THE BIOLOGY OF FOSSIL ABUNDANCE

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ABSTRACT

Many patterns of fossil abundance are very similar to abundance patterns of living species. Examples include: body size abundance, geographic range distributions, community abundance, paleoenvironmental patterns and abundance, greater temporal and spatial abundance variation in rare species than in common species, correlation of abundance density and geographic range, and species-area curves as seen in "species-time" curves. These patterns are apparently preserved despite many known taphonomic biases because there must be some correlation between relative living and fossil abundance. Suggested reasons for this correlation include time-averaging, which accumulates even rare species through time, and the fact that most abundance patterns compare groups with relatively constant phylogenetic influences on depositional processes. The importance of abundance and rarity has been greatly overlooked in paleontology. The described fossil record is based mainly on the 6-7% most abundant and widespread species. Most of the widely discussed interpretations of past events, such as paleocommunity persistence and biosphere extinctions, are thus based on exceptionally abundant, broadly adapted species. Better understanding of the biological origins of fossil abundance can greatly improve the accuracy of our interpretations of past events.

Keywords: Abundance, rare species, populations, taphonomy, foraminifera.

RESUMEN

Muchos patrones de abundancia de fósiles son muy similares a los de las especies vivientes. Entre los ejemplos se incluyen: abundancia de tamaño corporal, rangos de distribución geográfica, abundancia comunitaria, patrones paleoambientales, mayor variación temporal y espacial de la abundancia en las especies raras que en las comunes, correlación de la densidad de la abundancia y la distribución geográfica, y curvas especie-área como si fueran curvas especie-tiempo. Estos patrones se conservan, aparentemente, a pesar de los múltiples sesgos tafonómicos conocidos, porque debe haber alguna correlación entre la abundancia de los fósiles y la de sus parientes actuales. Entre las razones sugeridas para esta correlación se incluyen el promedio temporal que, a través del tiempo, acumula incluso las especies raras, y el hecho de que la mayoría de los patrones de abundancia comparan grupos con influencias filogenéticas relativamente constantes sobre los procesos de depósito. La importancia de la abundancia y la rareza apenas ha sido tenida en cuenta en paleontología. El registro fósil descrito se basa principalmente en el 6-7% de las especies más abundantes y extendidas. De este modo, la mayoría de las interpretaciones ampliamente discutidas de eventos del pasado, como la persistencia de las paleocomunidades y las extinciones de la biosfera, se basan sobre especies excepcionalmente abundantes y ampliamente adaptadas. Una mejor comprensión de los orígenes biológicos de la abundancia de los fósiles puede mejorar en gran medida la precisión de nuestras interpretaciones de los eventos pasados.

Palabras clave: Abundancia, especies raras, poblaciones, tafonomía, foraminíferos.

INTRODUCTION

The rapidly growing field of taphonomy has produced many insights about how fossilization can distort biological information. Biases in preservation, changing depositional rates, erosion, and many other processes have the potential to produce fossil assemblages that are very different in composition from the original living communities and populations (Kidwell and Flessa, 1995).

This paper reviews evidence that fossil abundance patterns, despite taphonomic processes, often closely correspond to known abundance patterns of living organisms. While incompleteness and biases undoubtedly occur, the fossil record of abundance apparently still contains considerable information about

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I. Abundance of Size

Size-frequency - both fossil and living "community" (multi-taxic) assemblages show a strongly right-skewed frequency distribution of size (most individuals are small).

II. Geographic Range Abundance

Geographic range-frequency - both fossil and living species (and genera) show a strongly right-skewed frequency distribution of geographic range (most species are local).

III. Species Abundance in Communities

Species-frequency - both fossil and living "community" (multi-taxic) assemblages show a strongly right-skewed frequency distribution of species (most species are rare).

IV. Environmental Abundance Patterns

Paleoenvironmental abundance patterns - ranked abundance distributions of fossil species have the same paleoenvironmental patterns of modern species living in similar environments.

V. Correlation of Local Density and Geographic Range

Correlation of density and range - in both fossil and living organisms, geographic range tends to positively correlate with local abundance density: geographically widespread species also tend to be locally abundant.

