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RATES OF SPECIES-LEVEL ORIGINATION AND EXTINCTION: FUNCTIONS OF AGE, DIVERSITY, AND HISTORY

Global-scale data on the Oligocene to Recent planktic foraminifers and coccoliths from the tropical Pacific and Atlantic Oceans are employed for quantitative testing of alternative models (Red Queen and Stationary Hypotheses) of the relationship between speciation rates, extinction rates, taxonomic diversity, abiotic events, and history of the paleosystem. The results demonstrate that although the Law of Constant Extinction is supported by the data, the theoretical implications are quite ambiguous because the two considered models appear as end-members of a continuum.

K e y   w o r d s: Evolution, extinction, Red Queen Hypothesis, Foraminiferida, Coccolithophorida.

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INTRODUCTION

Numerous interacting determinants characterize evolving biological systems. A common partitioning of the character-environment interaction, essential to studies of natural selection (Sober 1984), separates abiotic from biotic factors of 'environment'. Causal prominence to the biotic factors of the selective regime is given by the Red Queen Hypothesis of Van Valen (1973). This hypothesis is based on a zero-sum assumption that what one species gains, other species must lose or counter with evolutionary change. The oft-cited historical forerunner of this evolutionary postulate is Darwin's (1859) statement that, "the most important of all causes of organic change is one which is almost independent of... altered physical conditions, namely, the mutual relation of organism to organism... if some of these many species become modified and improved, others will have

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to be improved in a corresponding degree or they will be exterminated".
The alternative emphasis on character evolution tracking change in the
abiotic environment is also of long-standing tradition (Lyell 1832).

Stenseth and Maynard Smith (1984) more recently identified as alter-
native evolutionary modes, amenable to study on the geological time scale
of speciation and extinction, the Red Queen condition "characterized by
continuing... extinction and speciation" and the Stationary condition,
a zero-force state, "with... no extinction or speciation". In the former,
continuing speciation and extinction are expected even in abiotically
stable environment, whereas in the latter, "evolutionary change occurs
only in response to changes in the physical environment". Hence, in the
Red Queen mode, evolution has a significant autonomous component,
while in the Stationary mode, speciation and extinction are viewed as
externally or non-biotically driven processes. Arguing that either mode
is plausible in theory, Stenseth and Maynard Smith (1984) reasoned that
the issue was empirical and resolution lay with historical data from the
fossil record.

THE FALLACY OF THE EXCLUDED MIDDLE

Our analyses of extinction and speciation data from the fossil record
(Hoffman and Kitchell 1984) were motivated originally by this petition
for empirical testing. In translating these theoretically distinct models
into predictions for testing, however, a major difficulty, referred to as
'the fallacy of the excluded middle' (Dr. Donald R. Strong, personal
communication), is apparent. The environment of natural systems changes
continually (Chesson and Case 1986). Even taxonomic turnover introduces
a biotic composition that, over sufficiently long time scales, is continually
in flux as the inevitable outcome of originations and extinctions. As
a consequence, the natural world, over geologically long periods of time,
more frequently experiences the 'middle' condition of changing both
biotic and abiotic components of the selective environment with no
sustained periods of environmental stasis. Yet a constant abiotic environ-
ment is the requisite condition under which predictions of the Red
Queen/Stationary models diverge (Hoffman and Kitchell 1984).

A dilemma for quantitative testing that is unambiguous emerges. The
requisite condition rarely occurs over the speciation/extinction time scale,
and biotic and abiotic factors are not necessarily independent. There is
a feedback: abiotic factors may influence biotic interactions. There is no

way of distinguishing between primary biotic factors and secondary biotic change initiated by abiotic factors. Moreover, constancy of speciation and extinction rates need not mean necessarily that biotic factors predominated, but only that whatever selection forces were acting were doing so in a fairly constant manner. Time-dependent rates of speciation and extinction are similarly ambiguous in that the 'time' effect could be due to either biotic or abiotic causal factors.

Consequently, our present analyses are directed to specific questions that can be more adequately asked of such data from the fossil record. These include: to what extent are species-level rates of speciation and extinction (i) age-independent or age-dependent, with age referring to a taxon's duration; (ii) time-independent or time-dependent, with time referring to the actual, historical time scale; and (iii) diversity-independent or diversity-dependent, with diversity referring to the number of extant taxa per division of geological time.

We will quantitatively compare patterns of variation in the probabilities of speciation and extinction over biologic (species duration) time versus absolute (geologic) time, using single-factor *versus* interactive-factor descriptions. We will show that (i) the data are sufficient to discern key temporal patterns, (ii) the null hypothesis of independence on past history, or the Law of Constant Extinction, cannot be rejected, and yet (iii) the two evolutionary models presented by Stenseth and Maynard Smith (1984) represent end members of a continuum.

SELECTING DATA FROM THE FOSSIL RECORD: TEMPORAL AND GEOGRAPHIC CHARACTERISTICS

To best meet the requisites for testing the Red Queen versus Stationary models, the data sets to be analyzed should be global in nature, with fine temporal resolution, in an environment generally more homogeneous than most, and over a geologic time interval characterized by background rather than mass extinction. We will here utilize the unrivaled geographic and temporal scope of the fossil record of marine planktic organisms, made available to paleontologists by the Deep Sea Drilling Project (DSDP). In such deep-sea records, numerous species occur in large quantities in sequences that are relatively continuous and well-dated (e.g., Malmgren et al. 1983, Sorhannus et al. 1988, Fenster et al. 1989).

The present study, however, will differ from our earlier study (Hoffman and Kitchell 1984) in several important ways. The data will be compiled from a more homogeneous paleoenvironment, as discussed below. The absolute time component will be standardized to 1 Myr intervals, ridding the analytical models of the complicating factor of variable time lengths over which data are aggregated. And we will assess the degree

Table 1

Deep Sea Drilling Project sites and reports utilized

Sites	Reports
13	Maxwell *et al.* 1970 Init. Repts. DSDP 3
23, 24, 25, 26, 27, 29, 30, 31	Bader *et al.* 1970 Init. Repts. DSDP 4
53, 54, 55, 56, 57, 58, 59, 60	Fischer *et al.* 1971 Init. Repts. DSDP 6
62, 63, 64, 65	Winterer *et al.* 1971 Init. Repts. DSDP 7
69, 70, 71, 72, 73, 74, 75	Tracey *et al.* 1971 Init. Repts. DSDP 8
76, 77, 78, 79, 80, 81, 82, 83, 84	Hays *et al.* 1972 Init. Repts. DSDP 9
142, 144	Hayes, Pimm *et al.* 1972 Init. Repts. DSDP 14
146, 147, 148, 149, 150, 151, 152, 153, 154	Edgar, Saunders *et al.* 1973 Init. Repts. DSDP 15
155, 156, 157, 158, 159, 160, 161, 162	Van Andel, Heath *et al.* 1973 Init. Repts. DSDP 16
165, 166, 167, 171	Winterer, Ewing *et. al.* 1973 Init. Repts. DSDP 17
199, 200, 202	Heezen, MacGregor *et al.* 1973 Init. Repts. DSDP 20
209, 210	Burns, Andrews *et al.* 1973 Init. Repts. DSDP 21
286, 287, 288, 289	Andrews, Packham *et al.* 1975 Init. Repts. DSDP 30
290, 291, 292	Karig, Hyle *et al.* 1975 Init. Repts. DSDP 31
314, 315, 316, 317, 318	Schlanger, Jackson *et al.* 1976 Init. Repts. DSDP 33
319, 320, 321	Yeats, Hart *et al.* 1976 Init. Repts. DSDP 34
353, 354, 355	Supko, Perch-Nielsen *et al.* 1977 Init. Repts. DSDP 39
364	Bolli, Ryan *et al.* 1978 Init. Repts. DSDP 40
366, 367	Lancelot, Seibold *et al.* 1978 Init. Repts. DSDP 41
419, 420, 421, 422, 423, 424, 425, 426, 427	Rosendahl, Hekinian *et al.* 1980 Init. Repts. DSDP 54
445, 446	de Vries Klein, Kobayashi *et al.* 1980 Init. Repts. DSDP 58
447, 448, 449, 450, 451	Kroenke, Scott *et al.* 1981 Init. Repts. DSDP 59
458, 459	Hussong, Uyeda *et al.* 1982 Init. Repts. DSDP 60

Sites	Reports
462	Larson, Schlanger *et al.* 1981
	Init. Repts. DSDP 61
494, 495, 496, 497, 498,	Auboin, Von Huene *et al.* 1982
499, 500	Init. Repts. DSDP 67
502, 503	Prell, Gardner *et al.* 1982
	Init. Repts. DSDP 68
504, 505	Cann, Langseth *et al.* 1983
	Init. Repts. DSDP 69

of temporal correlation between speciation and extinction histories, on the one hand, and measures of the intensity and timing of abiotic environmental change, on the other.

