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BIODIVERSITY RESEARCH

Understanding regional species diversity through the log series distribution of occurrences

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Abstract. The distribution of benthic foraminifera around the continental margins of North America is extensively documented. Data from 2673 localities consists of a synonomized list of 2329 species (S) and 61 369 occurrences (n). Here, the margins are divided into five geographical regions: Pacific (PA), $S = 965$, $n = 19\,014$; Arctic (AR), $S = 458$, $n = 7342$; Atlantic (AT), $S = 878$, $n = 10\,034$; Gulf of Mexico (GM), $S = 849$, $n = 18\,011$; Caribbean (CR), $S = 1188$, $N = 6968$. As for many other organisms, species richness is lowest in the Arctic and highest in the Caribbean. In each region, the distribution of species richness and occurrences is a log series. Consequently, the entire series of species occurrences is predicted by the single proportionality constant, α. After log series rarefaction, differences in species richness among areas are nearly all accounted for by species occurring ≤ 10 times. Most of the differences are accounted for by species occurring once, less by twice, and so on. For example, species occurring once account for 81% of the difference in species richness between the Atlantic and Caribbean, and those occurring once and twice account for 87% of the difference. Most rare species have no fossil record and most endemic species are rare. Probably most of these species evolved recently indicating more origination in species-rich areas. High origination might also be coupled with less extinction. Although each of the five regions can easily be distinguished by differences in composition, in all regions the 10 most abundantly occurring species exhibit nearly equal proportions of occurrences. No region is dominated by only one or two species. All regions exhibit the log series distribution, have nearly equal proportions for abundant species, and differ only in the number of rare species that coexist. Thus, from the point of view of the distribution of occurrences, the most striking aspect is the similarity among regions.

Key words. regional species diversity, log series, occurrences, foraminifera

INTRODUCTION

Because abundance data are often unavailable, biogeographers (e.g. Brown, 1988) sometimes lament that mathematical distributions and diversity indices cannot be used on biogeographical data. However, Hayek & Buzas (1997) showed how species occurrence data can be used as a surrogate for those of abundance. Consider an area sampled by M stations or localities. A species represented by one individual also occurs at only one station. A species represented by two individuals may occur at one or two stations, and so on. The maximum number of individuals for the most abundant species may be quite large, but the maximum number of occurrences for a species is M. Another way of thinking about occurrence data is to imagine a sampling device so small that only a single individual can be captured during sampling. The species with the highest densities will appear in the greatest number of samples and the less abundant in fewer. For benthic foraminifera species occurring at only a few localities are almost always represented by only a few individuals. Consequently, for these species which comprise the majority, the number of occurrences and the number of individuals are similar in number. The few abundant species, however, often have many more individuals than occurrences because the latter is restricted by the number of localities sampled. The relationship

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is consistent enough so that on a log scale, density (abundance) can be predicted from occurrences. Hayek & Buzas (1997) demonstrated that except for the most abundant species, the predicted density from a regression on occurrences matches the observed density of benthic foraminifera in a traverse from the northern Gulf of Mexico. Therefore, the number of occurrences can be used as a surrogate for density.

We can use occurrences in their own right because they do measure abundance or density, but on a different scale, one on which the variance associated with individuals is largely dampened, which is a desirable property. Using this line of reasoning Buzas *et al.* (1982) substituted N occurrences for N individuals and showed that the number of species and the number of occurrences fit a log series for molluscs and benthic foraminifera quite well. We will further examine this relationship here.

At the species level, differences in distribution with depth and latitude are readily apparent for most benthic marine organisms including the foraminifera. If we were to list desirable attributes for a group of organisms that would well qualify the group for biogeographic studies at the species level, we might list: 1) ubiquitous distribution; 2) easily sampled; 3) high density; 4) many species; 5) good preservation providing an excellent fossil record; 6) large number of researchers; 7) many years of study. The benthic foraminifera have all of these attributes. Culver & Buzas (1980, 1981, 1982, 1985, 1986, 1987) compiled and taxonomically standardized all the existing data on the distribution of benthic foraminifera around the continental margins of North America. In the present study, we will consider the five geographical regions: Pacific (PA); Arctic (AR); Atlantic (AT); Gulf of Mexico (GM); Caribbean (CR). We will use these data sets to further our understanding of the biogeography of benthic foraminifera with particular emphasis on the significance of the distribution of species occurrence for species diversity. Because the data for benthic foraminifera are so extensive, any insights gained can serve as a model that can be tested for other groups of benthic organisms.

