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Species–time curves and population extremes: Ecological patterns in the fossil record

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ABSTRACT

Accumulation of species in geological time follows species–time curves that are similar to species–area curves, as predicted by Preston. The *z*-values of these fossil species–time curves range from 0.30 to 0.36, similar to species–area curves produced by sampling islands and other widely separated habitats. We suggest that such *z*-values in species–time curves occur because the episodic nature of fossil deposition essentially produces temporal 'islands' of widely spaced samples. We also find that marine fossil species tend to exhibit increased variation of abundance with time (reddened spectra) in ways that are consistent with marine abundance patterns measured across much shorter ecological time-scales. This adds further support to the view that physical parameters in the ocean vary over larger temporal and spatial scales than on land, including geological scales.

Keywords: fossil, population, species–area, species–time.

INTRODUCTION: SPECIES ACCUMULATION IN TIME

Do species accumulate in regular patterns through time? Preston (1960) hypothesized that annual censuses in a fixed area would reveal a species–time curve, fitting a function similar to a species–area curve: $\log S = c + z(\log A)$. (A is area for the species–area curve and would be substituted by time for the species–time curve.) While species–time curves have received much less attention than species–area curves, there is increasing interest in how species accumulate in both ecological (Rosenzweig, 1995; Gaston, 1996) and geological (Rosenzweig, 1995) time-scales. A main goal here is to extend Rosenzweig's (1995, 1998) initial attempts to describe fossil species accumulation in geological time via species–time curves. We show, using data from fossil foraminifera, that species–time curves at geological scales do follow species–area patterns as hypothesized by Preston (1960). We also suggest, using a previously published model of spatio-temporal fossil deposition (McKinney and Allmon, 1995; McKinney, 1996; McKinney *et al*., 1996), how these patterns of temporal accumulation may arise.

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In the second part of the paper, we show that another ecological temporal abundance pattern, that of population extremes, is found in the fossil record. We extend the work of Arino and Pimm (1995), who found that, at time-scales of less than 100 years, species in marine ecosystems have larger abundance increases than species in terrestrial and freshwater ecosystems. We show that, when analysed with the same method as Arino and Pimm (1995), fossil marine foraminifera show patterns of abundance fluctuations that are very similar to modern marine patterns. This is true despite the enormous difference in temporal scale: 100 years or less for modern species, versus many thousands of years for our fossil samples. This similarity may occur because the physical variables driving abundance patterns operate over many time-scales and often have a 'reddened spectrum' (more time = more variation) at those scales (Steele, 1986).

SPECIES–TIME CURVES: PATTERNS

Preston (1960) hypothesized that temporal sampling of an area, such as by annual censuses, would produce a species–time curve with the same general pattern as a species–area curve (Rosenzweig, 1995). In theory, this pattern would occur because, as with species–area curves, successive temporal samples would accumulate progressively fewer new species and so produce z-values of less than 1. We discuss the processes that could create this pattern (such as finding rare or vagrant species with successive samples) in the next section. First, we present further evidence bearing on whether such patterns even exist.

At ecological scales, annual censuses of birds and moths produce z-values ranging from 0.13 to 0.31, respectively, when calculated on log–log plots (Rosenzweig, 1995). At geological scales, our main focus in this paper, we are aware of only two previous data sets that have been published. These are the studies of Rosenzweig (1995) and McKinney *et al.* (1996), who reported z-values of 0.36 and 0.33, respectively. As seen in Table 1, these two studies used very different rock units, from different palaeoenvironments, of different ages (Palaeozoic versus Cenozoic) and of different biotas (benthic invertebrates versus foraminifera).

Table 1 also shows the results of new data, presented here in Fig. 1. Figure 1 consists of log–log plots of abundance data of late Eocene to early Oligocene foraminifera representing three different palaeoenvironments. '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

Table 1. Values of z for various ecosystems, estimated with log–log plots

Location	Time span	Palaeoenvironment	z	Source
Nicolet River (Quebec)	3–4 Ma	muddy benthos	0.36	Rosenzweig (1995)
Drill core (Georgia)	1–2 Ma	offshore carbonate	0.33	McKinney *et al*. (1996)
Brooksville (Florida)	1–2 Ma	nearshore carbonate	0.33	Fig. 1
Sepulga River (Alabama)	1–2 Ma	offshore carbonate	0.38	Fig. 1
Red Bluff (Mississippi)	1–2 Ma	mid-shelf clastic	0.26	Fig. 1

Note: Apart from the Quebec data, all z-values show accumlation of foraminifera species in rocks from the early Cenozoic Era (late Eocene to early Oligocene). In all cases, r^2-values exceed 0.93.

