Latitudinal difference in biodiversity caused by higher tropical rate of increase

Martin A. Buzas*†, Laurel S. Collins‡, and Stephen J. Culver§

*Department of Paleobiology, Smithsonian Institution, Washington, DC 20560-0121; ‡Departments of Earth Sciences and Biological Sciences, Florida International University, Miami, FL 33199; and §Department of Geology, East Carolina University, Greenville, NC 27858

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Tropical diversity has generally exceeded temperate diversity in the present and at points in the past, but whether measured differences have remained relatively constant through time has been unknown. Here we examine tropical vs. temperate diversities from the Neogene to Recent using the within-habitat diversity measure Fisher's alpha of Cenozoic benthic foraminifera from the temperate Central Atlantic Coastal Plain and the tropical Central American Isthmus. During the Neogene, the mean value of alpha at temperate latitudes increased 1.4 times or 40%, whereas in the tropics it increased 2.1 times or 106%. Thus, while both areas exhibit an increase of diversity with time, past differences in the rate of increase have generated a more pronounced gradient today (164%) than existed in the Miocene (80%). These data disagree with the suggestion that the world reached an equilibrium number of species during the Paleozoic and demonstrate the need to consider both temperate and tropical components in global diversity assessments.

In the world today, most groups of taxa exhibit a steep latitudinal diversity gradient. The causes are much-debated (1), but temperate areas typically have fewer species than tropical areas (2, 3). The foraminifera are no exception; their regional species richness increases from boreal to temperate to tropical areas (4). Foraminifera are useful for paleobiodiversity studies because they are diverse, well preserved in fossil sediments, and abundant enough to conduct statistical tests of apparent diversity patterns. For foraminifera, the mean number of species within a habitat is an accurate reflection of regional richness (5).

At any particular locality the within-habitat species richness for benthic foraminifera is obtained by counting the number of species represented by a few hundred individuals in a few milliliters of sediment obtained by a corer or other sampling device. Using within-habitat richness to statistically analyze differences in space and time has an enormous advantage over using regional richness. The number of species within a habitat is statistically a random variable and its mean is a measure of central tendency with an associated variance. The total regional number of species, however, is an estimate of an unknown constant. Consequently, the former is easily analyzed statistically while the latter is not. Measurement of within-habitat diversity is also more tractable than regional richness. The number of species within a sediment sample is relatively easily determined, but a regional estimate of species diversity must necessarily compare all of the taxa among samples, which requires a complete taxonomic study of the entire fauna. In species-rich areas, a complete taxonomic evaluation takes many years to complete. The within-habitat approach also has the advantage of allowing researchers to use other researchers' data without extensive taxonomic standardization among samples and areas (6–8).

A problem with estimating the number of species (S) is that S is a function of the number of individuals (N) examined (9). In our temperate data set, the mean N per sediment sample is 200 with a minimum of 75 and a maximum of 468. In our tropical data set, the mean N is 600 with a minimum of 143 and a maximum of 1,539. One way to standardize is by the use of Fisher's α (10). Providing the data conform to a log series, and benthic foraminifera do (11), α, the parameter of the log series, is independent of N and is, consequently, extensively used as a measure of diversity (12). We use Fisher's α for our analysis and estimate its value from statistical tables (9).

The diversity data include both fossil and living species. The data set for the temperate region consists of specimens from formations of the Salisbury and Albemarle embayment of the North American Atlantic Coastal Plain, which range in age from early Eocene to Pliocene (13, 14). Specimens of extant temperate species are from an area just north of Cape Hatteras (15). The tropical fossil taxa are from formations in Caribbean Panama and Costa Rica, and range in age from Miocene to early Pleistocene (16). Specimens of living tropical species are from the Caribbean Sea in the same area of northwestern Panama (16). All of the studied specimens are from neritic habitats, which we inferred for the fossils from geological, sedimentological, and paleontological evidence (14–16).

During the Cenozoic, temperate within-habitat species diversity rose gradually and consistently (Fig. 1). An ANOVA on the $n = 298$ sediment samples belonging to five age groups from the Cenozoic of the temperate area yielded a probability of $P < 0.001$ for the F-ratio, indicating the αs are significantly different. A contrast (Scheffé S-method) between the Paleogene and Neogene indicates a significant difference with $P < 0.001$. Similarly, a contrast between Recent vs. Miocene is significant with $P = 0.035$. However, contrasts between Recent vs. Pliocene ($P = 0.138$) and Pliocene vs. Miocene ($P = 0.333$) are not significant because the increases over time were small.