THE LOG SERIES DISTRIBUTION OF OCCURRENCES

The mathematical relationship of the number of individuals, N, to the number of species, S, in natural populations and associated diversity indices have been a subject of intense inquiry for over 50 years (see Hayek & Buzas, 1997; for a review). One of the most elegant and successful distributions is the log series (Fisher, 1943). The log series is a special case, or limiting form of the negative binomial distribution. As originally used, the distribution predicted the number of species represented by one individual, two individuals, and so on. In the present context, we substitute occurrence for individual so that we predict the number of species occurring once, twice, and so on. The log series is written as:

$$S = -\alpha \ln(1-x) = \alpha x + \alpha x^2/2 + \alpha x^3/3 + \ldots + \alpha x^n/n \quad (1)$$

where S is the number of species, α a proportionality constant, x a constant close to 1 and n the number of occurrences. The right side of the equation allows for the prediction of the number of species represented by one occurrence (αx), two occurrences ($\alpha x^2/2$), and so on. Obtaining a value for the constant α is not simple and requires an iterative solution. However, Murray (1973) provides a graph for approximate values and Hayek & Buzas (1997) provide an extensive tabulation of α values for a given N and S. Once α is obtained, x is easily solved for by the equation:

$$x = N/(N+\alpha) \quad (2)$$

This distribution contains only one parameter, the constant α, which is often used as a diversity index. Because x is a number close to 1, it is easy to see that α is a number close to the number of species expected with one occurrence (αx).

RARELY OCCURRING SPECIES

Using the observed N occurrences and S species, we have calculated α and the number of species expected with 1, 2, . . ., N occurrences for the five areas around North America. Figure 1 shows the occurrences for the data from the CR grouped into $\log_2$ classes. The fit is quite good. Most of the species occur only a few times and, consequently, the portion of the log series with the rarer species is of most interest. Table 1 lists and Fig. 2 illustrates the predicted and observed occurrences for ungrouped data in the categories 1,2, . . ., 10 for the five regions.

Just as we used occurrences instead of individuals for our calculations of the log series, so too can we use the total number of occurrences to calculate the proportion of total occurrences each species represents. We can then calculate the Shannon (1948) information