The compiled data set is comprised of the global record of tropical planktic foraminifer and coccolith species. Excellent paleontologic data exist as a consequence of the biostratigraphic utility of these two major groups. The data set is global, based on all DSDP sites situated in the tropical (15°N to 15°S latitude) Pacific and Atlantic Oceans which have a reasonably well-preserved and well-studied record of these two groups of fossils. These DSDP sites, numbering 116 in all, are listed in Table 1. (DSDP sites 171, 292, 445, 458, and 459 are presently located to the north of the tropical belts due to northward motion of the Pacific Plate during the Cenozoic.)

The data set consists of the times of first appearance and last appearance and, consequently, total stratigraphic ranges, in the study area for all planktic foraminifer and coccolith species encountered in the Oligocene through Holocene, meaning all species present by the beginning of the Oligocene and those originating subsequently. This time interval of approximately the past 37 Myr was selected because it enables us to study a paleosystem following a major turnover, though not associated with a mass extinction (Corliss *et al.* 1984, Snyder *et al.* 1984), and over a long period of time under a regime of background extinction. Species known only from the present and lacking a fossil record are necessarily excluded from consideration.

The Oligocene through Holocene tropical Pacific to Atlantic paleosystem was chosen also for a number of additional reasons. A major oceanographic change, namely, the development of the cold bottom oceanic layer, took place at or close to the Eocene/Oligocene boundary (cf. Douglas and Savin 1975*a*, *b*, Kennett and Shackleton 1976, Keigwin 1980, Van Couvering *et al.* 1981, Benson *et al.* 1984). Since that time, however, the tropical oceans have been less affected by climatic and oceanographic events than the other oceanic water masses. The tropical oceans are also

relatively well-studied. In particular, major abiotic events that affected these oceans during the Oligocene through Holocene can be identified and interpreted from the geochemical evidence of stable oxygen and carbon isotopes (cf. Kennett 1983, Miller *et al.* 1987). Although there are some differences in the timing of appearance and disappearance of some species over this vast area (Thunell 1981, Keigwin 1982, Johnson and Nigrini 1985), the tropical Pacific and Atlantic Oceans were largely homogeneous and widely interconnected for most of the considered time span. They became separated only in the Pliocene, a few million years ago. The relative homogeneity of this paleosystem alleviates some of the problems we encountered in our previous study (Hoffman and Kitchell 1984). On the other hand, however, the restriction of scope to only the tropical system has required of us to compile our own data base rather than to make use of existing compendia (e.g., Stainforth *et al.* 1975, Kennett and Srinivasan 1983). In spite of some widespread hiatuses (e.g., Van Andel *et al.* 1975, Moore *et al.* 1978, Barron and Keller 1982), the Oligocene through Holocene record is quite complete in the tropical oceans, thus allowing for construction of a complete composite section. There also exists good stratigraphic time control with an average time resolution of 1 Myr, which is exceptionally good on the global scale for the fossil record.

The DSDP sites utilized in this study include a number of continuously cored sites that provide a complete composite section of the Oligocene (and even Upper Eocene) through Holocene. In addition to the Initial Reports of DSDP, listed in Table 1, which often give an incomplete record of the biota, we also used more comprehensive paleontologic studies (e.g., Keller 1980, 1981*a*, *b*, Thunell 1981, Biolzi 1982). We also included data from the classic monographs on land-based sections in the Caribbean Islands (e.g., Bolli 1957*a*, *b*, 1964, 1972, Bramlette and Wilcoxon 1967, Gartner 1967). The stratigraphic framework is based on a number of regional and global biostratigraphic and magnetostratigraphic syntheses (Bolli 1966, Blow 1969, Martini 1971, 1981, Burckle 1972, Berggren and Van Couvering 1974, Rayan *et al.* 1974, Stainforth *et al.* 1975, Keigwin 1976, Saito 1977, Burckle and Trainer 1979, Bukry 1980, Beckmann *et al.* 1981, Srinivasan and Kennett 1981*a*, *b*, Ellis 1982, Backman and Shackleton 1983, Keller *et al.* 1983, Kent and Spariosu 1983) and referred to the geomagnetic polarity time scale (Berggren *et al.* 1985). Oxygen and carbon isotopic data are derived from the global summaries provided by Miller and Fairbanks (1985*a*, *b*; Miller *et al.* 1987), which are also based on a number of DSDP sites that we consider.

Because we are concerned with maximum stratigraphic ranges over a large area and large number of DSDP sites, the well-known biases of the fossil record, including core contamination and reworking of fossils, in any particular core have a more restricted effect on the reliability of

our data, compared to most published studies. In order to minimize these biases, however, we took into account both the sedimentologic and paleoceanographic setting of the micropaleontologic records.

We would also like to mention the relevant caveats. This is a taxon-bound study. As is true of all taxic studies in evolutionary paleontology, of which there is a long tradition (e.g., Simpson 1944, 1953, Van Valen 1973, 1984, Raup 1976a, b, 1986, Sepkoski 1978, 1979, 1984, Stanley 1979, Gould and Calloway 1980, Ward and Signor 1983, Valentine 1985, Prothero 1985, Knoll 1986), anagenesis and cladogenesis are frequently not distinguished. Ideally, taxic and morphometric data should be combined, but this is not yet possible except for isolated cases. The generality of these results depends, as a consequence, on what constitutes a species within these groups, and whether or not the species concept was uniformly applied by workers in the field. We undertook an appopriate effort. On the other hand, radiolarians were omitted from this study because their fossil record is more poorly-described and the species concept is more ambiguously applied within this group. Other caveats include: the recognition and extent of pseudoextinction and phyletic transformation, in that the former will inflate extinction and the latter will inflate speciation; migration effects on the paleosystem (the data set does not distinguish between species origination and immigration, because we have selected a geographically bound paleosystem in order to examine the patterns of turnover within the system); and the levels of uncertainty and sources of error in the data on both species and time.

THE PREDICTION OF CONSTANT EXTINCTION

Van Valen's (1973) stated intention was to document empirically the intuitive expectation that biologically young taxa had a higher probability of extinction than long-lived taxa. Instead, the data revealed that the probability of extinction of an ensemble of taxa is remarkably independent of biologic time, or whether a species has been in existence a long or a short time. Van Valen termed this empirical pattern the Law of Constant Extinction. To account for this unexpected empirical result, the Red Queen Hypothesis was proposed, although the empirical result of constant extinction independent of taxon longevity does not really require such a hypothesis (Hoffman 1983, Hoffman and Kitchell 1984). Rather, the Red Queen Hypothesis is one means of resolving the paradox that emerges if one expects species to be adapting continually throughout biologic time and if one assumes that such adaptations increase the overall probability of persistence.

The Law of Constant Extinction is lawlike in that it describes the statistical behavior of a large group of taxa. Testing such a prediction is

scale-dependent: to find evidence of constancy means that the data behave with a statistically constant probability with respect to age or duration, at a given temporal resolution. When ordered by the time of origination, each species in the data set under consideration has a unique time of origination (first appearance) and a unique time of extinction (last appearance) within the sampled paleosystem. There is a wide range of species durations, and the set of presently extant species include both long-ranging and recently originating species (cf. Kitchell 1987: fig. 5). It is only while considering the whole ensemble of taxa that regularity may appear.

