TIME COMPONENTS OF COMMUNITIES

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ABSTRACT

When surveying a modern community with a good fossil record, two components are recognizable: species with a fossil record (immigrants to the Recent, I) and species without a fossil record (originating in the Recent, O). How many species will emigrate into the future is, of course, unknown. If we treat a slice of time in the past as representing the "present", older geologic time-slices as the past and younger geologic time-slices as the "future", four components are recognizable. The I's can be divided into immigrants which become emigrants, IE, and immigrants which become extinct, IX; while the O's are those originating that emigrate, OE, and those originating which become extinct, OX. Thus, the total number of species observed is S = IE + IX + OE + OX. The "future" consists of emigrants in time, E = IE + OE. The question arises as to whether or not information gleaned from such an approach is transferable to modern communities. With this in mind, we selected five Cenozoic time-slices and examined these four components of benthic foraminifera in the Salisbury-Albemarle Embayment (SAE) of the North American Atlantic coastal plain.

In all the fossil communities the species are distributed about equally ($\pm 10\%$) between O and I components. The OX component averages about half of the O species and are often rare. These species can be regarded as failed "evolutionary trials" and are a minimum estimate for extinction. Of the five fossil communities, three are balanced where OE = IX so that I = E and the total number of extinctions is TX = IX + OX = O. In balanced communities all of the components can easily be predicted, if one is known. In the two unbalanced communities, OE > IX so that E > I. In these two cases, IX is small and, consequently, TX ≈ OX.

Based on our observations of the fossil foraminiferal communities of the SAE, we would predict that about half of the observed species in a modern community will be extinct within two to three million years. A minimum estimate, the OX component, constitutes about a quarter of the observed species. While many of the OX species occur rarely, survivorship of species with a fossil record (I) cannot be predicted on the basis of abundance.

Consideration of the time slices also indicates that the local foraminiferal community depends on continual transfer of species into and out of a regional species pool. Consequently, if other organisms behave like foraminifera, any conservation efforts must be directed toward a large geographic area.

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INTRODUCTION

When surveying the modern inhabitants of an area, the researcher often has no information on the past history of the species in the taxonomic group under consideration. Thus, the observer is restricted to the present (the current time-slice) to explain the observations. However, if the group has a good fossil record, then the geologic history of some of the species may be known. The researcher now has more latitude for explaining the observations. Species may be divided into those with a fossil record (immigrants to the present time) and those without a fossil record which, we presume, originated recently. In this case, the past and present are known, but the surveyor of a modern fauna or flora cannot obtain information on the future of the species being surveyed. How the past and present affect the future will always remain as mere speculation. The purpose of this paper is to examine how the diversity of (on a geological time scale) communities is produced.

When surveying the fossil inhabitants of an ancient time-slice, the researcher does not have these restrictions. One fossil time-slice may be regarded as the "present", older time-slices become the past, and younger time-slices the "future". Unlike the modern community which can be divided only into immigrant (with a fossil record) and originating (no fossil record) species, the fossil community = time-slice can be divided into four categories (Buzas and Culver, 1994, 1998, 2001; Barry and others, 1995; Foote, 2000): 1. Immigrants-emigrants (fossil record in both older and younger time-slices); 2. Immigrants-extinct (fossil record in older, but no record in younger time-slices); 3. Originating-emigrants (no fossil record in older, but a fossil record in younger time-slices); 4. Originating-extinct (fossil record only in the time-slice under study). Thus, providing the group has a well documented fossil record, the "past", "present", and "future" of the species comprising the fossil community is obtainable.

Utilizing the four groups listed above, we examine the benthic foraminiferal communities in five Cenozoic time-slices of the Salisbury and Albemarle embayment (SAE) of the U. S. Atlantic Coastal Plain. We show how diversity depends on the dynamic relationship between events occurring outside of the observed community as well as within it. We also examine whether observations made on communities where the "future" is known are useful for predicting the future of species comprising modern communities.