VI. Temporal Abundance Variation

Greater variation in rarer species - rare living and fossil species tend to exhibit greater relative fluctuations in abundance through time.

VII. Spatial Abundance Variation

Greater variation in rarer species - rare living and fossil species tend to exhibit greater relative variations in abundance throughout their spatial distribution.

VIII. Species-area curves: Accumulation in Time and Space

Spatial distribution in stratigraphic samples - sequential stratigraphic samples produce a "species-time" curve that is mathematically similar to a species-area curve. This is because fossil deposition is a process that preserves spatial abundance patterns through time.

Table 1. Some of the most important fossil abundance patterns that are the same as abundance patterns of living organisms.

the biological processes that produced it. Fossil abundance patterns of: body size, geographic range, and environment are generally the same as those found in living organisms. This is true even when we examine the finer details of species abundance variation in time and space.

How can these abundance patterns of living species be preserved, given the wide variety of taphonomic processes that can potentially cause gaps and distortions in the fossil record (e.g., Kidwell and Flessa, 1995)? Two reasons will be suggested. One is the process of time-averaging, which allows even rare species to be preserved as fossils through the cumulative deposition and "averaging" of sediment over long geological time spans. Another reason is that most abundance patterns involve analyses of species in the same higher taxic categories such as families or orders. Species within such phylogenetic categories share many of the same traits that influence fossilization so that taphonomic biases are consistent across all species.

The importance of fossil abundance is difficult to overemphasize. Virtually every aspect of paleontology relies, at least indirectly, on abundance of individual fossils as a source of information. These range from the practical, such as biostratigraphic zones based on fossil abundance, to the theoretical, such as paleocommunity and clade dynamics. Indeed, neglect of species abundance patterns has probably seriously distorted our perception of many (perhaps most) important paleontological studies because paleontologists have tended to study mainly common fossil species. Common species are easier to obtain and provide better sample sizes, but they also often have different biological traits and dynamics than rare species (Gaston, 1994). Raup (1988), for example, notes that most estimates of past biosphere extinction rates may be ten times too low because they omit the higher extinction rates of rare species. At the paleocommunity level, McKinney *et al.* (in press) discuss how the apparent ecological stasis of fossil communities is misleading because the data omit many rare species that may have high rates of ecological turnover (local extinction and recolonization) and have little interaction with other species.

BIOLOGICAL PATTERNS IN FOSSIL ABUNDANCE

The terms "abundance" and "rarity" have assumed many meanings in the scientific literature (Gaston, 1994). While there are many variations, the basic definition of abundance usually relies on two criteria: 1) local population density (*i.e.,* number of individuals per area) or 2) geographic range. "Rare species" thus typically refers to species that have low local population densities, a restricted geographic range, or both low density and restricted range. Population density and geographic range tend to be correlated among related species, discussed below, so that rare species tend to have both types of rarity.

This paper examines both geographic range and local population densities in fossils. Also, it examines environmental, community, and other spatial/temporal correlates of abundance that are similar in both fossil and living organisms. Table 1 outlines eight types of abundance patterns that apparently show this similarity. I will now briefly discuss each of the patterns.

Abundance of Size. Both fossil and living multi-species groups (communities and clades) show strongly right-skewed ("hollow curve") body size distributions, with smaller sizes being much more common. Examples include: May (1988) and Dial and Marzluff (1988) for living organisms; Murray (1991) for fossil foraminifera and McKinney (1986) for fossil echinoids. As discussed by May (1988) and Dial and Marzluff (1988) most explanations for the origin of this distribution in living groups have focused on the fact that smaller organisms can partition the physical environment into smaller parts.

Geographic Range Abundance. Both living and fossil clades show strongly right-skewed distributions of geographic ranges of their component species. Gaston (1994) reviews a number of examples for clades of living species. Fossil examples include Hansen (1980) and Jablonski (1986). Explanations for the biological origin of this pattern have focused on the reasons why most species are rare. As reviewed by Gaston (1994), this is probably because most species are limited by some type of habitat specialization or physiological tolerance. Only a few species ("eurytopes") are broadly adapted and physiologically tolerant enough to be widespread.