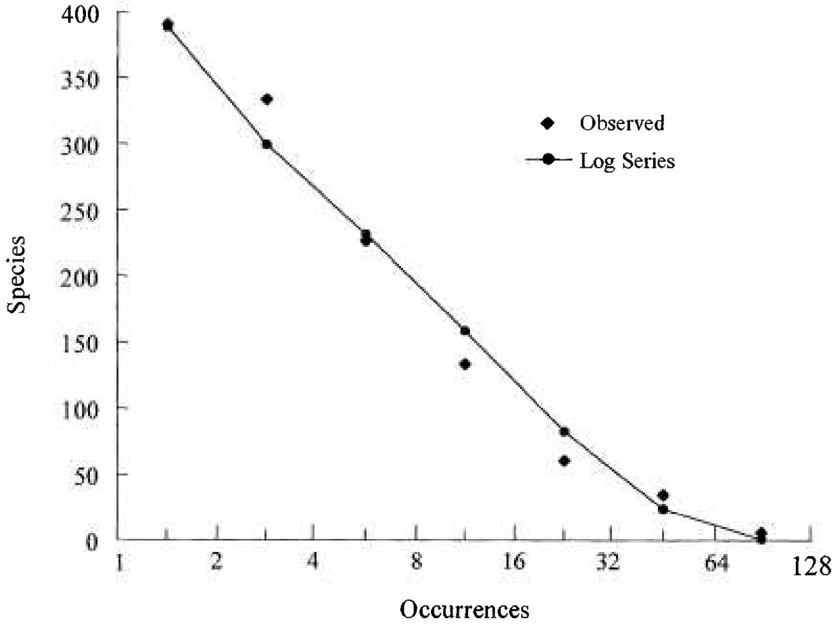

Fig. 1. Number of species and occurrences observed and predicted from a log series for Caribbean data (Culver & Buzas, 1982). Data are grouped into $\log_2$ classes. The total number of species, S, is 1188, the total number of occurrences, *N*, is 6968, and the parameter α of the log series is 412.

function, H, for occurrences. The familiar relationship is:

$$H = -\sum_{I=1}^{S} p_i \ln p_i \qquad (3)$$

where in this case p_i = occurrences of species I divided by the total number of occurrences. For a log series, the expected value of the information function is:

$$H = \ln\alpha + 0.58 \qquad (4)$$

where 0.58 is Euler's constant and α is the parameter of the log series (Bulmer, 1974). Once H is calculated, a measure of evenness, E, can be calculated by:

$$E = e^H/S \qquad (5)$$

where e is the base of the natural logs (Buzas & Gibson, 1969). The two are related by the decomposition equation

$$H = \ln S + \ln E \qquad (6)$$

which allows us to measure species richness and evenness within the same system (Buzas & Hayek, 1996, 1998; Hayek & Buzas, 1997). Because the value of E is between 0 and 1, $\ln E$ is always negative. Now $H_{max} = \ln S$, so that (6) indicates that H is the maximum species richness minus the amount of evenness. Equation 6 also shows that once H is determined by (3) or (4), E is fixed by (6) and the value can be determined either by (5) or (6). Note also that because α is a constant (4) indicates that H is a constant and (6) requires that as the number of species increases ($\ln S$), the evenness ($\ln E$) must decrease by the same amount to satisfy (6).

The observed and expected values of H and E for a log series are also shown in Table 1. The expected and observed values all agree reasonably well. The values of α are in general agreement with a ranking of the areas by the observed number of species. However, the AT now becomes more diverse, in terms of α, followed by the PA. In all areas, the majority of species occur rarely. This suggests that the great increase in diversity observed in the CR results from the presence of many rarely occurring species.

Table 1 indicates wide variation in the total number of occurrences among areas and, in order to effectively compare the areas, standardization is required. The CR has the highest diversity and the lowest number of

Table 1. Number of species (S), number of occurrences (N), number of ubiquitous species, number of endemic species with (%), number of localities, and the observed (O) and predicted (P) values for a log series around North America. Pacific (PA); Arctic (AR); Atlantic (AT); Gulf of Mexico (GM); Caribbean (CR)

	PA	AR	AT	GM	CR
S = number of species	965	458	878	849	1188
N = number of occurrences	19 014	7342	10 034	18 011	6968
Ubiquitous	112	112	112	112	112
Endemic	420(43)	107(23)	159(18)	182(21)	458(38)
Localities	999	368	542	426	338
α	215	108	232	185	412
x	0.9888	0.9855	0.9774	0.9898	0.9442
$H_{observed}$	6.03	5.09	5.94	5.88	6.35
$H_{log\ series}$	5.95	5.26	6.03	5.80	6.60
$E_{observed}$	0.43	0.36	0.43	0.42	0.48
$E_{log\ series}$	0.40	0.42	0.47	0.39	0.62