What does such regularity mean? If the per taxon probability of extinction does not depend on a taxon's past history, then the pattern of extinction probabilities should conform to a Poisson process. In other words, Van Valen's (1973) Law of Constant Extinction can be restated as a statistical description of an aggregate of random failures. Such a pattern says that the probability of background extinction does not depend on past history, the system lacks memory, and the causes of failure are unpredictable (Hoffman and Kitchell 1984). Such a pattern is well described by the exponential distribution.

It is worth noting that testing whether extinction rates are temporally constant (that is, constant over absolute or geologic time) is quite different from testing whether such rates are age-(or duration-)constant. Conroy and Nichols (1984) combined the biologic and geologic time criteria by stating that age-independent "taxonomic survivorship curves can only be assured if extinction rates are constant with respect to both taxon age and absolute time. Therefore, we believe that the question of temporal variation in extinction probabilities is very relevant to Van Valen's Law." We disagree. As we demonstrated previously (Hoffman and Kitchell 1984), and as we also show below, extinction probability may be constant with respect to a taxon's age but non-constant with respect to absolute time.

THE EMPIRICAL BEHAVIOR OF BACKGROUND EXTINCTION

Survival analysis: biologic time

The Law of Constant Extinction was derived from inspection of age-specific survivorship graphs that purported to show "almost uniform linearity for extinct taxa" (Van Valen 1973). It is a well-known feature of survivorship graphs that a constant mortality process will appear as an exponential pattern. Log transformation of the survivorship axis recasts the exponential curve as a linear function. Although Van Valen reported that the survivorship curves were surprisingly linear, Raup (1975) applied a test developed by Epstein to determine whether the linearity was

statistically significant, the standard measure of surprise. By simulating survivorship data, however, we have subsequently shown that the Epstein test is too sensitive to the lower tail of the distribution to provide an adequate test for age-independency (Hoffman and Kitchell 1984).

We have formulated several mathematical models that contrast independence of biologic time with various types of dependency on biologic time. The underlying assumption of survival analysis is that the survival of a species depends only on the age of a species. The only parameter included in survival analysis is duration time. Survival times represent duration times, or lengths of time between the known first appearance of each species in and its final disappearance from the set of 116 DSDP sites. Because not all taxa are extinct, standard methods are used to deal with censored data, or extant species whose total durations are undetermined. These survival times are then grouped into million-year intervals for analysis. We have, however, not applied any resampling program to compensate for differences in encounter probability among these million-year intervals (e.g., Nichols and Pollock 1983, Conroy and Nichols 1984).

Ordering of the data on all species permits the sequential derivation of the proportion of species that survive each duration interval. The slope of this function provides an overall estimate of the probability of extinction of the group. The shape of this function may or may not be exponential, or log-linear. However, it is only exponentiality that is related to age-independent survival. While formulating the problem this way, a key variable is the probability of becoming extinct this way, for each age group, given that a species reaches that age. This probability is frequently referred to as the hazard rate for that age. It is conditional probability of extinction, conditional on the species reaching a given age. The problem of estimating hazard rates has been considered extensively by statisticians. One approach is to assume that the probability of going extinct at a given age follows a certain parametric form. Well-studied examples are the Weibull and Gamma distributions. A second approach, used here, is not dependent on these parametric assumptions. Instead, one fits a general model or a series of models to the hazard probabilities and compares the estimates under these models to those under a constant hazard model. A more complete description of the analytical methods is given in our earlier article (Hoffman and Kitchell 1984).

We are primarily interested in testing the hypothesis of a constant, or age-independent, hazard rate against a simple age-dependence in rates. To do this, we compare a constant hazard rate model (the baseline model; cf. Wimsatt 1987) to models which assume that the hazards are linear in some transformation of age. The transformations of the age of a species that we have considered are the log of age, the negative reciprocal, and the square root. The best of the age-dependent models is then compared

to the baseline model to test the significance of the difference between age-independency and age-dependency.

To assess the alternative hypotheses of age-independency and age-dependency, we compare the deviance between empirical data and these several models of extinction probability. Each model is fit using a logistic regression on the observed hazard rates by the method of maximum likelihood. Logistic regression is necessitated by the fact that one is dealing with proportional-type of data: i.e., the proportion of species extinct per time interval. This method assumes that the observations are independent binomial random variables. It is assumed that the probability of surviving a given age interval is the same for all species reaching that age, and that the survival or extinction of any one species does not affect the survival or extinction of any other species in the same age interval. These assumptions may not be valid in all cases. Further, we make the assumption that the probability of surviving the t-th age interval is a logistic function of the age interval. The age-independent model is compared to several age-dependent models, to provide a measure of significance and to discriminate between types of age-dependency. For a more complete description of the methods see Hoffman and Kitchell (1984).

Comparisons of the empirical data with the best-fit age-independent model and the best-fit age-dependent model are displayed in figures 1 and 2. The deviances, degrees of freedom, and differences in deviance
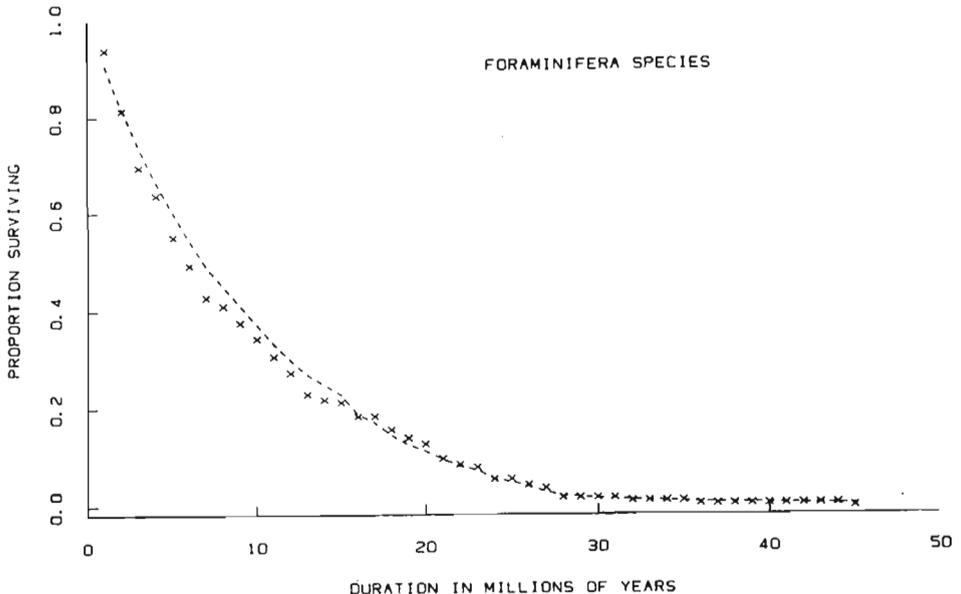