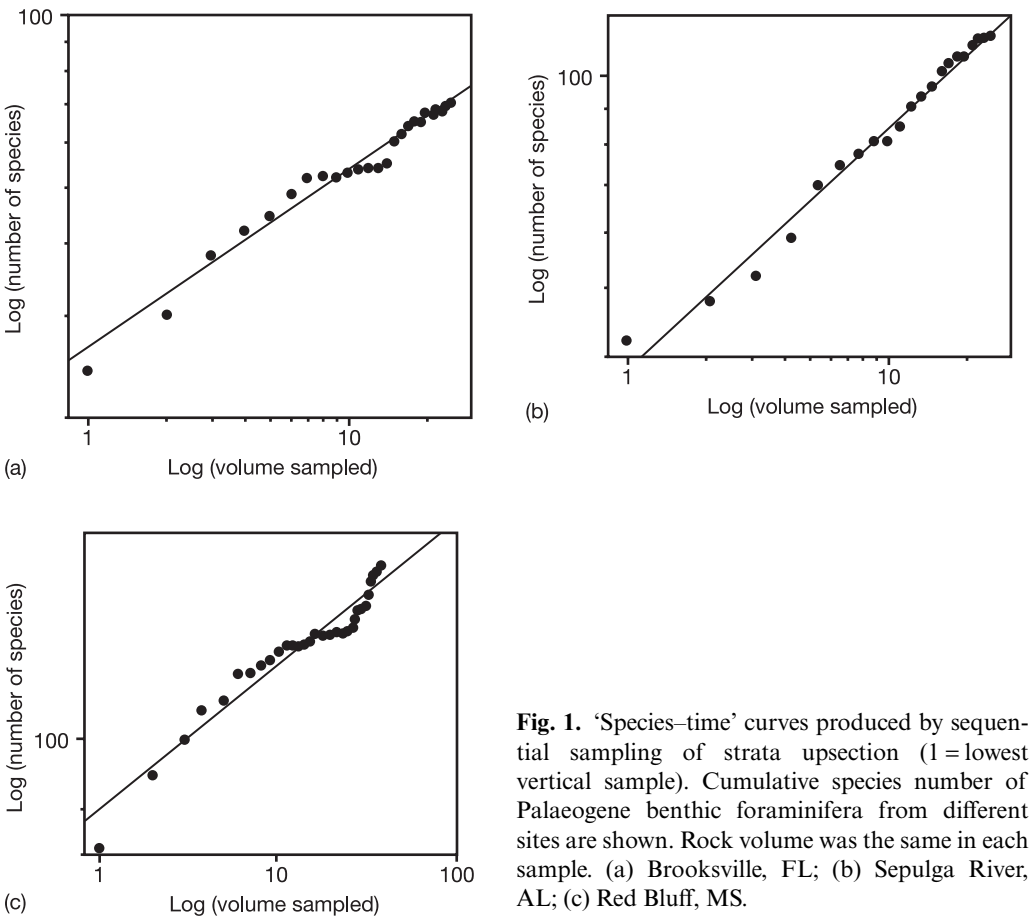

Fig. 1. 'Species–time' curves produced by sequential sampling of strata upsection (1 = lowest vertical sample). Cumulative species number of Palaeogene benthic foraminifera from different sites are shown. Rock volume was the same in each sample. (a) Brooksville, FL; (b) Sepulga River, AL; (c) Red Bluff, MS.

sample was the same volume and samples were taken at roughly equally spaced stratigraphic (vertical) intervals. We have found that high variation in sample spacing will produce species–time curves that are not straight in log–log space. They 'wobble' even more than those in Fig. 1 because closely spaced samples accumulate few new species and produce flattening of the curve, compared with widely spaced samples that accumulate many new species with each sample (for further discussion of methods, see McKinney and Allmon, 1995; McKinney, 1996). The plots in Fig. 1 indicate considerable consistency of pattern, with *z*-values (Table 1) similar to the 0.36 found by Rosenzweig (1995). We hasten to note that all of the *z*-values in Table 1 are similar to those found in species–area curves derived from sampling islands. This is a very important point, to which we will return.