Occurrences	Number of species									
	PA		AR		AT		GM		CR	
	O	P	O	P	O	P	O	P	O	P
1	199	212	139	106	236	226	217	183	391	389
2	92	105	56	52	111	111	98	91	206	184
3	66	69	23	34	72	72	55	60	128	116
4	37	51	25	25	51	53	33	44	73	82
5	48	41	22	20	43	41	25	35	75	62
6	36	34	18	16	25	34	16	29	47	49
7	28	28	9	14	28	28	15	25	32	39
8	23	25	12	12	14	24	20	21	31	32
9	22	22	6	10	24	21	7	19	27	27
10	13	19	7	9	15	18	17	17	17	23
Total	564	606	317	298	619	628	503	524	1027	1003

occurrences (Table 1). Because we have identified the log series as the statistical distribution fitting the observations, the other four areas are rarified to $n = 6968$ occurrences (CR) and the number of species are estimated considering the value for α already calculated. The expected number of species for a log series with a given $N = 6968$ and the α for each area is:

$$S = \alpha ln(1 + 6968/\alpha) \qquad (7)$$

(Hayek & Buzas, 1997). The estimated number of species in each area (Table 2) is now in agreement with α, and the AT is more species rich than the PA (compare with Table 1). Using (2) we now calculate a new x for each area and using (1) estimate the number of species with 1, 2, . . ., 10 occurrences for each area. The excess number of species in the CR for each category is obtained by subtracting the number predicted for a log series for the CR from the corresponding estimated number of occurrences in each area obtained by rarefaction. By adding the excess in the CR in each category of occurrence to the total number of species estimated for each area by (7) an accumulation is formed, demonstrating how each area approaches the number of species in the CR (1188). Table 2 shows and Fig. 3 illustrates that the difference in species richness between the CR and the other areas is accounted for by species occurring 10 times or less. The importance of rarely occurring species is even more striking when we consider that most of the difference is made up mostly of species occurring once, less so by those occurring twice, and so on. For example, in the PA, species occurring once make up 935/1188 = 79% of the difference, once and twice 86%, once, twice, and thrice 90%. The other areas show a similar pattern. The log series gives a quantitative estimation of how rare species