GEOLOGIC SETTING

The Cenozoic deposits of the middle Atlantic Coastal Plain of the U.S. were laid down in the Salisbury-Albemarle Embayments (SAE) separated on occasion by the Norfolk Arch (Fig. 1; Ward, 1984; Fig. 2; Buzas and Culver, 1998). The units incorporated in this study are the Eocene Nanjemoy and Piney Point formations; the Miocene Pungo River
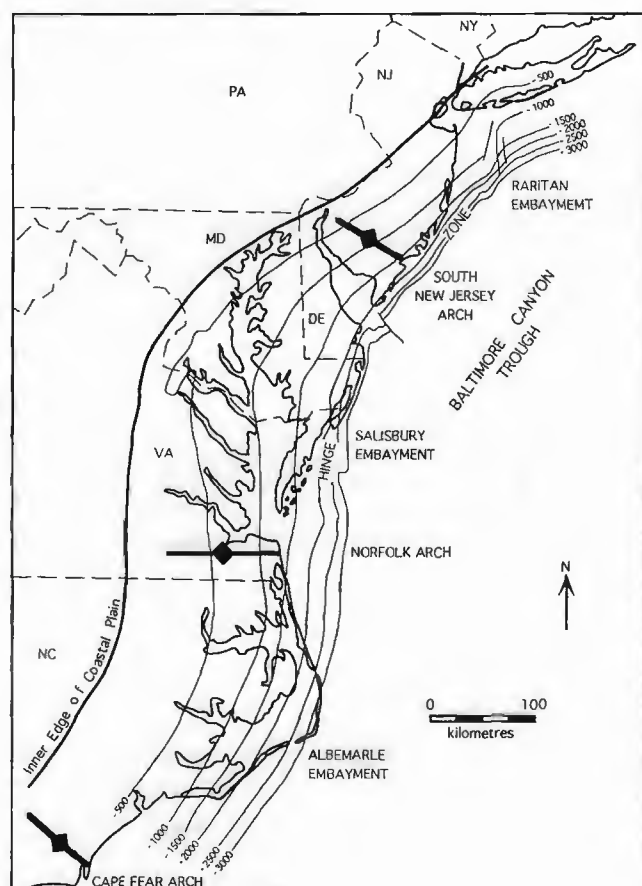
FIGURE 1. Structure contour map (m) of pre-Mesozoic basement of the middle Atlantic Coastal Plain of the U.S. showing major structural features and location of the Salisbury and Albemarle embayments (modified from Benson, 1984 and Olsson et al., 1988). DE, Delaware; MD, Maryland; VA, Virginia; NC, North Carolina.
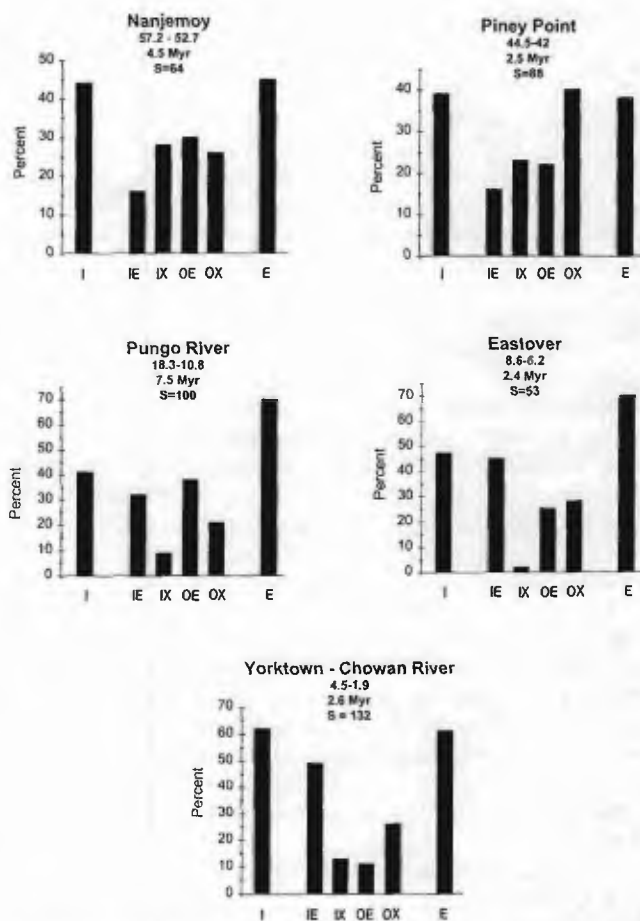

FIGURE 2. Bar graphs for five Cenozoic time-slices showing percentage of total species observed in the categories: immigrants (I), immigrants which become emigrants (IE), immigrants which become extinct (IX), originating which become emigrants (OE), originating which become extinct (OX), and emigrants (E).

and Eastover formations; and the Pliocene Yorktown and Chowan River formations.

