/IML code based on equation (3) used to generate Figure 1. For code details, see annotations embedded within the code.

```
%let Ev = 10*3.6*10**14; * - ecospace volume;
 * Ev = 1.3*10**18 - whole ocean volume;
 * Ev = 10*3.6*10**14 - 10m layer;
 proc iml;
 X = {0.000025 0.001 1}; * assumed average diameters of organisms;
 do i = 1 to 3;
 do coeff = 0 to 4 by 1;
 do expn = 0 to 30 by 5; * expn - an exponent for APS [average population size] in number of individuals;
 D = X[,i]; * D = diameter in meters;
 ABS = 1.35*1.33*3.14*(D/2)**3; * equation 2, ABS [average body volume] in m3;
 EV = &Ev; * EV - available ecospace;
 EO = 1/10**coeff; * EO - occupied ecospace;
 APS = 10**expn;
 div = ceil((EV/EO)/(ABS*APS));
 out = D| |ABS| |EV| |EO| |APS| |div;
 out2 = out2//out;
 end;
```

```
end;
end;
create new from out2;
append from out2;
close new;
data final;
set new;
Diam = Col1;
ABS = Col2;
EV = Col3;
EO = Col4;
APS = Col5;
div = Col6;
drop col1–col6;
proc print;
run;
quit;
```

Appendix 2

A SAS and SAS/IML code based on equation (5) used to generate Figures 2 and 3. The current parameter values are based on the "whale parameterization" discussed in the text. For code and output details, see annotations embedded within the code.

```
* MACROVARIABLES *;
* Ocean parameters;
%let V = 1.37*10**18; * - the volume of the ocean [m3],
maximum possible ecospace;
%let S = 3.6*10**14; * - the surface of the ocean [m3];
%let Ev = 10*&S; * - the ecospace volume of the ocean, which
can be computed using either V or S macrovariables above;

* Body size parameters;
%let Ymin = 3.3*10**−20; * - the volume occupied by an
individual in the smallest size class [m3];
%let Ymax = 172; * - the volume occupied by an individual in
the largest size
class [m3];
* Diversity model parameters;
%let a = 2.22488*10**7; * - dimensionless parameter (an
intercept of relation between #individuals and size);
%let b = 0.632*10**−6; * - dimensionless parameter (an
intercept of relation
species/individuals ratio and size);
%let c = −1.05; * - slope of log-log relation between
#individuals and size;
%let d = 0.75; * - slope of log-log relation between species/
individuals ratio and size;

proc iml;
do i = 1 to 100; * - this do-loop partitions body size range into
100 log-regular octaves;
if i = 1 then Z = &Ymin;
else Z = 10**(log10(Z) + ((log10(&Ymax) − log10(&Ymin))/
99 ));
Ind = (&a*Z**&c); * - total number of individuals in a size class;
SpInd = (&b*Z**&d); * - number of species per individual in a
size class;
D = Ind*SpInd; * - diversity of a size class;
BS = Ind*Z; * - biovolume of the size class;
DM = 2*(((3*Z)/(4*3.14159265358979))**(1/3)); * - body diam-
eter for a given size class;
out = Z||DM||BS||Ind||SpInd||D; * - data summary;
DD = DD//D;
BV = BV//BS;
TIND = TIND//Ind;
sum = sum//out;
end;
DIV = DD[+,]; * total diversity;
TNI = TIND[+,]; * total number of individuals;
APS = TNI/DIV; * APS [average population size [mean
#indiv. per species]];
TBV = BV[+,]; * Total biovolume occupied;
TBVC = BV[+,]*(1/0.74); * Total biovolume occupied corrected
for hexaognal packing [1/0.74];
ABV = BV[+,]/TNI; * ABV [average body volume [m3]];
ABS = 2*(((3*ABV)/4*3.14159265358979))**(1/3)); * ABS [aver-
age body size - diameter [m]];
Ev = &Ev;
EO = 100*TBV/Ev; * percentage of the ecospace occupied;
ND = (Ev*Eo)/((ABV*(1/0.74))*ABS);
print 'output summary' sum;
print 'total global diversity' DIV;
print 'total number of individuals' TNI;
print 'average population size [APS]' APS;
print 'total biovolume' TBV;
print 'total biovolume corrected for hexagonal packing' TBVC;
print 'average body volume' ABV;
print 'average body size [ABS]' ABS;
print 'ecospace volume [EV]' Ev;
print 'ecospace occupation [Eo]' Eo;
print 'naive diversity' ND;
create rep1 from sum;
append from sum;
close rep1;
data rep2;
set rep1;
size = col1;
diam = col2;
biov = col3;
Ind = col4;
SpInd = col5;
Div = col6;
drop col1–col6;
if diam < 0.000025 then group = 1; * group 1 = prokaryotes;
if 0.000025 <= diam < 0.001 then group = 2; * group 2 =
protists;
if diam >= 0.001 then group = 3; * group 3 = multicellular
organisms;
proc sort;
by group;
proc print;
proc univariate data = rep2 noprint;
by group;
var Div;
output out = rep3 sum = sum;
proc print;
run;
quit;
```

Appendix 3

How Large Was Noah's Ark?

Using the whale parameterization, we can estimate the number of species existing simultaneously globally (note that "kinds," referred to in the Bible, denotes organisms that can produce offspring of the same kind, which is the technical definition of the species). If we limit population size of each species/kind to two individuals (a male and a female) and restrict the data to eukaryotes only, the resulting biovolume of marine eukaryotes would be $6.2*10^{12}$ m^3. Obviously, the continents represent a much smaller ecosystem than the oceans. Let us therefore assume that the biovolume occupied by male-female sets of all land-dwelling eukaryote species would represent only 0.1% of the biovolume estimated above for the marine eukaryotes. This is an extremely conservative estimate, as it posits the difference of three orders of magnitude between oceans and land. However, even this conservative number means that the biovolume of organisms that Noah had to load on the Ark must have been on the order of 600 million cubic meters. To offer a perspective, the largest ships built in recent times all have carrying capacities well below one million cubic meters (e.g., TI Europe, Knock Nevis, Batillus-class supertankers). Noah's Ark must have had capacity at least a thousand times higher than the largest supertanker (note here that Noah's Ark, as described in cubits in Genesis, would have been much smaller than a modern supertanker). Finally, note that our estimate of the Ark's capacity is naively conservative because it assumes that all animals were packed like canned sardines. Also, the postulated Noah's Ark, as gigantic as it is, does not allow for any space to store food needed to ensure survival of organisms.