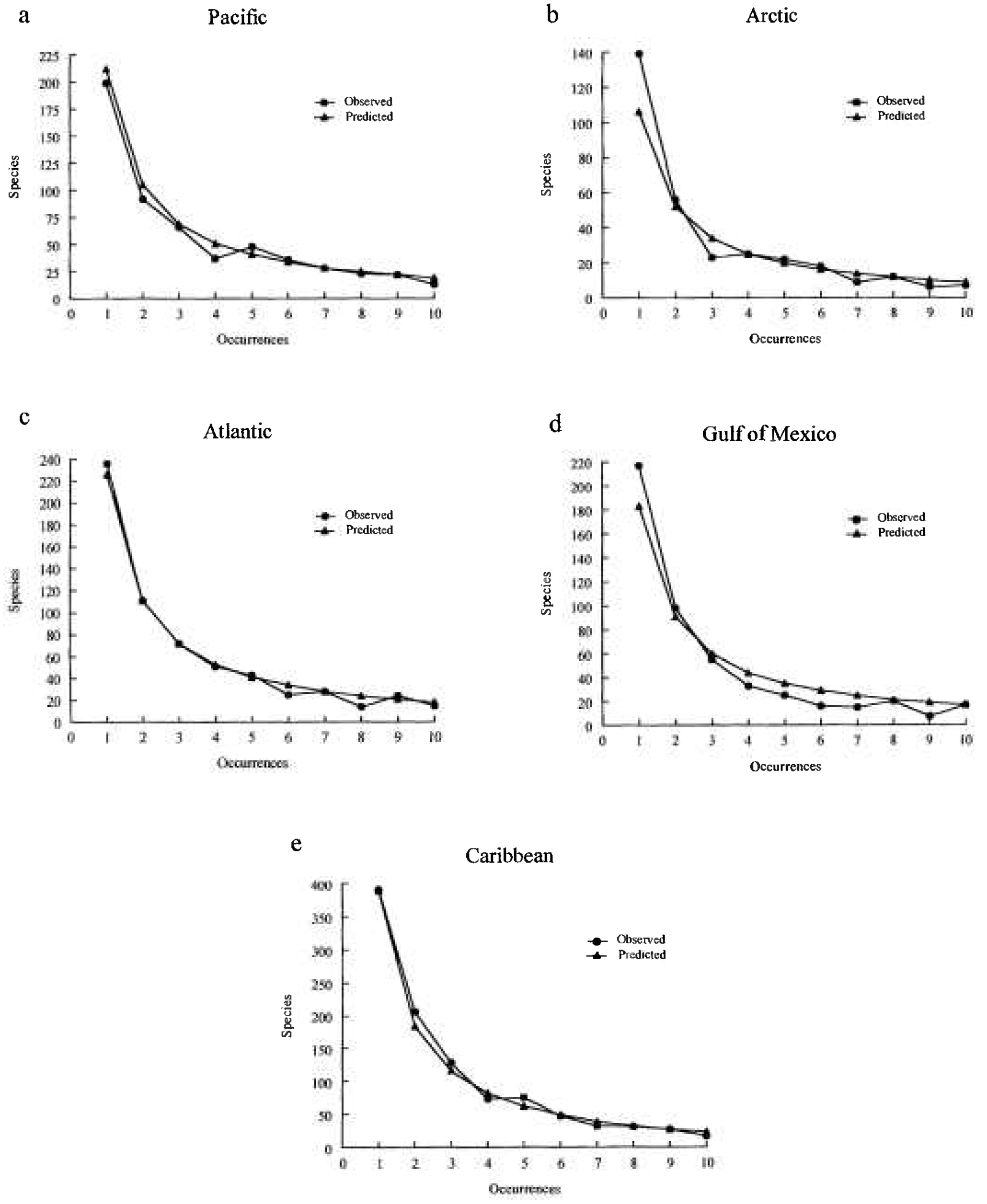

Fig. 2. Number of species and occurrences observed and predicted from a log series for occurrence categories 1, 2, …, 10. (a) Pacific data from Culver & Buzas (1985, 1986, 1987); the total number of species, S, is 965, the total number of occurrences, *N*, is 19 014, and the parameter α of the log series is 215. (b) Arctic data from Culver (unpublished); the total number of species, S, is 458, the total number of occurrences, *N*, is 7342, and the parameter α of the log series is 108. (c) Atlantic data from Culver & Buzas (1980); the total number of species, S, is 878, the total number of occurrences, *N*, is 10 034, and the parameter α of the log series is 232. (d) Gulf of Mexico data from Culver & Buzas (1981); the total number of species, S, is 849, the total number of occurrences, *N*, is 18011, and the parameter α of the log series is 185. (e) Caribbean data from Culver & Buzas (1982); the total number of species, S, is 1188, the total number of occurrences, *N*, is 6968, and the parameter α of the log series is 412.

Table 2. The number of species (S) expected in each area was estimated by rarefying to $N=6968$ (CR) by equation 7. The values of α estimated for each area (Table 2) were used to calculate a value of x from equation 2 and equation 1 was used to estimate the number of species expected with 1, 2, . . ., 10 occurrences in each area. The value estimated for the CR (Table 2) was subtracted from each corresponding estimate to obtain the excess in the CR for the categories of occurrence 1, 2, . . ., 10. By accumulating these values with the expected number of species in each area obtained through rarefaction, the difference between the species richness in the CR and other areas is accounted for by observing how quickly equivalent species richness is reached

	PA	AR	AT	GM	CR
N	6968	6968	6968	6968	6968
α	215	108	232	185	412
x	0.9701	0.9847	0.9678	0.9741	0.9442
S	754	451	797	676	1188
Occurrences					
1	935	734	962	885	0
2	1018	866	1037	981	0
3	1069	948	1083	1040	0
4	1103	1005	1114	1080	0
5	1128	1047	1137	1110	0
6	1147	1080	1154	1133	0
7	1161	1105	1167	1150	0
8	1172	1125	1177	1163	0
9	1181	1142	1185	1174	0
10	1188	1156	1191	1183	0
Totals	1188	1156	1191	1183	1188