The Nanjemoy Formation, deposited during a transgression into the Salisbury Embayment, is divided into the Potopaco Member, a very fine grained, clayey glauconitic sand and the overlying silty, fine, shell-rich glauconitic sand of the Woodstock Member, both deposited in an open marine, shallow shelf setting (Ward, 1984; Ward and Powars, 1991). The Nanjemoy Formation accumulated during the early Eocene between 57.2 and 52.7 Myr, and spans calcareous nannofossil zones NP10 to 13 and planktonic foraminiferal zones P6 to P9 (Bybell and Gibson, 1991; Poag and Commeau, 1995).

The immediately overlying Piney Point Formation was deposited in the Salisbury Embayment during the most extensive Cenozoic transgression (Ward and Powers, 1991). It is a richly fossiliferous, glauconitic sand deposited in a warm temperate, fully marine, shallow-to-middle shelf environment in a broad embayment (Ward, 1984; Gibson and others, 1991). The Piney Point Formation accumulated during the middle Eocene between 44.5 and 42.0 Myr, and spans calcareous nannofossil zones NP16 and 17 and planktonic foraminiferal zones P11 to P15 (Bybell and Gibson, 1991; Poag and Commeau, 1995).

The Pungo River Formation was deposited in the Albemarle Embayment during the early to middle Miocene (Snyder, 1988), it is composed of sands rich in phosphorites as a result of periodic upwelling spilling onto a middle-to-outer-shelf, open marine environment (Gibson, 1967, 1983; Snyder, 1988). The Pungo River Formation is represented by three episodes of deposition, each approximately 1 Myr in duration, between 18.2 and 12.0 Myr, and spans planktonic foraminiferal zones N6 to zone N12/13 (Snyder, 1988).

The Eastover Formation was deposited in the Salisbury and Albemarle embayments during the late Miocene at a time when the Norfolk Arch had little effect on patterns of deposition. These clayey sands and sandy clays comprise the lower Claremont Manor Member, characterized by a low diversity molluscan fauna indicative of deposition in an inner shelf embayment, and the Cobham Bay Member with higher diversity faunas, indicating open shelf, normal salinity conditions (Ward, 1984). The Eastover Formation was deposited in the late Miocene between 8.6 and 6.2 Myr; although a slightly younger age is a possibility (Culver and Goshorn, 1996).

Early Pliocene Yorktown Formation deposition, like that of the Eastover Formation, straddled the Norfolk Arch. Four

members (Sunken Meadow, Morgarts Bearch, Rushmere, Moore House) represent three transgressions that extended varying distances across the coastal plain (Ward, 1984). In the Salisbury Embayment the Yorktown is characterized by inner shelf deposits, but in the Albemarle Embayment the molluscan and foraminiferal faunas suggest deeper middle-to-outer-shelf environments (Gibson, 1983; Snyder and others, 2001). The Yorktown Formation is assigned to planktonic foraminiferal Zones N19 and N20, between 4.5 and 3.0 Myr (Dowsett and Wiggs, 1992; Krantz, 1991).

The Chowan River Formation overlies the Yorktown Formation, but its locus of deposition is in the Albemarle Embayment (Ward, 1984). These inner-to-middle-shelf, silty sands (Snyder and others, 2001), with trace fossils and molluscan and foraminiferal faunas indicating normal marine salinities, are assigned to plankton zone N21 (Cronin and others, 1984) and were deposited in late Pliocene between 1.9 and 2.4 Myr (Krantz, 1991).

There is a hiatus of only 0.6 Myr between the Yorktown and Chowan River formations. Of the 92 species that occur in the Chowan River Formation, 82 also occur in the Yorktown Formation. The similarity of the faunas and the relatively short hiatus between the formations prompted us to treat the Yorktown-Chowan River formations as a single community (Buzas and Culver, 1998).

METHODS AND DATA

Foraminiferal data from each stratigraphic unit utilized in this study are compatible in terms of the sampling scheme, processing protocol, and taxonomic concepts. We used data from two micropaleontological laboratories; S.W. Snyder's at East Carolina University and S.J. Culver's at Old Dominion University for Nanjemoy Formation (Vredenburg and Culver, unpublished data); Piney Point Formation (Jones and Culver, unpublished data); Pungo River Formation (Snyder and others, 1988); Eastover Formation (Culver and Goshorn, 1996); Yorktown Formation; and Chowan River Formation (Snyder and others, unpublished data; 2001).