Species Abundance in Communities. It has long been known that most species in living communities are rare (Williams, 1964; review by Gaston, 1994). As with geographic range, this is commonly explained by noting that most species are relatively specialized (Lawton *et al.,* 1994). Indeed, much of Brown's (1995) recent book on "macroecology" concerns the ecology and evolution of niche-based abundance, *i.e.,* why most species evolve to be rare in communities while only a few species can numerically dominate. This may also partially explain why there is a strong correlation between geographic range and local community abundance (density) of individuals in many groups of organisms (reviews in Lawton *et al.,* 1994, and Gaston, 1994). The narrower niches of relatively specialized species may tend to restrict both their geographic ranges and their ability to reach high abundance densities in communities (Brown, 1995).

The precise pattern of species rarity in living communities is one of exponential decline. In other words, species represented by one individual are the largest class of species, species with two individuals are the next largest class, and so on. Only a few species have many hundreds or thousands of individuals (*e.g.,* Williams, 1964; Gaston, 1994). A variety of models, such as the "broken stick", log-normal, and log-series, will fit this exponentially declining abundance pattern in living communities (review in May, 1975).

The same exponentially declining pattern of species rarity is found in nearly all fossil communities. Buzas *et al.* (1982), Koch (1987) and CoBabe and Allmon (1994) are examples that show this when species abundance in a fossil "community" assemblage is measured in terms of volumetric abundance in the sediment or rock. These papers also show how to deal with the large problem of sampling error that arises with all these rare species: even if exactly the same fossil assemblage is resampled, some rare species will disappear in the next sample while new rare species will appear. Indeed, CoBabe and Allmon (1994) infer that only about 5% of the fossil molluscan species in their data are common enough to provide reliably consistent data on abundance distributions. Up to 60% of the fossil species are too rare to provide reliable data no matter how intensively the rocks are sampled. Buzas *et al.* (1982) and Koch (1987) suggest statistical techniques to test if two samples are sufficiently different in their composition of rare species to be considered as truly distinct (beyond differences of sampling error). These are also discussed in CoBabe and Allmon (1994).

A detailed discussion of how taphonomy affects this abundance pattern in fossils has, to my knowledge, not been made. However, Fursich (1990) reviews how fossil assemblages are usually time-averaged communities, with living communities existing many years apart being superimposed. He also cites several studies showing that numerically dominant species in communities often become numerically dominant in the time-averaged assemblage. An example of such a study is Staff *et al.* (1986).

Paleoenvironmental Abundance Patterns. The models used to fit community species abundance, such as broken stick, log-series and log-normal noted above, can be used to interpret the origin of such patterns in the community (May, 1975). These same models have been applied to the fossil record (*e.g.,* Buzas *et al.,* 1982; CoBabe and Allmon, 1994) although mainly for purposes of description rather than explanation. An important exception is Murray's (1973) use of the log-series model to interpret community abundance patterns in foraminifera in terms of paleoenvironments.

In the log-series model, one can characterize diversity by the "alpha index" which is relatively robust to sample size and easy to calculate (Williams, 1964; Murray, 1973). As seen in Figure 1, alpha can be measured as the slope of the line when number of individuals in each sample are plotted against number of species found in that sample. Alpha is approximately equal to the number of species in each sample represented by just one individual (Buzas *et al.,* 1982). Communities with low alpha values therefore have relatively low species diversity.

The data in Figure 1 are taken from samples of fossil Eocene-Oligocene benthic foraminifera from Florida, deposited in largely nearshore shelf-sea sediments (McKinney and Frederick, 1992). Murray (1973) describes how modern benthic foraminifera in shelf-sea environments of normal salinity have alpha values between 5 and 16. Nearshore, hyposaline shelf-seas have values below 5. The abundance data in Figure 1 are thus in agreement with their origin in a nearshore shelf sea with fluctuating sea level that sometimes approached normal salinity during high sea level.