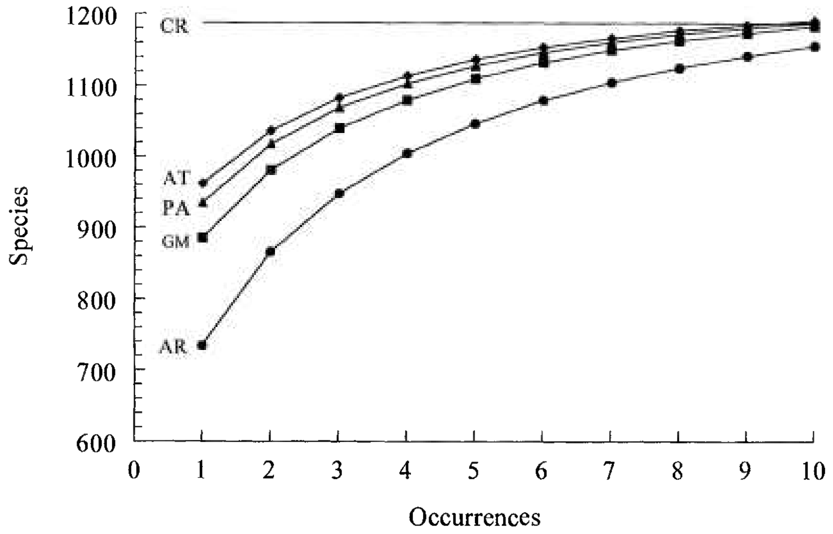

Fig. 3. The total number of species expected in each region after taking into account excess species in the CR in the categories of occurrence 1,2,. . .,10. See Table 2 for explanation.

Table 3. The number of occurrences for each of the 10 most abundantly occurring species in each of the five areas were totalled. The proportion of each of the I species (p_i) was calculated by dividing the number of occurrences of the ith species by the total

Species rank	PA p_i	AR p_i	AT p_i	GM p_i	CR p_i
1	0.1299	0.1432	0.1924	0.1327	0.1307
2	0.1254	0.1360	0.1344	0.1230	0.1293
3	0.1067	0.1129	0.1023	0.1116	0.1178
4	0.1027	0.1023	0.0962	0.1026	0.1121
5	0.0972	0.0871	0.0878	0.0948	0.0977
6	0.0916	0.0858	0.0824	0.0888	0.0948
7	0.0891	0.0838	0.0802	0.0882	0.0891
8	0.0861	0.0832	0.0756	0.0864	0.0805
9	0.0856	0.0832	0.0748	0.0864	0.0761
10	0.0856	0.0825	0.0740	0.0852	0.0718
Total	0.9999	1.0000	1.0001	0.9997	0.9999
Total top 10 occurrences	1986	1515	1310	1666	696
$\lambda=\Sigma\ p_i2$	0.1023	0.1048	0.1126	0.1027	0.1042
$E=e^H/S$	0.9884	0.9772	0.9475	0.9871	0.9793

contribute to the difference in species richness. Regardless of the hypothesis used to explain differences in species richness, these results show that the difference in species richness among areas is due to rare species.

ABUNDANTLY OCCURRING SPECIES

For each of the five regions, the occurrences of the 10 most abundantly occurring species was summed and the proportion of this total for each species tabulated (Table 3). In all regions, the difference in the proportions from the most abundant to the least is small, and the values are similar. An effective way to measure the concentration of the classification, especially when there are an equal number of categories (Hayek & Buzas, 1997), is Simpson (1949) which is written:

$$\lambda=\sum_{i=1}^{S} p_i^2 \qquad (8)$$

If all the proportions are equal, then the value of λ is 1/S or 0.1000 where S = 10. The results (Table 3) show that the proportion of occurrences for the five areas are not only similar, but also indicate a high degree of evenness. We also include E (5), another measure of evenness for which a value of E = 1 would indicate complete equality of the proportions (6). The evenness exhibited by all five areas is strikingly high and similar. The AT is less even than the other four regions because of slightly more dominance of the AT's most abundantly occurring species. However, the confidence interval for λ (Hayek & Buzas, 1997) in the AT is 0.08–0.15, and all the areas easily fall within the interval. In terms of the proportions of occurrences of the 10 most abundantly occurring species, all five areas are similar, and all allocate the occurrences nearly equally among the abundant species. The great disparity among areas when species richness was considered is no longer evident.