Processing in all studies used a 63-μm sieve for concentrating foraminifera. Choosing specimens involved random selection. Specimen identifications were confirmed by comparisons with material in the Cushman Collection (Smithsonian Institution) The standardization of Culver and Snyder's taxonomic concepts was furthered by additional comparative work by Culver and Buzas. Numerical abundance was recorded and species proportions were calculated for all taxa. Details of field and laboratory methods are found in Snyder and others (1988, 2001), and Culver and Goshorn (1996).

Three hundred and fifty-six species were identified in a total of 66,002 specimens extracted from 354 samples (Table 1). Over 10,000 specimens were used for each time-slice. The geographic location, worldwide, of the published record of each taxon and the age (in million years) of each of those records that proved to be of conspecific material was recorded. This information was extracted from the card catalogue in the Smithsonian's Todd Library that includes each record for every species recorded in the published literature up to the 1960s. Information for the last thirty years was compiled from a literature search in the Todd Library

TABLE 1. Foraminiferal data for six formations of the Salisbury-Albemarle Embayment.

Formation	Number of samples	Number of individuals	Number of species
Chowan River	9	2033	92
Yorktown	33	8525	122
Eastover	66	10391	53
Pungo River	115	11627	100
Piney Point	59	16323	88
Nanjemoy	72	17103	64
Totals	354	66002	356

and from information on slides (often of unpublished comparative material) in the Cushman Collection at the Smithsonian. In all, this extensive search utilized over 7,000 publications (Culver and others, 1987).

The worldwide distributions of species came from 142 formations, most from the North American Atlantic and Gulf of Mexico coastal plains. The biostratigraphic assignment of these formations was derived from the U.S. Geological Survey CD-ROM compilation of such data. The age of earliest occurrence of each species was defined as the midpoint of the lowermost planktonic microfossil zone occurring in the formation where the species was found. A similar approach was used for dating last occurrences. Berggren and others (1985a, b) provided the chronostratigraphic framework.

THE COMPONENTS: IMMIGRATING AND ORIGINATING SPECIES

When viewed as a time-slice equivalent to the present day, each stratigraphic unit (formation) contains a fossil assemblage (paleocommunity) consisting of immigrants, I (recorded in older time-slices), and originators, O (not recorded in previous time-slices). In order to examine the past, "present" and "future" of the species comprising the fossil communities, the two categories can be subdivided again because we know which species became emigrants, E, to younger time-slices. Consequently, the total number of species observed in each of the five communities studied here is divided into four components: 1. immigrants-emigrants (IE); 2. immigrants-extinct (IX); 3. originating-emigrants (OE); 4. originating-extinct (OX). Summarizing, the I are those species with a past. The IE are those species that have a "future" while the IX are species that were last observed in the time-slice under observation. The O species have no past and were first observed in the time-slice under observation. These species can also be divided into those with a "future" (OE) and those which were observed only in the time-slice (OX).

The percentages of these components in each of the five communities is shown in Figure 2. We also include in this figure, as the first column, the percentage of the total species that are immigrants (I = IE + IX), and, in the last column, the percentage of the total species that are emigrants (E = IE + OE). If the first and last columns are equal or nearly so (I ≈ E), then no net change in the number of species emigrating to the regional species pool occurred during the deposition of the unit (Buzas and Culver, 1994, 1998). We refer to this situation as one of balance. Note also that the

column OX contributes nothing to the number of E nor I. On a balance sheet or accounting ledger, OX would simply be added and then subtracted. These OX species were called "loopers" by Buzas and Culver (1998). They were referred to as "singletons" by Alroy (1996) and Foote (2000), but this term has a long and common usage (Preston, 1948; Hubbell, 2001) in the ecological literature as a species represented by one individual. Consequently, the use of the term "singleton" for taxa restricted to a single time interval is likely to cause confusion.

The plot for the Nanjemoy Formation (Fig. 2) shows a balance between I and E. Although a large number of species belong to the category IX, their number is matched by the number of OE. The Piney Point Formation (Fig. 2) exhibits a similar trend and illustrates that although the proportion of loopers, or OX, is much larger than in the Nanjemoy, it contributes nothing to the final number of E.