Unlike the temperate diversification, the increase in tropical diversity is large (Fig. 1). An ANOVA on the $n = 75$ sediment samples belonging to three age groups from the Neogene of the tropics yielded a $P < 0.001$ for the F-ratio. Contrasts between Recent vs. Pliocene ($P < 0.001$) and Pliocene vs. Miocene ($P = 0.001$) are significant, reflecting large changes over time.

We do not believe that there is any significant taphonomic loss of species over time. The neritic benthic species we have analyzed are mostly calcareous and robust. In the temperate fauna, the lack of any significant difference between the Pliocene and Recent supports this conclusion. In the tropical fauna, the αs for the 1.4 mega-annum (millions of years ago) Swan Clay Formation are nearly identical with the Recent Bocas del Toro reef.

In the temperate area during the Neogene, α increased from 10 to 14, 1.4 times or 40%, while in the tropical area the increase was from 18 to 37, an increase of about 2.1 times or 106%. For the temperate area, the increase in α during the Cenozoic was from 5 (early Eocene) to 14 (Recent), 2.8 times or 180%. Unfortunately, no suitable comparative data are available at present for the tropical Paleogene, either in the form of published literature or museum collections. During the Miocene, the increase in the diversity gradient from temperate ($\alpha = 10$) to tropical ($\alpha = 18$) was 1.8 times or 80%. Today, the difference

†To whom reprint requests should be addressed. E-mail: Buzas.Marty@nmnh.si.edu.