Correlation of Species Density and Range. As noted above, a basic pattern found in many living groups is that geographic range correlates with local abundance: widespread species tend to be locally abundant and endemics tend to be of low population density (Gaston, 1994; Lawton *et al.,* 1994). This same pattern has been found in a number of fossil studies such as Cretaceous mollusks whereby species that are locally rare in the sediment also tend to be geographically restricted (Buzas *et al.,* 1982). Other examples are reviewed in Levinton (1988) and McKinney (in press). In most of these examples, it can be readily seen that this pattern is not solely an artifact of sampling because moderately abundant species are found in far fewer localities than expected from random occurrence.

Greater Temporal Abundance Variation in Rarer Species. Many ecologists have argued that rare species tend to show greater fluctuations in population abundance through time (reviews in Gaston, 1994; Gaston and McArdle, 1994). For example, abundance counts of rare living species through time often have higher coefficients of variation (CV's) than CV's for common species. Because the CV equals standard deviation of abundance divided by the mean abundance of each species, the higher CV's of rare living species indicates greater relative abundance fluctuations through time. These higher CV's in living populations of rare species are sometimes used to infer greater density-independent population controls than abundant species whose lower CV's may indicate more density-dependent controls based on biotic interactions (Gaston and McArdle, 1994).

Again, there is fossil evidence for the same general pattern, with rare fossil species showing greater relative fluctuations in abundance through time. For example, CoBabe and Allmon (1994) analyzed abundance counts of stratigraphic samples of Cenozoic mollusks and found that abundant species had more consistent CV's than rare species, indicating greater variation in abundance for rare species. Similarly, McKinney and Frederick (1992) showed that abundance fluctuations of Cenozoic foraminifera were enhanced by a "red shift", indicating that the abundance time series had greater relative swings in magnitude with time.

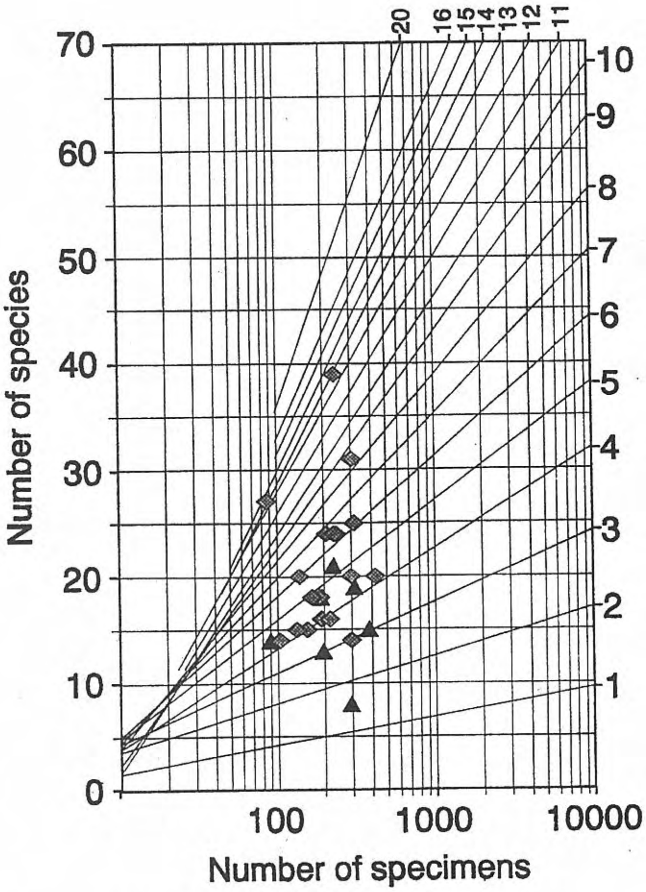

Figure 1. Alpha values can be measured as the slope of the line obtained when number of individuals (specimens) is plotted against number of species, for each sample (Murray, 1973). Slope values here are similar to those obtained from samples of benthic foraminifera in modern ecosystems of the same environment as the fossil (Paleogene) samples.