The Miocene Pungo River Formation (Fig. 2) has a percentage of E far outweighing the percentage of I. This is achieved through a decrease in IX and an increase in the number of OE. In the Miocene Eastover Formation (Fig. 2), the percentage of E once again far outweighs that of I. The number of OE is similar to the Paleogene formations. However, there is almost no IX. The large number of E in these formations represents the "Miocene diversity pump" (Buzas and Culver, 1998) which is also recognized in bivalves (Crame, 2000, 2001).

The difference between OE and IX components can also be understood through rates of origination and extinction. In the Pungo River Formation, $(OE - IX) = (38 - 9) = 29$ species (Table 2). Buzas and Culver (1998) used the concept of net change, defined as $(E - I)/I$, to integrate the contribution of origination and extinction. Thus, for the Pungo River Formation, $(70 - 41)/41 = 0.7073$, and $0.7073 \times 41 = 29$. Because the Pungo River Formation has a duration of 7.5 MY, the net change per million years is 0.0943. Calculating the more traditional origination and extinction rates (Foote, 2000) produces the same result. In our notation, origination equals $(OE + OX)/S/7.5$ or 0.0787 where S is the total number of species. Extinction equals $(IX + OX)/S/7.5$ or 0.0400. The difference is 0.0387 and $0.0387 \times 100 \times 7.5 = 29$. In contrast, the earlier Piney Point Formation has $(OE - IX) = (19 - 20) = -1$. The net change is $(33 - 34)/34 = -0.0294$ and $-0.0294 \times 34 = -1$. Because the Piney Point Formation has a duration of 2.5 MY, the net change per million years is -0.0118. Origination is $(19 + 35)/88/2.5 = 0.2455$ and extinction $(20 + 35)/88/2.5 = 0.2500$. The difference is -0.0045 and $-0.0045 \times 88 \times 2.5 = -1$. If we do not consider the duration of the formations, the net change in the Pungo River Formation is 0.703 and in the Piney Point Formation -0.0294. If we divide these by the duration of the formations, we obtain 0.0943 and -0.0118, respectively. Thus, the net change is higher in the Pungo River Formation per million years and the fact that the duration is three times longer produces a substantial increase in emigrant species "the Miocene diversity pump."

The data for the Pliocene Yorktown and Chowan River formations (considered as a single unit because of the similarity of their faunas and their near contemporaneity) are also shown in Figure 2. Like the Paleogene formations, there is, once again, a near balance between I and E. This time, however, the balance is achieved by the few extinctions in IX and low numbers of OE. If we view these two formations separately, we observe many species originating in the Yorktown Formation and emigrating into the Chowan River Formation (Buzas and Culver, 1998). However, durations are short because they become extinct in the Chowan River Formation. When the two are considered as a unit, these species become OX or loopers.

When viewed from the standpoint of information available to an observer in the past, each of the communities under consideration consists of I and O species. We know, however, that a complete picture consists of IE, IX, OE, and OX. Examination of Figure 2 indicates that a balance between I and E in three of the five communities is achieved when the number of IX species is matched by the number of OE species. Therefore, in the balanced situation, if we can estimate any one of the four components, because we know O and I, we have the entire ensemble. And if we can estimate the components IE and OE, we can predict the "future."

For the immigrant group (I), we know not only that these species occurred in older geologic time-slices, but we also know their age. By subtracting the age of first occurrence of a species from the beginning of the age of the time-slice under consideration, we have the age of a species at the time of entry into the time-slice. If older species are more likely to become extinct than younger species, then the mean age of IE should be less then the mean age of IX. In all communities, the mean ages between IE and IX were not significantly different as judged by a t-test. Thus, survival does not depend on the age of the species upon entering a time-slice.

We next considered the O group. In Figure 2, we notice some variation between the sizes of the OE and OX group from community to community. To obtain an average, we divided the total number of species in the OX category in all communities by the total O species in all communities to obtain the proportion $123/227 = 0.5419$. Recall, that if the fossil horizon were viewed as the equivalent of a modern community, the number of O and I species would be the only information available. To calculate the predicted values for each component in each community, we multiplied O by the proportion 0.5419 to obtain an estimate of OX. We then have $OE = O - OX$ and, in the balanced situation, $OE = IX$ while $IE = I - IX$. We can thus predict the number of species of each component in each community given the number of O species and I species and the proportion of the OX species. The results are shown in Table 2. For the three communities in the balanced situation where I equals E, the predicted values for the four categories are quite close. The total number of species becoming extinct within a time-slice (TX) is $TX = IX + OX$. The predicted and observed values are within a species of the observation (Table 2). Notice also that in the balanced situation, because $IX = OE$, $TX = OE + OX = O$. Consequently, the total number of extinctions is equal to the number of O species even though all species in this group may not become extinct. Using only the proportion $OX/O = 0.6214$ from the three balanced communities, the predictions are even closer for these communities (Table 3).