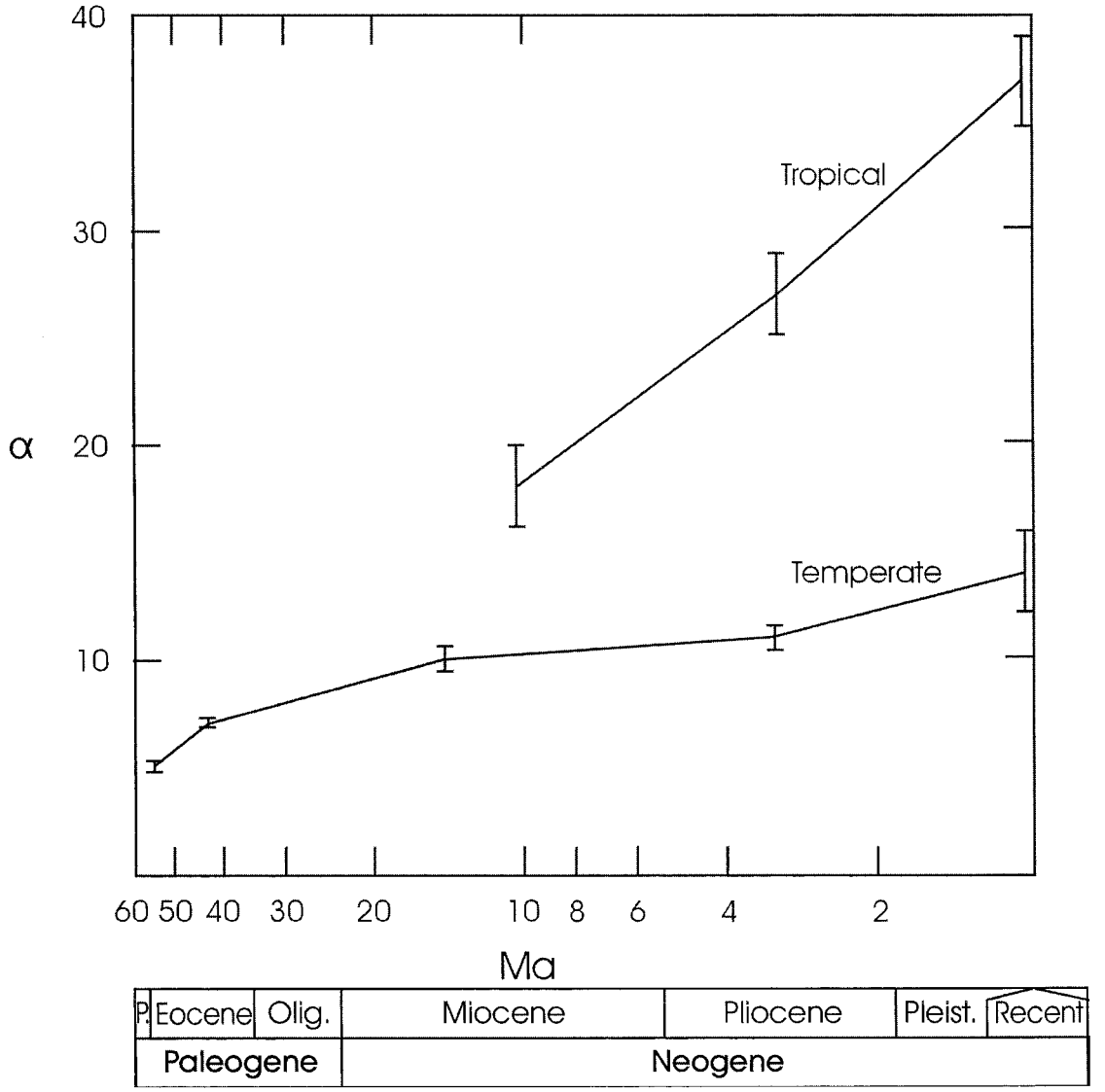

Fig. 1. Within-habitat species diversity trends represented by mean values of α with standard errors for the Isthmus of Panama (tropical) and the Atlantic Coastal Plain (temperate). Ma, mega-annum (millions of years ago).

from temperate (α = 14) to tropical (α = 37) is 2.6 times or 164%.

At temperate latitudes on the Atlantic Coastal Plain, a substantial number of the fossil benthic foraminiferal species are rare and restricted to a particular formation or time-slice. The proportion they constitute (about 28%) of the total number of species within a formation does not vary in any systematic way, contributing no measurable bias to the data set (14). The species involved have relatively short durations (17) and can be regarded as evolutionary "trials." Data from the Pliocene Yorktown-Chowan River formations suggest that if species survive after about the first 2 million years of their existence, they become part of the group with an expectation of normal species duration regardless of abundance (17). This latter group of long-lived species, which originates and then emigrates and immigrates (into a later time-slice), accounts for the overall increase in temperate species diversity with time. In the overall ledger for the Cenozoic of the Atlantic Coastal Plain, origination exceeds extinction and the Miocene is a particularly large diversity pump (13, 14). With time, there is an accumulation of long-lived species that, with the addition of newly originating species, increases the diversity. At each successive time interval, the mean duration of species with a previous fossil record (that is, those originating earlier and immigrating into the time interval) increases. Consequently, the mean partial duration of extant species with a fossil record is greater than for species with a complete fossil record (17). Like species diversity, the mean duration of the temperate benthic foraminifera is increasing with time. The log series distribution is characterized by a long "tail" of rare species (9) and, consequently, differences between high and low diversity areas are due to species that occur rarely. Taxonomic standardization of all extant species occurring on the North Atlantic Continental margin yielded 878 species and on the Caribbean margin 1,188 species (4). About 80% of this difference is accounted for by species occurring at only one locality (4). Most of these rare species are endemic to a continental margin and overall the Caribbean has 38% endemism while the Atlantic margin has only 18% (4). Taken together, the inferred high rate of origination and extinction in the tropics (18) and its many rare and endemic species suggest a much larger component of short-lived evolutionary trials than in the temperate realm. In this way, a gradient between temperate and tropical faunas can be maintained.

The tropical increase in diversity may have resulted from an accumulation of long-lived species over time (17), as with the temperate taxa. In addition, the physical oceanic changes produced by the Neogene closure of the tropical Eastern Pacific-Caribbean seaway have been associated with increased diversification in benthic foraminifera (16, 19).

The patterns of origination and extinction that determine diversity appear to vary between temperate and tropical latitudes as well as within the tropics. On the Atlantic Coastal Plain, Neogene foraminifera experienced an extinction of about 40% during the Pliocene, but origination was sufficient to prevent decreased diversity in the modern temperate fauna (14, 15). The large increase in diversity of benthic foraminifera off the Central American Isthmus agrees with the observed pattern in common species that origination greatly outweighed extinction, which was very low (5%) during the Pliocene (19, 20). In contrast, mollusks experienced a substantial extinction event during the Pliocene in both the temperate NW Atlantic and Caribbean. Some researchers estimate a maximum Pliocene diversity with a decrease toward the Recent (21–25), while others suggest either stasis or an increase toward the Recent (26–29).

Our results of increasing Neogene diversity are congruent with earlier synoptic diversity studies that document a major marine increase in post-Paleozoic species diversity that continued into the Cenozoic (30). Unlike those studies, however, the current data are not biased by possible sampling artifacts (31), because we measured within-habitat rather than cumulative regional diversity. The data do not shed light on the recent proposal that Paleozoic marine diversity is similar to Paleogene levels, but they disagree with any inference that the world may have reached an equilibrium number of species during the Paleozoic (32). Most importantly, the foraminiferal data demonstrate the differing and changing temperate and tropical components of diversity through time (Table 1, which is published as supporting information on the PNAS web site, www.pnas.org).

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