Greater Spatial Abundance Variation in Rarer Species. A valid criticism of the fossil evidence just noted for greater temporal variation in rare species is that a stratigraphic sequence cannot be directly interpreted as a time series. A main reason is that a stratigraphic section records spatial, or lateral, abundance variation as well as temporal variation. This is because populations within the community often migrate across the area of deposition so that lateral facies and abundance changes are translated into vertical stratigraphic changes.

This is shown in Figure 2 in that an area of deposition (= a stratigraphic section) can be considered to be moving through populations of organisms composing a community (also see McKinney and Allmon, 1995;

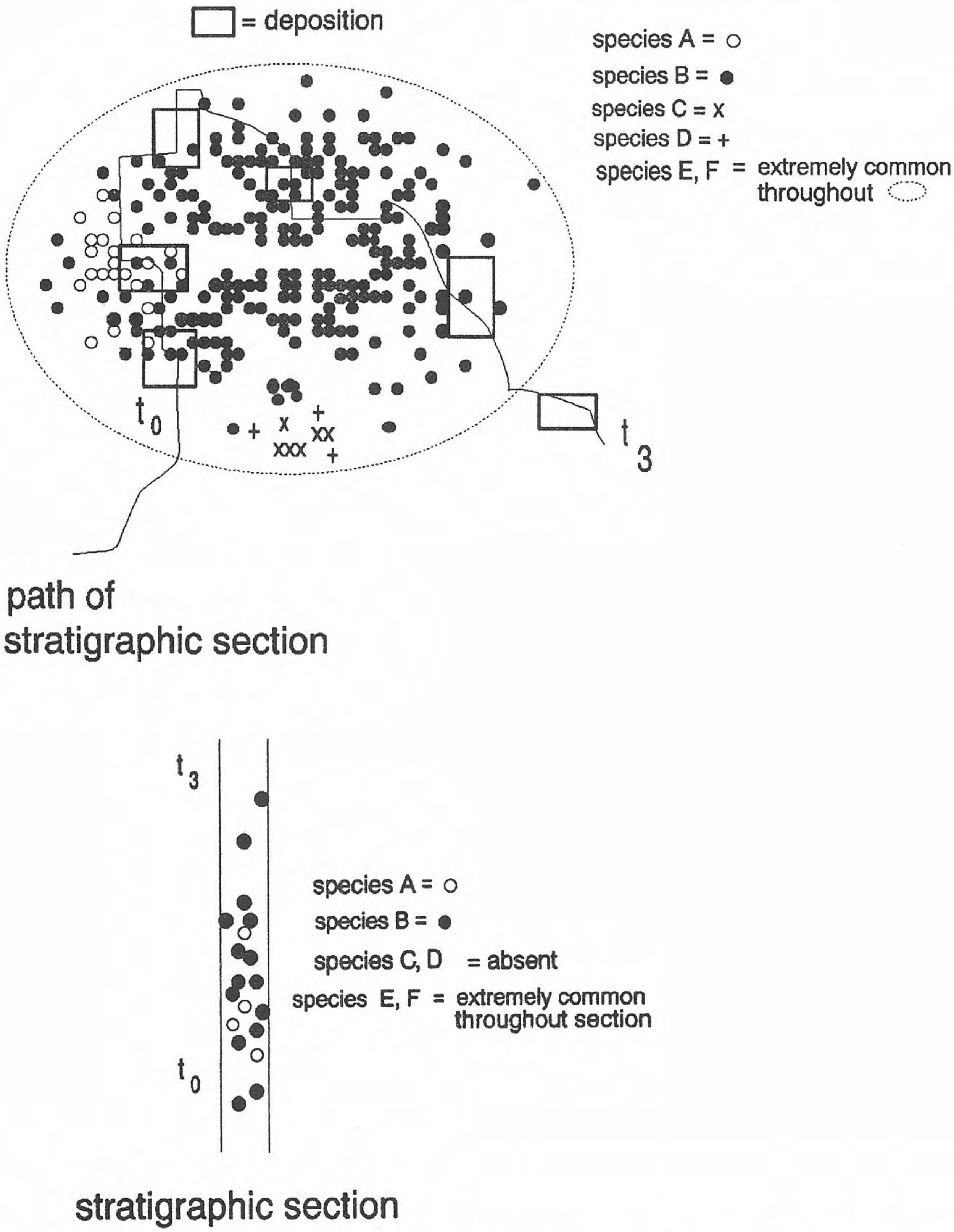

Figure 2. Top: Formation of a stratigraphic section can be modelled as a localized area of deposition that horizontally moves through spatially coexisting populations of species. Symbols (*e.g.*, x) represent individuals of designated species and illustrate the "patchy" distribution of most species. Deposition only occurs at certain areas shown by box. Ultimate pathway of section is shown, with t0 and t3 indicating arbitrary early and later times when the section reaches the given point shown. Bottom: Stratigraphic section depicting vertical distribution of fossilized individuals of species. Note that species with localized and sparse spatial distribution also show localized and sparse vertical distribution.

McKinney *et al.*, in press). In reality of course the populations are moving across the area of deposition, with only a few or no individuals being preserved. But it is easier to visualize the path of a single particle through a matrix of populations than the reverse. Figure 2 illustrates how some individuals (shown by symbols) of various species are deposited, but only at certain times depicted by the box because deposition is episodic and the fossil record incomplete (*e.g.*, Palmquist, 1993). Note that the populations of different species shown in Figure 2 are usually not moving across the area of deposition in unison (at the same rate). The individualistic behavior of different species means that species will often migrate independently in different directions as demonstrated by Valentine and Jablonski (1993) and Roy *et al.* (1995). Figure 2 is thus a "snapshot" of the community at a single point in time but showing the ultimate path of the stratigraphic section through a period of time (from t0 to t3).