Fig. 1. Results of survival analysis for planktic foraminifer species, with data grouped into million-year intervals; crosses denote the original data, dashed line denotes the age-independent model of constant extinction probability, which is the best-fit model (see Table 2).
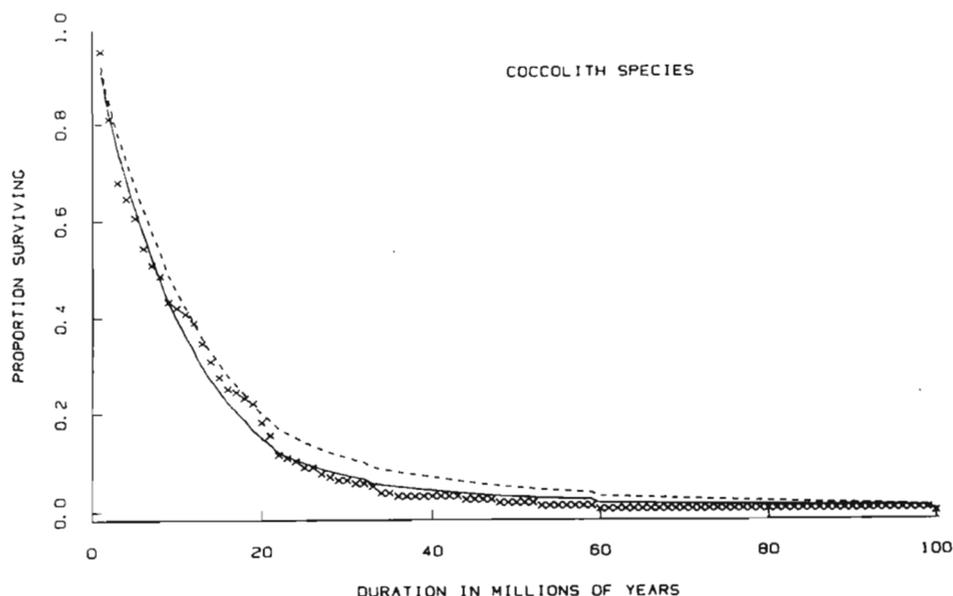
Fig. 2. Results of survival analysis for coccolith species, with data grouped into million-year intervals; crosses denote the original data, dashed line denotes the best-fit age-independent model, solid line denotes the best-fit of the tested age-dependent models, which is the best descriptor of the data (see Table 2).

Table 2

Summary of age-independent and age-dependent survival models; deviance and associated degrees of freedom are provided for each model, chi-square statistic (d.f. = 1) is given in lower line for each model comparison

Taxonomic group	Age-indepen- dent model	Age-dependent models:		
		linear	logarithm	reciprocal
foraminifers	51.76; 44	51.57; 43	51.61; 43	51.51; 43
		0.19	0.15	0.25
coccoliths	81.28; 99	76.19; 98	78.70; 98	81.12; 98
		5.09	2.58	0.16

between the various age-dependent models and the age-independent model are given in Table 2. For planktic foraminifers, the best-fit model is the age-independent model. None of the models that included age has a significantly better fit than this model, which suggests that the hazard is constant over age and is estimated as a hazard of 9.35%. Such a slope of constant extinction probability predicts a mean species duration of 10.7 Myr. The coccolith survivorship data are not best fit by the age-independ-

ent model but rather by the linear age–dependent model. This age–dependent model, however, is the only one to fit the data significantly better than the constant hazard model (p < .05). This suggests that the hazard (or probability of extinction) is decreasing at a statistically constant rate for all ages. The age–independent, or constant hazard, model estimates a hazard of 7.85%, and a mean species duration of 12.7 Myr.

Polycohort analysis: geologic time effect

If we replace the biologic axis of duration time with the geologic axis of absolute time, the behavior of extinction changes from statistically continuous to a combination of continuous and discontinuous. This is illustrated by Kitchell (1987: fig. 7) who presented the actual, historical trajectories of survivorship. Each trajectory represents the cumulative decay (by extinction) of a 'polycohort' of species, wherein the polycohort is defined as species extant per 1 million-year interval. The progressive decline in the number of surviving species as the polycohort ages introduces some bias toward stepping. For both the planktic foraminifers and coccoliths, however, the interval from 37 to 22 Myr is characterized by a fairly smooth or constant decay pattern, whereas the interval from 22 to 0 Myr is distinctly more stepped. Such a stepped pattern is evidence of alternating periods of quiescence and activity in extinction (Raup 1986).

Interactive effects of age and time

Extinction probability may be dependent jointly on age and absolute or geologic time, particularly if the abiotic environment experiences nonconstant change. In addition, the behavior of extinction probability may differ among origination of true cohorts. Consequently, we are interested in the results of an analysis that will compute the extinction probability surface for a series of true cohorts as a function both of duration (biologic) time and absolute (geologic) time. The method involves an application of logistic regression and is discussed in more detail by Hoffman and Kitchell (1984). To permit comparison between the results of the previous study and the present study, we have used the same smoothing values (see Craven and Wahba 1979) and have similarly scaled extinction probability (z-axis) to range between 0 and 1.

The extinction probability surfaces, plotted in figures 3 and 4 as functions of origination time and absolute time, are inclined, thus indicating that younger cohorts have an increasingly higher probability of extinction. The interactive effects of origination time (age of cohort) and geologic time are revealed as local highs in the extinction probability surface. The oldest foraminifer cohort, for example, has a pronounced peak in extinc-

tion at 35—27 Myr, whereas the next two origination cohorts experience the same time interval with little effect.
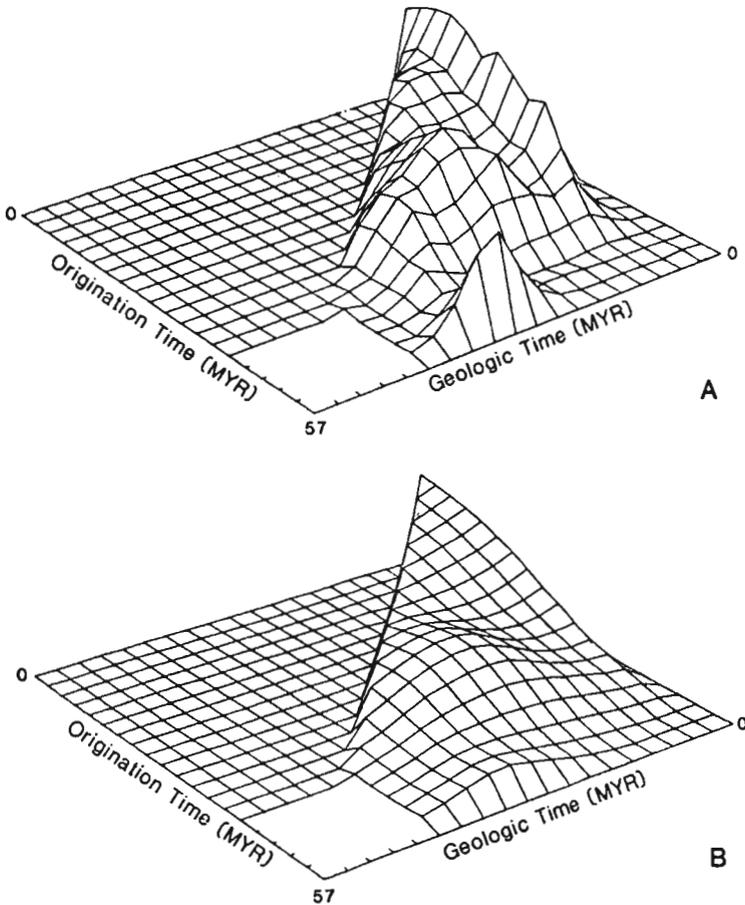

Fig. 3. Plots of the extinction probability surface (z-axis) as a function of origination time and geologic time for planktic foraminifer species. Lines parallel to the geologic time axis represent true cohorts (species originating during a given time interval); the diagonal reflects the sequential time of origination of each cohort; species are grouped into cohorts on 3-Myr basis; the unlined portion of the extinction probability surface represents the pre-Oligocene data which necessarily record solely origina-tions but no extinctions. The z-axis is scaled, for purposes of comparison, to have the same range of extinction probability, from 0 to 1. A — smoothing values of -12, B — smoothing values of -9 (see Craven and Wahba 1979)