Importantly, the data in Fig. 1 are derived from a wide range of palaeoenvironments. The palaeoenvironments and sampling location are shown in Fig. 2. The Florida data are from a limestone quarry in central Florida described in detail in McKinney and Frederick (1992). These rocks were deposited in an offshore carbonate palaeoenvironment (Fig. 2). Figure 2 also shows the locations and palaeoenvironments of the other data sets, from Alabama, Mississippi and the Georgia core data. [A detailed description of the geological sites sampled and faunal lists obtained can be found in Frederick (1994).] These data thus cover

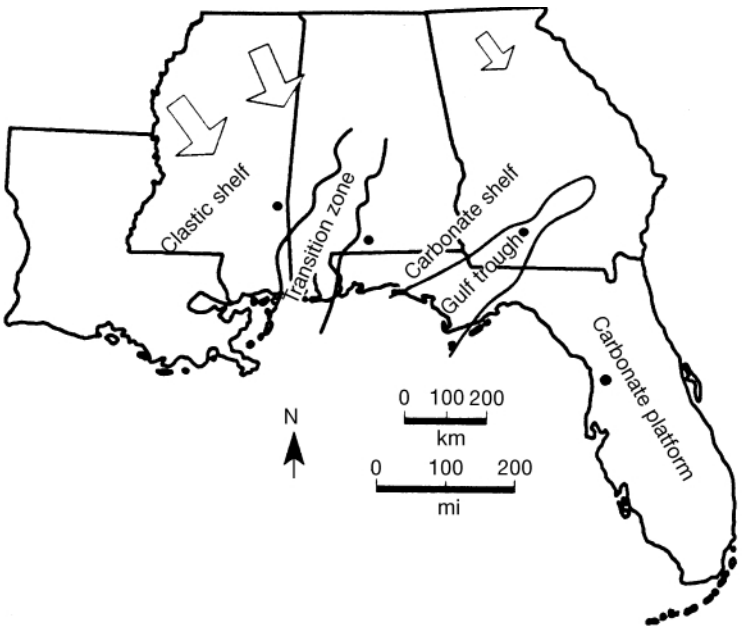

Fig. 2. Locations and palaeoenvironments of all fossil samples (except Quebec) in Table 1. Arrows show direction of sediment movement from land. A detailed description of the geological sites sampled and faunal lists obtained can be found in Frederick (1994).

palaeoenvironments ranging from mid-shelf clastic to offshore carbonate. Thus, the *z*-value consistency is rather striking, given the potential for different rates of sedimentation and preservation.

SPECIES–TIME CURVES: PROCESSES

Gaston (1996) noted that areas of moderate size rarely show equilibrial diversity patterns on ecological time-scales because new species are being added as temporal sampling continues. He discussed three basic ways that species are added during successive censuses in ecological time: reduced sampling error, vagrants and colonists (Gaston, 1996). We have organized these into a framework that also includes geological time, shown below. Note that the four categories on this list simply identify the accumulating species in terms of their origin. The role of physical change in bringing these individuals into the area will be discussed shortly.

I. Additions in ecological time (days to thousands of years)
   1. *Newly sampled species*: rare species that were present but previously unsampled. Scale = days to decades.
   2. *Vagrants*: species that do not normally reside in the area but occur temporarily on a regular or irregular basis. This could include recurring extinction–colonization cycles of metapopulation dynamics (Hanski and Gilpin, 1997). Scale = days to decades.

3. *Colonists*: species that are introduced into the area and become permanent residents. Scale = hundreds to thousands of years.

II. Additions in geological time (thousands to millions of years)

1. *Newly evolved species*: speciation produces new vagrants and new colonists. Scale = many thousands to millions of years.

Each process is ranked in approximate order of importance at increasingly large time-scales. Sampling additions and vagrants are most important at fine day-to-decade time-scales, while evolution takes many thousands of years to add species to the area by adding new vagrants or colonists. Intermediate to these temporal extremes is colonization, which, before human intervention, usually occurred over scales of hundreds (islands) to many thousands (continents) of years, according to fossil data on biotic interchange (Vermeij, 1991). Before the rapid spread of human-introduced biotas, organisms relied on the removal of geological barriers, the creation of land bridges and other much slower natural processes for colonization.