A main advantage of the model is how it specifies the link between the spatial and temporal dynamics of deposition. For example, Figure 2 depicts how rare (and often locally restricted) species migrate into the area of deposition and are sometimes preserved (*e.g.*, species A). Other, often very localized species, such as species C and D, are never preserved because they never migrate over the area of deposition. This also illustrates how spatial abundance variation within a species is recorded as vertical stratigraphic variation. Decreased abundance in species B, for example, toward the edges of its geographic range would be recorded as decreased stratigraphic abundance around the earliest and latest appearance of species B in the stratigraphic section as shown in Figure 2.

If stratigraphic sampling intermixes spatial and temporal abundance variation, then why does the fossil data noted above agree with the ecological data which is based only on temporal variation? I suggest the answer is that rare species exhibit greater abundance variation than common species in both time and space. There is emerging evidence for this in ecological studies that analyze the spatial and temporal changes in abundance of living species. Maurer (1994) and Brown (1995) discuss rigorous statistical evidence, mainly from birds, that species with "patchy" or highly variable population distributions in space also tend to have highly variable fluctuations in population abundance in time. Thus, common, widespread species show little tendency for drastic temporal abundance change anywhere in their geographic range while rarer species seem to show greater relative abundance variation in both time and space (Maurer, 1994; Brown, 1995).

If true, then the intermixing of temporal and spatial abundance variation in the fossil record will record the greater variation in rare species in both time and space. Indeed, the fossil record will provide a more complete view of abundance variation than ecological data that is based only on temporal abundance data.

Species-Area Curves: Abundance Accumulation in Space and Time. Given the depositional process shown in Figure 2, we might predict that a vertical sequence of stratigraphic samples would follow a "species-area" curve. This curve is common in ecology where cumulative plots of the number of new species identified increases in a regular way with increasing area (May, 1975; Rosenzweig, 1995). In the case of fossils, we might expect such a curve because, as the depositional area of Figure 2 traverses populations of different species, the process is similar to taking random samples of species in an expanding area. Indeed, detailed analysis by Springer and Miller (1990) showed that spatial variability in fossil assemblages does preserve patterns of spatial variability in living communities. May (1975) discusses how the species-area curve will result where area, or in this case volume, sampled is roughly proportional to the number of individuals sampled. The only difference with fossils is that we are increasing the number of individuals sampled by more increasing our sample size stratigraphically (vertically) instead of spatially (horizontally).