DISCUSSION

When numerical abundance data (densities) or relative abundance data (species per cent of the total) are recorded at stations, one species often dominates a fauna. The range in values (usually in per cent of the assemblage), however, is large, and ranges from different geographical areas and/or depths overlap so that generalizations on patterns are confusing (Gibson & Hill, 1992). By using occurrences, the effect of dominance is reduced and, on a regional scale, the distribution of the occurrences of abundant species is nearly equal (Table 3). Evidently, the variables which control distribution over a regional area vary sufficiently to prevent monopolization by one or a few species. Thus, consideration of occurrences presents us with a different viewpoint concerning the utilization of environmental resources and evolutionary strategy. A species may be dominant locally, but regionally, the distribution of occurrences is remarkably equitable.

Although the five areas of this study are easily discriminated by species compositions and species richness, the data on species occurrences all fit the log series. As equation 1 shows, the entire series of species occurrences is predicted by a single proportionality constant, α. Thus, the difference in species diversity among areas is measured by α, the parameter of the distribution which allows us to predict the number of species represented by 1, 2, , *n* occurrences (Table 1). This ability allows us to enumerate the contribution of rarely occurring species to the observed species richness (Table 2; Fig. 2). The difference in species richness among areas is due to rarely occurring species with the rarest contributing the most, the second rarest next, and so on (Table 3; Fig. 3). Consequently, any explanation concerning the difference in species richness among areas on a regional scale must explain why so many rarely occurring species exist in the lower latitudes.

One of the striking attributes of endemic species is that most of them occur rarely (Buzas & Culver, 1989, 1991). On the AT continental margin, of the 159 recorded endemic species, 143/159 = 90% occur less then 10 times and 79/159 = 50% occur once. The numbers for the CR are similar, where 447/458 = 98% of endemics occur less than 10 times and 231/458 = 50% of endemics occur once. In the AR, 87/107 = 81% of endemics occur less than 10 times and 46/107 = 43% occur once. Why are there three times more rare-endemic species in the CR than in the AT and five times more than in the AR?

In the modern fauna, most rare and endemic species do not have a fossil record and probably originated recently (Buzas & Culver, 1989, 1991). Many of these species will also have a short duration (Buzas & Culver, 1998). The data presented here show the differences in species richness among regions and with latitude are due to the increase in species with less than 10 occurrences and which, presumably, originated recently. Thus, the evidence indicates more origination at the lower latitudes (see also, Jablonski, 1993). Perhaps, the number of rare species is also enhanced by a longer period of survival in the low latitudes.

Similar to benthic foraminifera, marine prosobranch gastropods also exhibit a latitudinal gradient in species richness which Roy *et al.* (1998) correlated with solar energy input, represented by the average sea surface temperature. A hypothesis suggesting that the increase in solar radiation at lower latitudes enhances evolutionary speed and hence origination (Rohde, 1992) is supported by the observations made here. Other variables such as environmental variability, disturbance, patchiness and productivity may also influence the pattern (Sanders, 1968; Grassle, 1989, 1991; Stevens, 1989, 1992; Gooday & Turley, 1990; Loubere, 1997). The cautionary vision of Blackburn & Gaston (1996) that a single cause for all explanations may be unrealistic is noted. The data presented here indicate that regionally, occurrences are proportioned among species in a simple predictable way and no species dominates the entire area.

CONCLUSIONS

1. Species occurrences for five regions around North America fit a log series distribution.
2. Differences in species richness are due to rare species with less than 10 occurrences.
3. Most rare species have no fossil record and most endemic species are rare.
4. Most rare species probably evolved recently and species rich areas probably have more origination and less extinction.
5. On a regional scale, abundant species exhibit a nearly equitable number of occurrences.

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