TABLE 2. Observed and predicted values in five units of the SAE for the number of species in the categories: Immigrants-Emigrants (IE), Immigrants-Extinct (IX), Originating-Emigrants (OE) and Originating-Extinct (OX). For the predicted values the total I and O are a given, then, $OX = (0.5419)O$, $OE = O - OX$, $OE = IX$, $IE = I - IX$. Total number of species extinct, $TX = IX + OX$.

Unit	IE	IX	OE	OX	TX
Nanjemoy					
observed	10	18	19	17	35
predicted	11.5	16.5	16.5	19.5	36.0
Piney Point					
observed	14	20	19	35	55
predicted	9.3	24.7	24.7	29.3	54.0
Pungo River					
observed	32	9	38	21	30
predicted	14.0	27.0	27.0	32.0	59.0
Eastover					
observed	24	1	13	15	16
predicted	12.2	12.8	12.8	15.1	28.0
Yorktown-Chowan River					
observed	65	17	15	35	52
predicted	59.0	22.9	22.9	27.1	50.0

For the unbalanced Pungo River and Eastover formations the estimated values are not nearly as close, except for OX and OE in the Eastover. The exercise illustrates that with only the knowledge of I and O the assumption that about 55% of the O are OX, we can make a reasonable prediction about the "future" minimum extinctions. Interestingly, the predicted values of OX for the unbalanced communities are close to the observed values for TX because the IX component is so small.

THE COMPONENTS AND OCCURRENCES

In each unit, each species is designated as belonging to one of the four categories IE, IX, OE and OX. In addition to knowing the number of species in each category, we also know the number of occurrences of each species in the samples. Buzas and Culver (2001) showed through regression analyses that if the OX group is excluded, species durations are not statistically related to the number of occurrences. Abundantly occurring species are as likely to become extinct as rarely occurring species. Here, we examine for each

TABLE 3. Observed and predicted values in three balanced units of the SAE for the number of species in the categories: IE, IX, OE, and OX. Assuming I and O are given then $OX = (.6214)O$, $OE = O - OX$, $OE = IX$, $IE = I - IX$.

Unit	IE	IX	OE	OX	TX
Nanjemoy					
observed	10	18	19	17	35
predicted	14.4	13.6	13.6	22.4	36.0
Piney Point					
observed	14	20	19	35	55
predicted	13.6	20.4	20.4	33.6	54.0
Yorktown-Chowan River					
observed	65	17	15	35	52
predicted	63.1	18.9	18.9	31.1	50.0

TABLE 4. Results of one-way ANOVA on occurrences of each species in the groups IE, IX, OE, and OX.

Unit	Mean-square	df	F-ratio	p
Nanjemoy	2910.78	3	7.57	0.00
error	384.33	60		
Piney Point	901.81	3	3.66	0.02
error	246.28	84		
Pungo River	652.65	3	0.85	0.47
error	765.23	96		
Eastover	858.94	3	3.97	0.01
error	216.26	49		
Yorktown-Chowan River	391.94	3	3.38	0.02
error	115.96	128		