Figure 3 adds the important geographical dimension to the four categories above. The classical species–area (SPAR) patterns accumulate new species by spatial sampling of new habitats, as shown on the horizontal axis, indicating progressively more spatially distant samples. Conversely, the four categories of species–time (SPTI) accumulation, on the vertical axis, generally reflect the spatial origin of the species. Newly sampled species are rare species that occur in the immediate area. Vagrants tend to be 'sink' species from nearby habitats. Colonists are more permanent residents that immigrate from more distant habitats. There is also a strong geographical component to evolutionary additions. Rosenzweig (1995) discussed how distant provinces tend to have evolutionarily distinct biotas because of longer geological isolation.

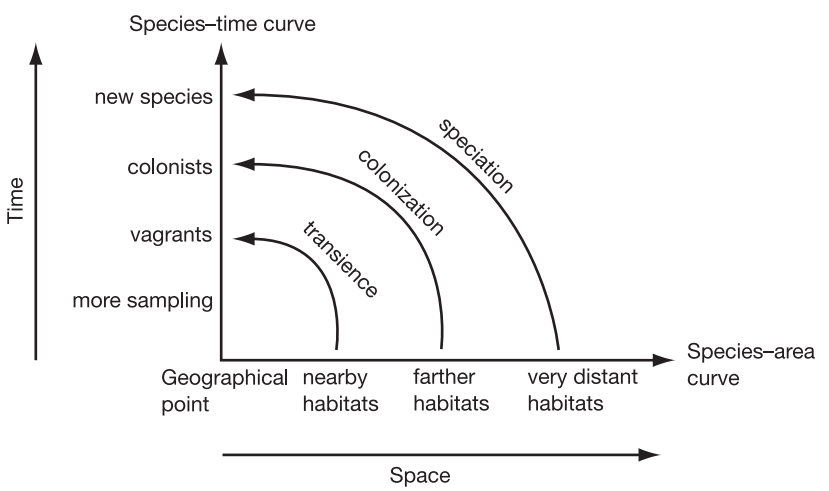

Fig. 3. Relationship between species–area (SPAR) and species–time (SPTI) curves. SPAR curves (horizontal axis) accumulate new species with more distant spatial sampling from a fixed geographical point. SPTI curves accumulate species with more distant temporal sampling at a fixed geographical point as new habitats traverse the point due to climatic, sea-level and other physical changes. Vagrants, colonists and evolutionary additions are names given to species that accumulate temporally in this way.

Figure 3 shows that species–time curves are produced over very long time-scales because the spatial location of habitats is not static. The fossil record shows that, over long time spans, shifts in climate, sea level and many other physical parameters cause shifts in habitat and lead to migration of species (e.g. Roy *et al.*, 1995). A fixed geographical point, such as in Fig. 3, will thus accumulate species over time in the same way as that of the species–area curve: new habitats are sampled. Furthermore, the lateral shifting of habitats over the region will tend to produce vertical samples in a sequence that reflect the horizontal pattern. Vagrants, colonists and evolutionary additions are names given to species that accumulate temporally in this way.

SPECIES–TIME CURVES IN THE FOSSIL RECORD

How does this framework help us understand the fossil patterns described above? A fossil sequence is usually a randomly sampled, gap-ridden temporal record of a tiny fixed spatial area. This is shown in Fig. 4, in that a stratigraphic section (= area of deposition) can be considered to be a 'particle' moving through populations of organisms composing a community. This model is discussed in detail elsewhere (McKinney and Allmon, 1995; McKinney, 1996; McKinney *et al.*, 1996) and is conceptually similar to the description given by Rosenzweig and Duek (1979). In reality, of course, populations move across the 'particle' (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 spatially varying set of populations than the reverse. This is especially true given that the populations of different species shown in Fig. 4 usually do not move in unison – that is, at the same rate or direction. The individualistic behaviour of different species (Brown, 1995) means that species will often migrate independently in different directions, as demonstrated by Roy *et al.* (1995). Figure 4 is thus a motion picture of the community, tracking its path over the area of deposition through space and time.