On the other hand, species durations, illustrated by Kitchell (1987: fig. 2C, D) as frequency distributions, have the expected hollow-curve distribution wherein short-lived species clearly dominate. Since it is extinct species that are responsible for the hollow-curve form of the distribution of species durations, this pattern is not an artifact of truncated durations of presently extant species.
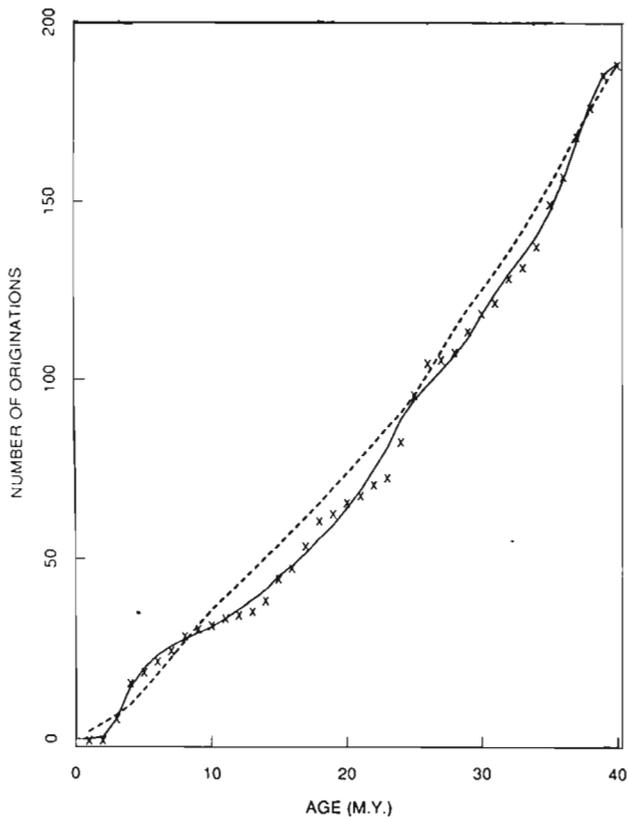
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Fig. 5. Comparison of models of planktic foraminifer species accretion as a function of age of the paleosystem; crosses denote the original data (or the cumulative number of species originations), dashed line denotes the best-fit model of diversity-independent accretion (model 1), solid line denotes the best-fit diversity-dependent model (see Table 3).
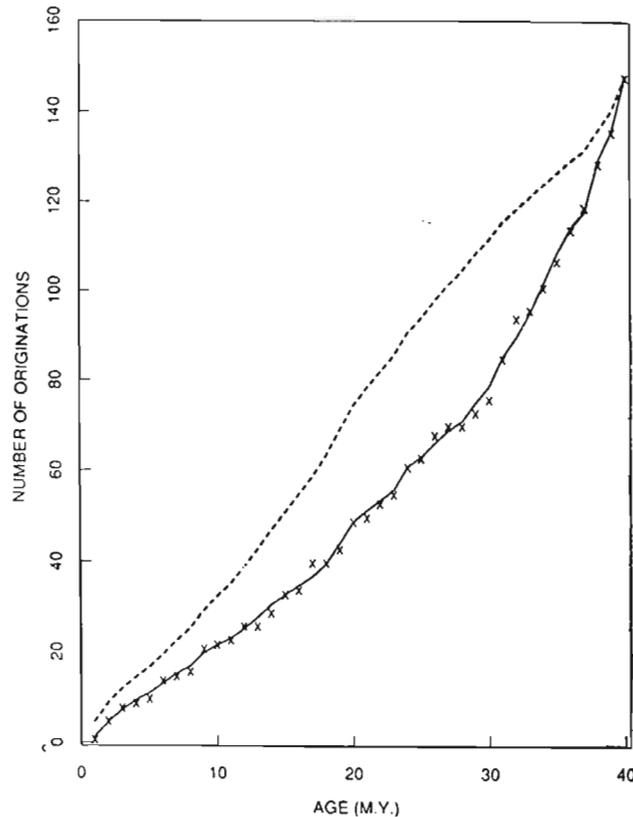
Fig. 6. Comparison of models of coccolith species accretion as a function of age of the paleosystem; see Fig. 5 for explanation.
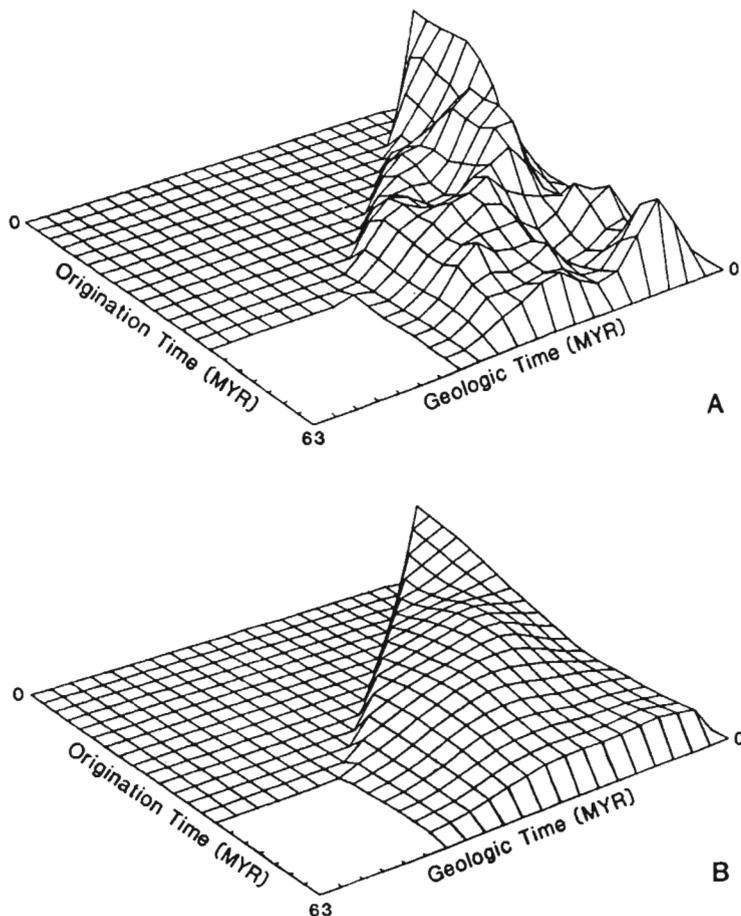
Fig. 4. Plots of the extinction probability surface (z-axis) as a function of origination time and geologic time for coccolith species; see Fig. 3 for explanation.

THE EMPIRICAL BEHAVIOR OF ORIGINATION

Accretion analysis: paleosystem time

We are also interested in deriving and testing models for the origination of species within these groups over the duration of the paleosystem. These analyses are also done on data grouped into 1 Myr intervals. Since these intervals are of equal duration, there is now no need to include a length-of-the-interval term (necessary in Hoffman and Kitchell 1984). For the purposes of analysis, the number of originations in a time interval is assumed to be a Poisson variable that might be dependent on the number of species extant at the beginning of an interval and the time at which the interval began. These variables are added sequentially to a baseline model, in order to assess the degree of dependency between

species age (or duration), diversity, and absolute (or geologic) time. The baseline, or diversity-independent, model assumes that the origination rate is constant for each time interval and not dependent on the number of species present:

$$O_i = e^\lambda \tag{1}$$

Each of the other three models examines diversity-dependence. The second model considered has the number of species originating in an interval dependent on the number of species present in the interval, but is otherwise constant:

$$O_i = D_i \cdot e^\lambda \tag{2}$$

A variation of this model assumes that the average number of originations is dependent on the number of extant species, but it does not force this relationship to be in strict proportion to their product. Rather, it assumes that the average is in proportion to the product of some power of each:

$$O_i = D_i^{\beta_1} \cdot e^\lambda \tag{3}$$

These models are discussed in terms of products and powers since a Poisson variable is modelled in terms of the natural logarithm of its mean. The final model relaxes the constant time assumption of equation (1), but is otherwise similar to equation (3):

$$O_i = D_i^{\beta_1} \cdot e^{\lambda(t)} \tag{4}$$

The estimated means derived from these methods are displayed graphically as accretion curves, representing the cumulative number of species that have originated since the beginning of the study period (figures 5 and 6). They are obtained as a cumulative sum of the predicted values. For example, the best-fit curve for the constant accretion, or diversity-independent, model is obtained by estimating the expected number of originations in each interval. These means are used to form the partial sum of all estimates up to that point in time.