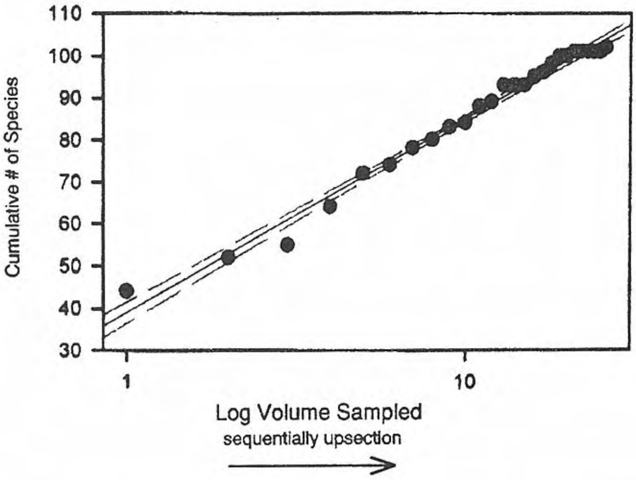

Figure 3. "Species-time" curve produced by sequential sampling of strata upsection (1 = lowest sample). Cumulative species number of Paleogene benthic foraminifera from a Georgia core are shown. Rock volume was the same in each sample but the samples were not equally spaced vertically due to sampling difficulties.

Figure 3 shows that fossil data do fit the classic species-area curve pattern, where "area" is volume of sediment sampled and "species" is number of new species identified with progressively stratigraphically sampling upsection. These data are for species of Eocene-Oligocene benthic foraminifera identified from volumetric samples taken from a core drilled in south Georgia. "Volume sampled" on the x-axis records the cumulative amount of sediment sampled, where 1 = volume of first (stratigraphically lowest) sample, 2 = volume of first plus second (stratigraphically next higher) sample, and so on. Each sample was the same volume. (Further discussion of data in McKinney and Allmon, 1995; McKinney *et al.*, in press).

Of great interest is that the z value of Figure 3 is 0.33, where z is the exponent of the equation $S=CA^z$. S is the

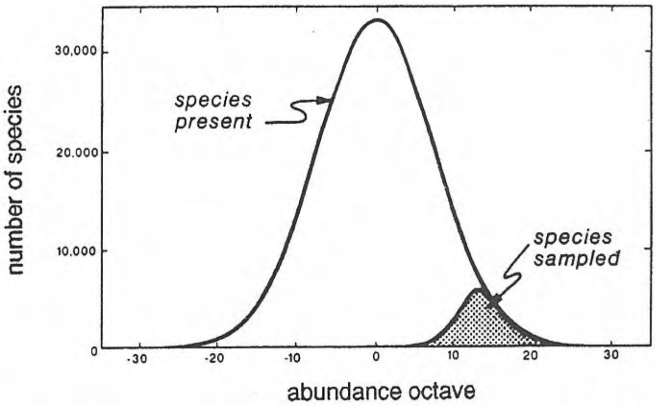

Figure 4. The large majority of species sampled from the fossil record are among the most abundant fossil species. In this figure, abundance "octave" is the logarithmic measure of fossil species abundance, as discussed in Sepkoski (1994). (Figure modified from Sepkoski, 1994).

number of species and A is area. For Figure 3, volume is substituted for area. This z-value is relatively high; it is typical of z-values for species-area curves calculated from oceanic islands (May, 1975; Rosenzweig, 1995). Rosenzweig (1995) found a similar z-value, of 0.36, in a similar curve of Ordovician species but plotting species versus time instead of volume. Such high z-values, according to May (1975), often indicate that the area being sampled is relatively heterogeneous, such as occurs when different islands are sampled. With fossils, we may infer that the heterogeneity occurs because much time often passes between pulses of fossil deposition (or stratigraphic samples are taken at widely spaced intervals) so that a relatively large variety of habitat variation is sampled as we sample upward in the stratigraphic section.

WHY ARE BIOLOGICAL ABUNDANCE PATTERNS PRESERVED?