If the model in Fig. 4 is valid, then we might predict that a vertical sequence of stratigraphic samples would indeed follow a species–time curve. This is because, as the

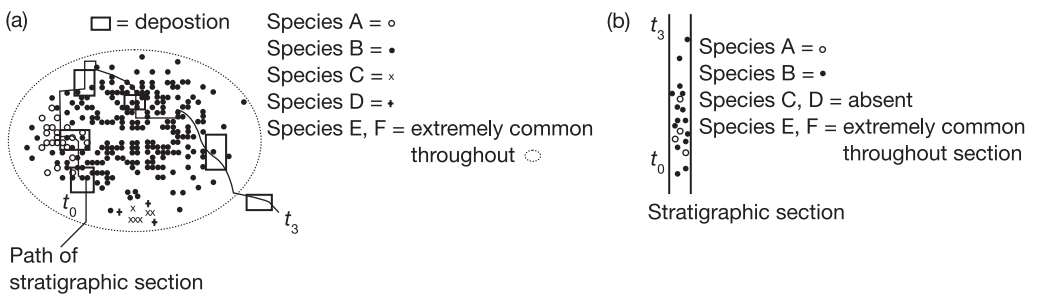

Fig. 4. (a) Formation of a stratigraphic section can be modelled as a localized area of deposition that moves horizontally through spatially co-existing populations of species. Symbols (e.g. ×) are individuals of designated species with the patchy distribution of most species. Deposition only occurs at certain areas shown by boxes. The ultimate pathway of a section is shown, with t_0 and t_3 indicating times when the section reaches the given point shown. (b) Stratigraphic section depicting vertical distribution of fossilized individuals of species. Species with a localized and sparse spatial distribution also show a localized and sparse vertical distribution.

'particle' (depositional area) of Fig. 4 traverses populations of different species, it is similar to taking random samples around an expanding area. As first noted by Williams (1943), sampling larger areas will tend to increase the number of habitats and individuals sampled and thus the number of species in the species–area curve (see Leitner and Rosenzweig, 1997, for recent theoretical insights). In our model of Fig. 4, increasing the area sampled is roughly proportional to increasing the sediment volume sampled. We can tentatively infer that the species–time curve occurs because the number of species preserved and sampled is roughly proportional to sediment volume preserved and sampled.

Note how this scenario introduces two important modifications to the temporal accumulation of species shown in Fig. 3: random samples and gaps between samples. Both of these modifications tend to increase the z-value of a species–area (and species–time) curve. Whereas nested adjacent subsamples tend to produce species–area curves with low z-values of 0.1–0.2, species–area curves of oceanic islands tend to be higher (Rosenzweig, 1995). The same is true of random samples taken within an area (Rosenzweig, 1995, fig. 2.3). In the case of sampling of strata, it is a continually expanding area (see fig. 5.2 in McKinney and Allmon, 1995). Such higher z-value slopes are produced because sampling non-adjacent areas increases the number of new habitats and thus species encountered with each sample (Williams, 1943; Rosenzweig, 1995).

It is therefore very interesting that the z-values in Table 1 range from 0.26 to 0.38. [This may also be true of species–time curves produced in ecological time, as in annual sampling of insects (Rosenzweig, 1995).] These values are typical of z-values for species–area curves calculated for islands (Rosenzweig, 1995). We might thus infer that the z-values in Table 1 result from an island effect, but each sample is an 'island' in time *and* space instead of only space. The heterogeneity among samples is apparently relatively high because time has passed and the 'particle' of Fig. 4 has moved a considerable distance from the previous sample. New populations and new microhabitats that are not closely adjacent in space *or* time are being sampled. Even the geological details seem to conform to this process: the lowest z-value in Table 1 is for the Red Bluff unit, which was an area near the continent that received rapid deposition (Fig. 2). The higher depositional rate would imply that the spatio-temporal 'islands' being sampled were less isolated in time and space for this unit. This would tend to produce lower z-values than those expected from islands (Rosenzweig, 1995).

POPULATION EXTREMES IN MARINE FOSSILS: RED SPECTRA

Studies (Pimm and Redfearn, 1988; Pimm, 1991; Arino and Pimm, 1995) indicate that, at ecological time-scales, population variability in most species increases with time. That is, population variation shows 'reddened spectra'. In addition, Arino and Pimm (1995) showed evidence that marine organisms tend to have larger increases in variability (redder spectra) in ecological time than terrestrial organisms.

Can these population variability patterns be seen in temporal patterns of fossil abundance? While there are many potential preservational problems, there is growing evidence that many original population abundance patterns are not completely erased by the fossil record (for reviews, see Kidwell and Flessa, 1995; McKinney, 1996). An example that is very relevant here is that living species tend to have abundance patterns that show spatial correlation: Areas of high abundance tend to be adjacent to other areas of high abundance (Maurer, 1994; Brown, 1995). This same spatial correlation is found in fossil species,

as illustrated by 'spaghetti' diagrams (Springer and Miller, 1990) and gradient analysis (Patzkowsky, 1995).