Table 3

Results from fitting diversity-independent and diversity-dependent accretion models (see text for explanation), reported as deviances, degrees of freedom, and chi-square statistics; chi-square values represent comparison between each model and the previous one; note that model (4) used cubic B-splines with 5 knots and hence has a loss of 4 degrees of freedom

Taxonomic group	model (1)	Accretion models:		
		model (2)	model (3)	model (4)
foraminifers	101.6; 39	86.2; 39	85.9; 38	45.7; 34
		15.4	0.3	40.2
coccoliths	92.9; 39	101.1; 39	82.6; 38	40.7; 34
			10.3	41.9

Table 3 lists the results from fitting each accretion model to the data in terms of deviances and differences in deviance between pairs of models, as well as the chi-square statistic of each comparison. The constant diversity-dependent model (2) provides a significantly better fit to the data than does the diversity-independent model (1), for both groups. The chi-square statistic is not significant for model (3). Model (4), however, provides a highly significant fit ($p < .001$) for the coccolith data. For foraminifers, the diversity coefficient (D_i) of model (2) is 0.7193 (standard error $= 0.1063$). For coccoliths, this coefficient is 0.9412 (standard error $= 0.1068$), which is not significantly different from 1; hence there is no significant difference between the models (2) and (3).

CORRELATION WITH ABIOTIC CHANGE

Rates of extinction and origination

Evolutionary turnover, powered either by extinction, or origination, or both, is characteristically continual. There are no quiescent intervals, on a global resolution time scale of 1 Myr, over approximately the past 37 Myr (figures 7 and 8). The history of each group is dominated by simultaneous origination and extinction activity. The diversity trajectories over these 37 Myr (figure 9) are consistent with an early phase of diversity increase, powered by originations in excess of extinctions, and a later phase, particularly for the coccolith data, when diversity is remarkably constant, indicating balanced rates of origination and extinction. A cross-correlation matrix shows that extinction rate and origination rate are highly intercorrelated ($p < .01$; Table 4).

This significant correlation between origination and extinction activity suggests either (i) an endogenous process whereby origination and extinction stimulate each other, either by extinctions providing an opportunity for successful originations, or originations leading to an overshooting with extinctions following as a correction, or (ii) simultaneous responses to external perturbations. To better examine the latter interpretation, the degree of correlation between originations and extinctions and the oxygen and carbon stable isotopic records were studied. Paleoceanographic events are generally recognized by anomalies in delta-13-carbon and delta-18-oxygen values (e.g., Savin *et al.* 1981, Kennett 1983, Keigwin and Keller 1984, Shackleton 1985, Keigwin and Corliss 1986). The isotopic record we have used is derived from Miller and Fairbanks' (1985*a, b*) time-series analysis of benthic foraminifer data on the global scale, providing values per Myr. Significant correlations ($p < .01$; Table 4) are present between both originations and extinctions and the delta-18-oxygen record. The highest correlations, however, are lagged for the foraminifer data, at 3 Myr for originations and 1 Myr for extinctions, for the oxygen isotopic
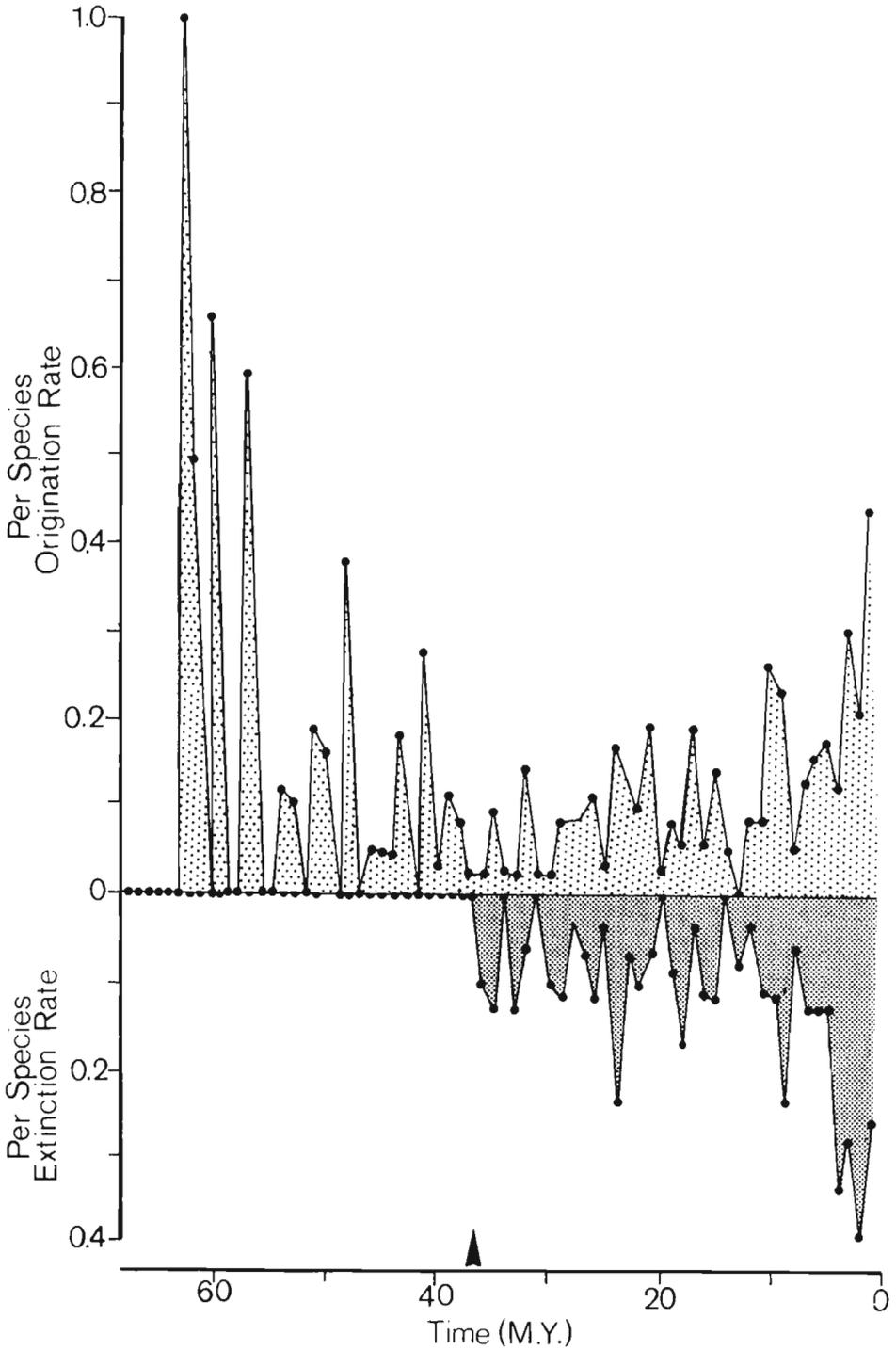
Fig. 7. Origination rate (light shading) and extinction rate (dark shading) of planktic foraminifer species calculated as a per species rate (that is, standardized for the number of extant species per time interval), as a function of geologic time; the arrow separates the pre-Oligocene origination history from the Oligocene-through-Holocene origination/extinction history.
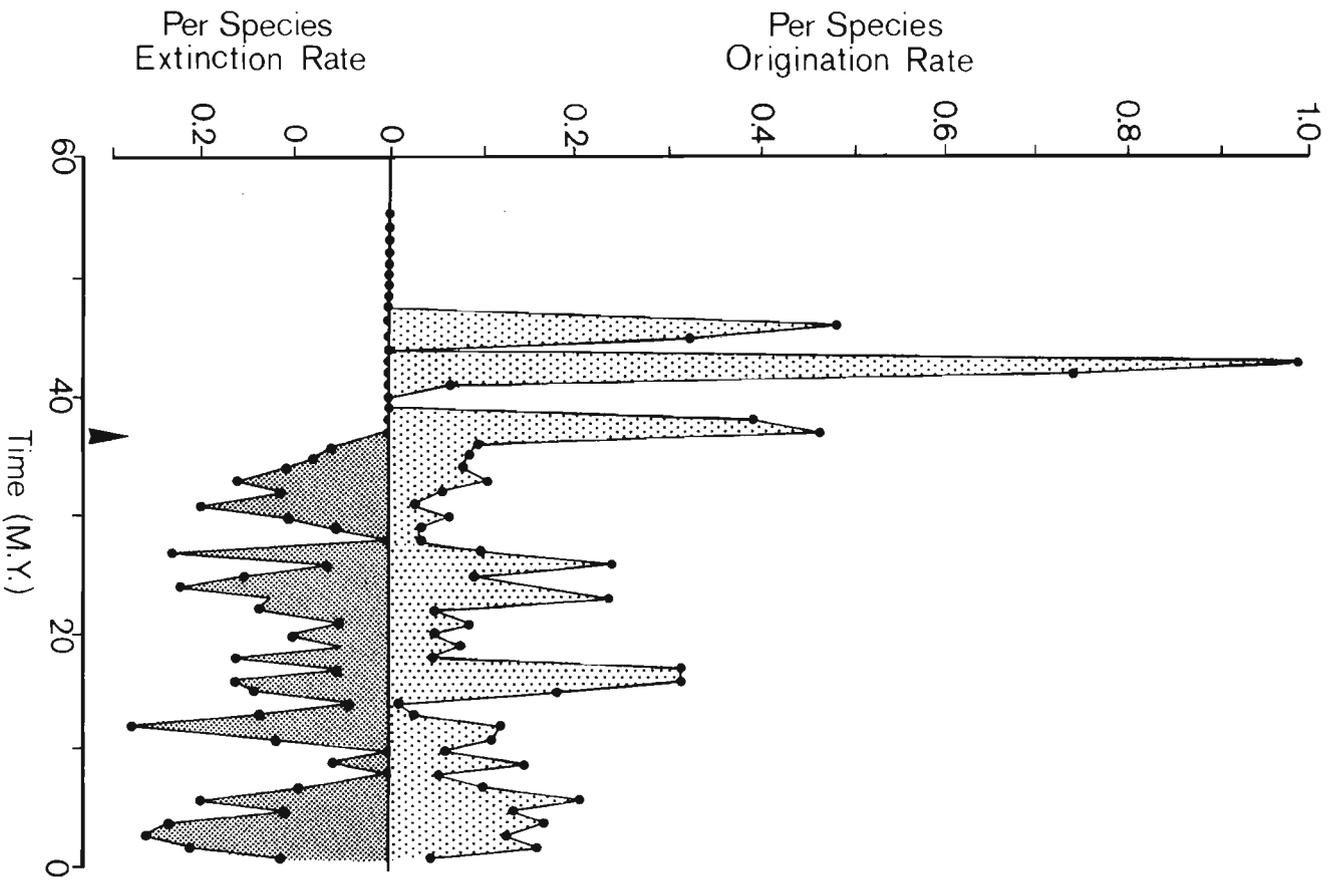
Fig. 8. Origination and extinction rate of coccolith species as a function of geologic time; see Fig. 7 for explanation.