of the units the number of occurrences of the species in each of the four categories. The null hypothesis is $\mu_{IE} = \mu_{IX} = \mu_{OE} = \mu_{OX}$, that is, there is not a significant difference in the mean number of occurrences for species belonging to each of the four categories. An abbreviated result of the five ANOVA's is given in Table 4 and the means of the four categories are shown in Figure 3. All of the ANOVA's except for the Pungo River are significant, meaning that the mean occurrences in the categories are not the same. The plots in Figure 3 indicate that for the Nanjemoy, Piney Point, and Yorktown-Chowan River, OX species have fewer occurrences. In other words, in balanced situations, OX spe-
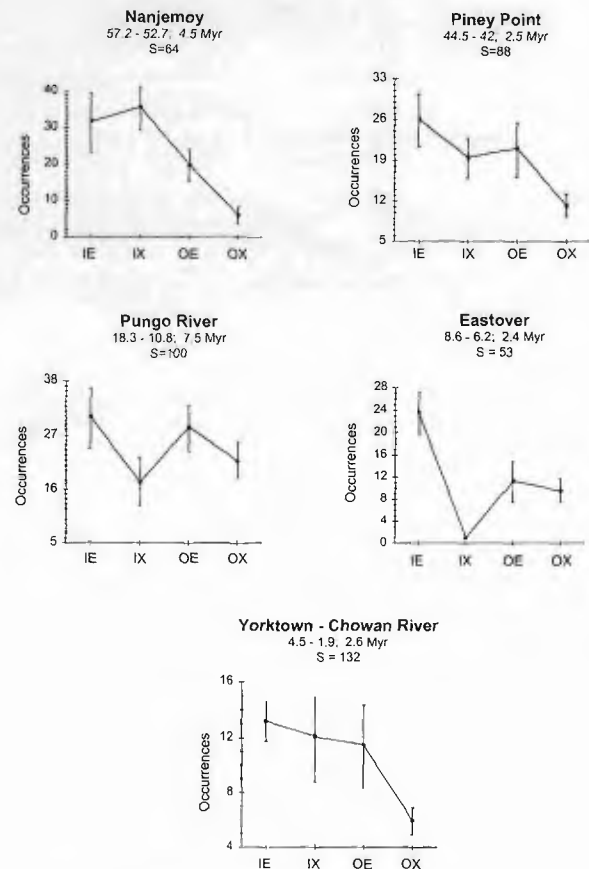

FIGURE 3. Plots for the four time components (IE, IX, OE, OX) of the mean number of occurrences at five Cenozoic time-slices. Error bars are one standard error.

TABLE 5. Post-hoc contrasts on significant ANOVA in Table 4. Values given are probabilities of F-ratio for the contrast.

Contrast	Nanjemoy	Piney Point	Eastover	Yorktown-Chowan River
IE vs OX	0.00	0.00	0.00	0.00
IE,IX,OE vs OX	0.00	0.00	0.70	0.01
OE vs OX	0.04	0.03	0.75	0.11
IX vs OX	0.00	0.06	0.58	0.06
IE,IX vs OE,OX	0.00	0.06	0.81	0.08
IE vs IX	0.62	0.24	0.14	0.71

cies are significantly rarer than species in the other categories. Based on the plots, six contrasts were performed. The results are shown in Table 5. For all four of the significant ANOVA's the contrast IE vs OX is significant, and for all except the Eastover, OX vs the rest is significant. Recalling the lack of significant difference in the ages at entry of IE vs IX, here we note in all cases the contrast IE vs IX is not significant. Consequently, species in the two categories face an equal likelihood of extinction because they cannot be discriminated by either age or number of occurrences.

The contrasts indicate that for balanced units, the OX group has a lower mean number of occurrences than the other groups. We would expect, then, that the majority of species with low occurrences in the O group would belong to OX. Table 6 shows O species from balanced units occurring <8 times and indicates that about 75% of these would belong to the OX category. Consequently, if these communities are thought of as a modern community, we would expect that the majority of species in the known O group or component which occur only a few times are the most likely to become extinct in the near future.

A major problem arises from the difficulty in recognizing a balanced versus an unbalanced situation when only I and O are known. As shown in Table 4, the Pungo River does not have any significant difference in the mean number of occurrences among the components. This suggests that unbalanced situations may lack the differentiation observed in the balanced units. However, the Eastover ANOVA is significant, which may negate such a simple solution. Nevertheless, the contrasts shown in Table 4 indicate fewer significant differences for the Eastover than the other groups. The Eastover also has only one species in the IX group and may not be typical.

DISCUSSION AND CONCLUSIONS

A paleocommunity consists of taxon belonging to four time components: immigrants-emigrants (IE), immigrants-extinct (IX), originating-emigrants (OE), originating-extinct (OX). If the observed time-slice is viewed as the present, and nothing is known of the future, only I and O species can be discriminated. This is the situation we would encounter when surveying a modern marine community of organisms with a good fossil record. To predict the emigrants (E) of the future we need to know E = IE + OE. Examination of the four time components in the fossil record of five Cenozoic communities in the Salisbury-Albemarle Embayment indicates that three are in balance where I = E. In this situation, IX = OE, and because I and O are

TABLE 6. Values of OE and OX for <8 occurrences in balanced units. ( ) is proportion OX/total.