In addition, spatial and temporal patchiness are correlated in a number of living species. Widespread species show little tendency for drastic temporal abundance change anywhere in their geographical range, whereas rarer species seem to show greater relative abundance variation in both time and space (Maurer, 1994; Brown, 1995). Similarly, in fossils, CoBabe and Allmon (1994) showed that the coefficient of variation for the abundance of rare fossil species increased with increased number of stratigraphic samples taken, whereas it did not increase in common species.

Such agreement between living and fossil abundance patterns tentatively implies that we might also find Arino and Pimm's reddened spectral patterns of increasing abundance variation in the fossil record. Table 2 shows the results of an analysis of fossil foraminifera abundance by McKinney and Frederick (1992). Using the same methods as Arino and Pimm (1995), Table 2 shows H (Hurst exponent) values derived from rescaled range analysis, where increasing H-values indicate an increasing tendency for population (abundance) variation with time (for a discussion of H calculation, see McKinney and Frederick, 1992; Arino and Pimm, 1995). Table 2 indicates that foraminifera species with

Table 2. Number of geological stages that species persisted and the H-value of those species

Geological stages	Foraminifera species	H-value
4 +	*Guttulina irregularis*	1.10
	Cibicides pseudoungerianus	0.68
	Globullna gibba	0.27
	Mean	0.68
3–4	*Pyrgo inornata*	1.28
	Mississippiana monsouri	0.83
	Nonion advena	0.83
	Mean	0.98
1–2	*Operculinoides willcoxi*	1.44
	Eponides ocalana	1.44
	Cassidulina moodyensis	1.33
	Miliola newberryensis	1.24
	Reussela eocena	0.90
	Nummulites vanderstocki	0.80
	Camagueyia perplexa	0.73
	Rotalia cushmani	0.59
	Spiroloculina bidentata	0.57
	Operculinoides ocalanus	0.57
	Mean	0.96

Overall mean for all foraminifera species: 0.91, s.d. = 0.35.

Data from McKinney and Frederick (1992).

less abundance variation tended to persist longer in the fossil record (number of geological stages), as is often expected from ecological variation patterns (Pimm, 1991).

Furthermore, the mean H-value of 0.91 is in line with the findings of Arino and Pimm (1995) for marine species. Specifically, in a compilation of 58 species, Arino and Pimm (1995) found the following mean H-values: marine 1.02, freshwater 0.78 and terrestrial 0.72. They suggested that these patterns occur because, as Steele (1986) demonstrated, 'physical variables in marine systems have strongly reddened spectra, while terrestrial systems do not' (Arino and Pimm, 1995, p. 440). Our findings thus support their evidence and interpretation, although it is very tentative (e.g. the standard deviation of $H = 0.35$ in Table 2). Because our data describe variability across much larger time-scales (on the scale of hundreds to thousands of years), we can infer that, as predicted by Steele (1986) and Pimm (1991), the reddened spectral patterns of physical and biotic abundance should extrapolate across many time-scales. Indeed, the Hurst exponent itself is fractal and is thus ideal for such analyses.

CONCLUSIONS

Preliminary evidence indicates that two basic abundance patterns that occur at ecological time-scales also seem to occur at geological time-scales. Preston's (1960) conjecture about a close parallel between species–area and species–time curves appears to be valid at many scales. The basic origin of the general pattern of both curves lies the asymptotic nature of spatial and temporal sampling, whereby successive spatial and temporal samples discover fewer new species. That temporal sampling produces z-values over 0.25, typical of island and heterogeneous spatial sampling, may reflect the temporal discontinuous, episodic nature of most temporal samples available at ecological but especially geological time-scales.

The other basic ecological abundance pattern, that most species have increased abundance variation with time (reddened spectra), also seems to be detectable at geological time-scales. In agreement with data from ecological scales, the marine fossil species analysed tend to show highly reddened spectral values. This concurs with Steele's (1986) suggestions that physical parameters in the ocean vary over larger temporal and spatial scales than on land. It also concurs with the work of McGowan and Walker (1993), who showed that biotic processes in the oceans parallel this abiotic pattern by varying across larger spatio-temporal scales than terrestrial biotic patterns.

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