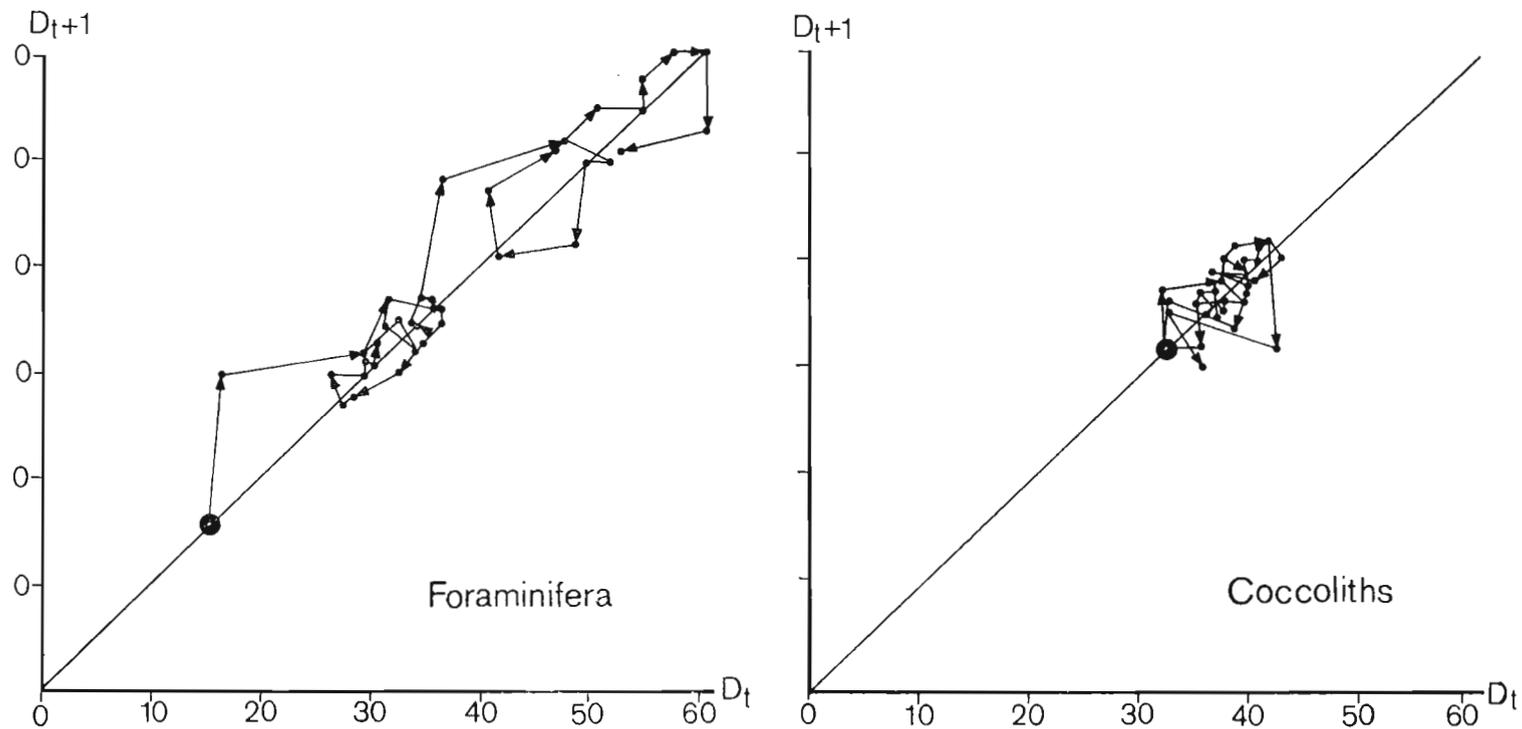Fig. 9. Phase plane trajectories of planktic foraminifer and coccolith species diversity at time t versus time t+1, over the past 37 Myr; intersection of the trajectories with the 45° line represents a constant, or potential equilibrium, diversity.

signal (Table 4). For the coccolith data set, the highest correlations are not lagged, and are similarly more significant (p < .01; Table 4) for the oxygen isotopic signal.

Table 4

Correlation matrix of origination rates, extinction rates, oxygen isotope record, and carbon isotope record for coccolith species (upper right matrix) and foraminifer species (lower left matrix); ** p < . 01, * p < . 0.5; (0) zero lag, (−1) 1 Myr lag; (−3) 3 Myr lag

	Origination rate	Extinction rate	Delta-18 oxygen	Delta-13 carbon
Origination rate	—	0.66 **(0)	0.53 **(0)	−0.36 *(0)
Extinction rate	0.51 **(0)	—	0.58 **(0)	−0.58 **(0)
Delta-18 oxygen	0.58 **(−3)	0.57 **(−1)	—	−0.58 **(0)
Delta-13 carbon	−0.37 *(−3)	−0.39 *(−1)	−0.58 **(0)	—

Paleoceanographic events and evolutionary turnover

Major paleoceanographic events within the temporal scope of this study, which begins with the Eocene/Oligocene boundary event placed at 37—36 Myr and evidencing a global change in climate and ocean chemistry associated with the origin of the psychrosphere (Corliss et al. 1984; see also Benson et al. 1984), include the following: the mid-Oligocene event placed at 31—30 Myr, the terminal Oligocene event at 25—24 Myr, the mid-Miocene event at 15—14 Myr, the terminal Miocene event at 6.2—5.5 Myr, and the Pliocene event at 3.2—2.5 Myr. A comparison of the timing of these events to the origination and extinction data (cf. figures 7 and 8) shows again that there are no quiescent million-year intervals, nor any unique bursts of origination/extinction activity solely associated with these 'events'. These results are unlike the interpretations presented by Wei and Kennett (1986). These results do underscore the general testing problem in that although quiescent periods in the abiotic environment are the requisite conditions under which the predictions of the models diverge, they are not characteristic of the historical record at this time scale.