Unit	OE	OX	Total
Nanjemoy	7	13 (0.65)	20
Piney Point	5	17 (0.77)	22
Yorktown-Chowan River	8	27 (0.77)	35

known, if any of the four components can be estimated, so can the entire ensemble. Using the ratio from all communities of OX/(OE + OX), we estimated the components and found a very good fit between predicted and observed components. The estimate of the total number of extinctions and emigrants is within one species. Analyses of occurrences in the four components indicates that the OX group can be expected to form the majority (75%) of O species with less than 8 occurrences (Table 6).

Translating the lessons learned to a modern community with a good fossil record is, of course, somewhat tenuous. Given I and O, we would expect a reasonable estimate of the components, if the community is balanced (I = E). In this case, we would also expect a reasonable estimate of the total number of future extinctions TX = IX + OX or O (even though the extinctions would not all be from the O group). We would also expect that the majority of species in the rarely occurring portion of the O group will consist of OX. However, these species account for only about a third of all extinctions within a unit. Clearly, rarity cannot be the sole criterion for recognizing species in danger of extinction (Gaston, 1994).

Even in the unbalanced situation some insight is gained by the approach offered here. The estimate of OX is reasonable, but we have not been able to estimate IX with accuracy. Consequently, because IX ≠ OE, the total number of extinctions cannot be reliably estimated. However, the OX estimate still gives a minimum number for the expected number of extinctions and in the two unbalanced units the predicted OX is very close to the observed TX (Table 2). The lack of a significant difference in the mean number of occurrences among components in the Pungo River Formation suggests that unbalanced situations might be recognized in this way when only I and O are observed as in a modern community.

Regardless of balance, the OX group (loopers) consists of a quarter to a third of the species observed in a unit, and about 50% of the O group. These species, which do not emigrate in space and time, have short species durations. If a species is successful and enters the OE group to become a subsequent I, then it is likely to enjoy a long species duration (mean about 21 Myr) typical of benthic foraminifera (Buzas and Culver, 1984, 1991, 1994; Hayward and others, 1999).

Consideration of the time components of marine communities also gives insight as to how species diversity is produced and maintained. Because some immigrant species must inevitably become extinct, in order to maintain diversity they must be replaced from the originating group. The data (Table 2) indicate that on the average slightly less than half of the species originating (O) are suitable replacements (OE). The remainder, OX, are failed evolutionary trials.

The worldwide stratigraphic distribution of the 356 species studied were traced to 142 geologic formations. Most of these formations (86%) are located in the North American Atlantic coastal plain, Gulf of Mexico coastal plain, or the Caribbean. The species occupying these areas constitute the regional species pool for the I portion of the local diversity observed in the SAE. At any particular time slice, only about half of the available species are immigrants into the SAE, and of the emigrants from the SAE, only about one-quarter ever return to the embayment during a subsequent transgression (Buzas and Culver, 1998). There is, then, a constant interchange of species from regional pool to local community and back again so that any understanding of local communities must consider the regional or biogeographic aspects (Cornell and Lawton, 1992).

Except for the Eastover Formation, which probably represents a climatically mediated special case (Buzas and Culver, 1998), there is an increase in the total number of species in each formation during the Cenozoic (Buzas and others, 2002). The increase is more than expected from observation of local species richness alone. For example, 70 species emigrated from the Pungo River Formation, but 82 immigrated into the Yorktown-Chowan River formations (Buzas and Culver, 1998). The increase most likely reflects an overall increase in the regional species pool. Our observations do not suggest any species saturation and is most consistent with a type 1 community of Cornell and Lawton (1992) where local richness increases proportionately with regional richness.

Our inability to identify with certainty which species are OX and IX, and the dependence of local diversity on regional diversity makes local conservation efforts a precarious undertaking. The interaction of local and regional diversity certainly indicates that local conservation alone will not preserve species diversity. At the same time, preservation of regional diversity should insure restocking in a damaged local area when conditions permit. Clearly, more research with different cases and taxa as well as with different lengths of time-slices are required before the development of numerical limits on time components can firmly be established. Understanding the community in terms of time components, however, offers a remarkable insight as to how the system works and this insight can only come from paleoecology where the "future" is a known quantity.

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