There are many well-known biases in the fossilization process that can potentially distort the abundance relationships among fossil species compared to their relative abundance in life (Kidwell and Flessa, 1995). Differences in mineralogy, size, and habitat among species are but a few examples of traits that can cause differential preservation. Yet the abundance patterns discussed above implies that such distortion of ecological abundance may not occur. This inference is supported by a growing number of studies that directly compare known abundance of living species to their relative abundance in death assemblages, subfossil, and fossil remains. These studies show that there is a strong correlation between the relative abundance of a species in life and its relative abundance in death and fossil assemblages. Kidwell and Flessa (1995) review this evidence for molluscan remains and other taxa. Similar correlations have been reported by Staff *et al.* (1986), Miller (1988), and Fursich and Aberhan (1990) for a variety of taxa and communities.

There are undoubtedly many contributing factors that cause this strong correlation between living and fossil relative abundance (Kidwell and Flessa, 1995). I suggest that two such factors are of special importance to the abundance patterns discussed here. One is the process of time-averaging, which can produce "overcompleteness". As discussed by Kowalewski (in press), time-averaging allows even rare species to be preserved as rare fossils through the cumulative deposition and "averaging" of sediment over long geological time spans. For example, in his review of foraminifera paleontology, Murray (1991) states that time-averaging produces sediments with "a few common species present at all times and an ever changing number of minor species" (p. 44).

Another factor for this live:dead correlation is that many abundance patterns, including those reviewed here, involve analyses of species in the same taxonomic groups. Many influences on taphonomic processes such as deposition, are phylogenetic. Test or shell mineralogy, and behaviors such as burrowing, are examples of key biological traits that influence the chance of fossilization. When we analyze species within the same phylogenetic group, such as abundance patterns of gastropods or foraminifera, we are comparing species that share many of the same traits that influence fossilization. Taphonomic biases are thus consistent across all species. The result is that very abundant living species will become relatively abundant fossil species and rare living species will become rare fossil species (McKinney and Allmon, 1995).

DISCUSSION: THE NEGLECT OF FOSSIL ABUNDANCE

Traditional pursuits of paleontology, such as taxonomy and biostratigraphy, have been more concerned with the description and identification of fossil specimens than with their abundance. Even studies of evolutionary "dynamics" such as punctuated equilibrium and macroevolution have focused on morphometrics and species diversity without regard to the abundance of the fossil species being studied. One main reason is that the obvious potential taphonomic biases of fossil preservation have tended to promote the idea that fossil abundance may not be biologically or ecological informative. But by omitting rigorous consideration of abundance data, paleontologists have not simply omitted information. We have probably also distorted our perception of past processes at many scales ranging from paleocommunities through macroevolutionary dynamics.

Perhaps the most important distortion of our perception has come from the tendency of paleontologists to study mainly abundant species. As seen in Figure 4, Sepkoski (1994) has estimated that paleontologists have sampled mainly the most abundant 6-7% of fossil species. Gaston (1994) has noted the same problem in ecology, and for the same reason: Common species are obviously easier to obtain. But, as Gaston (1994) also discusses, common species often have different biological traits from rare species so that our omission of rare species may seriously bias what we think are "normal" biological dynamics. Many workers (*e.g.*, Stanley, 1990) have, for example, noted that rare species have much higher extinction and speciation rates than common species. By sampling mainly the most common species, we have probably greatly underestimated past extinction and speciation rates, as Raup (1988) has suggested.

Similarly, a focus on common fossil species may be a reason for the frequent interest in long-term paleocommunity stasis (*e.g.*, Brett and Baird, 1995). McKinney *et al.* (in press) discuss how the apparent ecological stasis of fossil communities may be misleading because the data omit many rare species that may have high rates of ecological turnover (local extinction and recolonization) and have little interaction with other species. The appearance of stasis may occur because widespread common species form the large bulk of the data. As Jackson (1994) has recently cautioned: "paleoecologists need to pay more attention to the relative abundances of species if we are to resolve the issue of how much community structure is more than just the sum of the component species parts." A major message of this paper is not only that paleontologists should pay more attention to abundance, but that fossil abundance apparently contains considerably more biological information than it has often been given credit for.

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