TESTING COMPLEX CAUSALITY AND CONTINUA

The fossil record provides partial information on notoriously complex systems of multiple causality. Our approach has been directed toward

the testability of propositions pertaining to the species level of the fossil record and geologic time scale. We have examined empirical patterns of species duration, and the degree to which these patterns may be powered by dynamics in species number, a crude measure of the biotic environment, and isotopic ratio changes, a more direct measure of the abiotic environment.

The original appeal to empirical testing, formulated by Stenseth and Maynard Smith (1984), was based on the expectation that the fossil record would provide an explicitly empirical test over the evolutionary time scale to distinguish between theoretically plausible but alternative evolutionary explanations of causality. One explanation, namely the Red Queen Hypothesis, predicted constancy of evolutionary activity in terms of extinction-origination in the absence of change in the abiotic environment; whereas the alternative, Stationary Hypothesis, predicted quiescent periods of no evolutionary activity in a constant abiotic environment. Both hypotheses predicted response in extinction–origination activity given extrinsic perturbations, or change in the abiotic environment. The difference is one of degree: the Red Queen Hypothesis posits that change in the abiotic environment is not the sole cause of evolutionary turnover, while the Stationary Hypothesis posits that it is.

The empirical issue is important. Accordingly, we have examined what data are anticipated from these hypotheses and how these expectations compare with data for two major groups whose fossil record provides an exceptional opportunity for global analyses at fine temporal resolution. We have identified several potential causal processes — taxon longevity, diversity, and absolute time differences in historical environments — and have attempted to evaluate their probable contributions to rates of speciation and extinction. These parameters were selected for study because they correspond to predictions of the two models envisaged by Stenseth and Maynard Smith (1984), and because they are measurable from the fossil record.

The quantitative analyses themselves are unambiguous: models of age- (or biologic time-), geologic time-, diversity-, and cohort-dependence have been evaluated with maximum likelihood techniques to determine the degrees of explanation afforded by each factor, as independent and interactive variables. Independent temporal evidence of paleoceanographic changes in climate and ocean chemistry were examined for the degree of similarity between the timing of events in the abiotic environment and responses in the extinction-origination data.

These analyses reveal that the probability of extinction considered as a function of biologic time is a continuous, stochastic process. The probability of extinction is remarkably constant, or independent of elapsed biologic time. Such a result, at the species level, is compatible with Van Valen's (1973) Law of Constant Extinction, a model of continuous back-

ground extinction. By contrast, the probability of extinction considered as a function of geologic time is both continuous and discontinuous. Analyses using cohorts of species that originated within 1 Myr intervals reveal an interactive effect between species duration and geologic time. In general, older cohorts had lower probabilities of extinction than younger cohorts. A comparison between Figure 9 of Hoffman and Kitchell (1984) and Figure 7 of Kitchell (1987) shows that the mid-Miocene event is much less pronounced in the global tropical data, suggesting that this event was experienced to a greater degree by higher latitude species, indicating a biogeographic element to the extinction response.

No time intervals were characterized, however, by evolutionary quiescence. For all million-year intervals, either originations, or extinctions, or both were observed. The dominant pattern was both origination and extinction within each time interval. The diversity coefficients were both less than 1, thus indicating no positive feedback between an increase in species number and an increase in extinction or origination.

The interpretation of these empirical results, as a means of deciding between the two alternative evolutionary hypotheses, however, is much more ambiguous. In theory, selection powered by biotic and abiotic parameters is quite distinct. In natural systems, however, the processes act simultaneously. As expressed by Quinn and Dunham (1983), "it is not possible in principle to perform 'critical tests' to distinguish between the 'truth' of processes occurring simultaneously."

Processes that vary over a continuum are similarly problematic. There may be a continuous range of predicted outcomes. Data retrieved from the fossil record necessarily incorporate simultaneous abiotic and biotic pressures, in addition to developmental and genetic and other factors. A priori, case histories from the fossil record are expected to lie along the continuum between theoretical end members. Consequently, we have been more interested in assessing relative contributions of simultaneously operating factors than in aligning ourselves with one or the other hypothesis. We have examined predictions of the models we formulated, which have sequentially incorporated variables of age-, time-, and diversity-dependence. Estimates of contributions of each variable to the overall pattern were made in order to quantitatively partition the observable components of an explanation.

We have shown empirically that the assumption of constancy of the environment does not hold. Constancy (equilibrium) has been a standard assumption of ecological theory over the past several decades (Chesson and Case 1986). Such theories tend to disregard, as unimportant, historical effects and environmental perturbations. Nonequilibrium theories represent a counterdevelopment. These nonequilibrium theories emphasize dynamic, and thereby temporal, features of natural systems, and are more suitable for evolutionary, or geologic, time scale studies. But if chance

factors and historical effects dominate, can natural systems have predict-
able patterns (Chesson and Case 1986)?

Numerous caveats are in order. All results are necessarily scale-
-dependent. Our results are derived from global data on extinction and
speciation, measured over one-million-year intervals. Extrapolation to
finer time scales would require independent testing. This is also a taxon-
bound study. The utility of these results for making inference about
evolutionary processes depends on what constitutes a species, whether
or not these criteria were uniformly applied, and the generality of proti-
stan patterns for evolution in general.

CONCLUSION

In conclusion, the type of data analyzed in this study is duration time,
as a consequence of time of origination and time of extinction. Expected
time to extinction has been proposed as the fundamental measure of
fitness (Cooper 1984), in particular for the purpose of macroevolutionary
investigations (Endler 1986). In the context of macroevolution, other
fitness measures are seen as derivatives of the expected time to extinction.
Expected time to extinction also requires, to be a predictable measure of
fitness, a complete knowledge of the environment and its dynamics. As
a consequence, one is at the impasse recognized by Maynard Smith (1982).
The development of a 'theory of environment' is needed in order to
explain, rather than merely describe, differences among species in their
expected time to extinction.

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TEMPO POWSTAWANIA I WYMIERANIA GATUNKÓW JAKO FUNKCJA DŁUGOTRWAŁOŚCI GATUNKU ORAZ ZRÓŻNICOWANIA I HISTORII PALEOSYSTEMU

Streszczenie

Empiryczne dane o stratygraficznym zasięgu planktonicznych otwornic i kokkolitów od oligocenu do holocenu na obszarze tropikalnego Pacyfiku i Atlantyku, pochodzące ze sprawozdań Deep Sea Drilling Project (tabela 1), poddane zostały precyzyjnej analizie statystycznej w celu przetestowania modelu Czerwonej Królowe:

i modelu Stacjonarnego ewolucji w systemie wielogatunkowym (por. Hoffman i Kitchell 1984, Stenseth i Maynard Smith 1984). Analizowano związki pomiędzy tempem powstawania i wymierania gatunków a długotrwałością gatunków oraz zróżnicowaniem taksonomicznym i historią paleosystemu (tabele 2—4; figury 1—9). Okazuje się, że co prawda prawo stałości tempa wymierania, które legło u podstaw modelu Czerwonej Królowej (Van Valen 1973), znajduje w tych danych mocne potwierdzenie empiryczne, jednak konsekwencje teoretyczne tego wyniku są niejednoznaczne, gdyż testowane modele nie stanowią dwóch wykluczających się stanów, lecz dwa skrajne ogniwa ciągłego spektrum możliwości.