A NONEQUILIBRIUM THEORY FOR THE RATE-CONTROL OF SPECIATION AND EXTINCTION AND THE ORIGIN OF MACROEVOLUTIONARY PATTERNS

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Abstract

Cracraft, J. (Department of Anatomy, University of Illinois at the Medical Center, P.O. Box 6998, Chicago, Illinois 60680, and Division of Birds, Field Museum of Natural History, Chicago, Illinois 60605) 1982. A nonequilibrium theory for the rate-control of speciation and extinction and the origin of macroevolutionary patterns. Syst. Zool., 31:348–365.—Macroevolutionary analysis focuses on the explanation of general patterns of diversity among monophyletic groups. Three general patterns can be recognized: radiation diversity in which species richness increases through time, reduction diversity in which richness decreases, and steady-state diversity in which it remains relatively constant. Most clades show some combination of these three patterns.

Clades also exhibit a pattern of phenotypic change that can be superimposed on the pattern of diversification. With speciation, descendant species can become either markedly apomorphic or remain plesiomorphic relative to the ancestral condition. There is no necessary correlation between a particular phenotypic pattern and a specific pattern of diversity.

Explanations of macroevolutionary patterns have been of two principal types: adaptationist and species selectionist. The adaptationist approach has explained patterns of diversity in terms of the occupation of “adaptive zones,” driven by natural selection. “Adaptive zones” are tautological constructs and lack ontological status. The other macroevolutionary explanation, species selection, is a pattern of species survival through time and as such is neither a process nor a theory of macroevolutionary change. A deterministic theory of macroevolution lies in explaining inter-cladal diversity patterns by variation in the rate-controls of speciation and extinction.

Speciation rate is controlled by factors intrinsic to species such as morphogenetic complexity (Wiley and Brooks, 1982) and by external factors. It is hypothesized here that the primary external rate control of speciation is lithospheric complexity, which relates directly to the number of geological and climatic barriers promoting geographic isolation. It is also proposed that plate tectonic activity controls extinction rates through mechanical influences on habitats and its effects on environmental climatic change. Extinction rates are postulated to be lower in environments of higher favorableness, which is defined in terms of relatively high mean annual temperature, low range of mean annual temperature, and high annual rainfall dispersed evenly throughout the year.

The interaction of relative environmental complexity and favorableness can be used to make predictions about diversity patterns among clades and to investigate the relative importance of internal morphogenetic complexity. [Macroevolution; diversity; speciation rates; extinction rates; lithospheric complexity; climatic change.]

It has been traditional within systematics and evolutionary biology to view macroevolution from two perspectives, which, at least historically, have been taken to be interrelated with one another (see especially Simpson, 1944, 1953). First, macroevolution is described in taxonomic terms, with emphasis on the analysis of patterns of diversity within superspecific (higher) taxa. A common example is the description and explanation of so-called “adaptive radiations.” The second perspective is to view macroevolution as the origin of major phenotypic (in the broad sense) characters or character-complexes, in contrast to minor phenotypic discontinuities often seen to define populations, species, or sometimes genera. Historically, however, the taxonomic component of macroevolution usually has been interpreted within the context of a transformation of the phenotype (Eldredge, 1979; Eldredge and Cracraft, 1980), particularly within paleontology, but this perspective is also found in much of the recent commentary.
on macroevolution generated by workers whose primary field of study is population genetics rather than systematics or paleontology (Lande, 1980; Templeton, 1980; Stebbins and Ayala, 1981; Charlesworth et al., 1982). Thus, in this latter view, macroevolutionary change is seen as an extrapolation of microevolutionary (within-population) change over a long time-scale: accumulated small phenotypic changes, said to be describable in terms of population genetic theory, are the principal evolutionary phenomena with which we should be concerned.

In recent years, however, an alternative conception of macroevolution has emerged, one that advocates not only its epistemological separation from microevolutionary analysis, but more importantly, its ontological separation as well (Eldredge and Gould, 1972; Stanley, 1975, 1979; Eldredge, 1979; Eldredge and Cracraft, 1980; Vrba, 1980; Gould, 1980). (Historically, paleontologists have maintained the epistemological, but not ontological, separation of microevolution and macroevolution, but now some population biologists seem to be the major proponents of this view.) This alternative conception of macroevolution, which sees the problem of evolution as primarily a question of the origin of taxonomic discontinuities (Eldredge, 1979; Eldredge and Cracraft, 1980), follows logically from two premises: (1) that basic taxonomic units (call them species) can be—and are—definable as discrete units in space and time, and (2) that the origin of such units (speciation) is not merely a problem of accumulating gene or genotype change. Given these, then, there is necessarily a disjunction between the patterns characterizing populations within a species (patterns of gene, genotype, karyotype, or phenotypic frequencies, for example) and those characterizing species or groups of species within and between clades. Indeed, the two premises seem to have significant conceptual and empirical support: (1) paleontology and systematics have demonstrated repeatedly the generality of species individuality in space and time, and (2) it has not yet proven possible to explain patterns of taxonomic differentiation, including the accompanying phenotypic discontinuities, with reference to a particular theory of gene or genotype change (Lewontin, 1974).

Within the framework of the taxic approach to macroevolution, patterns of diversity and phenotypic variation within and among clades are explained as a consequence of differential survival of species rather than as a necessary manifestation of the presumed "adaptive" characteristics of individual organisms within populations of each species. The patterns, therefore, are determined by differential rates of speciation and extinction, and the central problem of macroevolutionary analysis is the development of a deterministic theory to explain non-random variation in those rates.

This paper is an attempt to propose a mechanistic theory of speciation and extinction rate-control and relate it to possible explanations of macroevolutionary patterns. Because workers can have different perceptions of the importance of the questions being asked within the domain of macroevolutionary analysis, those macroevolutionary patterns that seem to require a general explanation will be specified first. Following that, some postulated explanations will be reviewed, focusing primarily but not exclusively on hypotheses which attempt to explain differential rates of speciation and extinction. Finally, an alternative theory for the rate-control of speciation and extinction will be introduced and applied to the problem of explaining macroevolutionary patterns.

MACROEVOlUTIONARY PATTERN

Two kinds of macroevolutionary pattern can be described, one involving differential species diversity (richness) within and between clades, and one having some component of character change superimposed on the pattern of taxonomic diversity. It is doubtful whether a pattern of character change can be considered independent of a pattern of diversity.
For example, most, if not all, trends are defined as much by a pattern of diversity as they are by the character-state pattern possessed by the species of the different clades. Likewise, patterns of geography may sometimes have their own intrinsic interest, but in the context of macroevolutionary analysis, they generally will not have significance unless combined with patterns of diversity and character change; many "adaptive" radiations, for instance, may have a distinct geographic pattern.

All patterns are defined with respect to time, either absolute or relative: given one time-scale a pattern may be apparent, but may disappear when taken within the context of a different time-scale. Macroevolutionary patterns always span "geological" time in contrast to "ecological" time, but macroevolutionary patterns themselves are not defined by a geological time-scale (contra Stebbins and Ayala, 1981:968–969); as used in this paper, macroevolutionary patterns are those relating to changes in species diversity within and between monophyletic groups (Eldredge and Cracraft, 1980: chapter 6). Moreover, some (perhaps many) microevolutionary patterns are also delimited in "geological" time.

As has been pointed out previously, macroevolutionary patterns must be defined in terms of a cladistic hypothesis for the group in question (Eldredge and Cracraft, 1980; Vrba, 1980; Cracraft, 1981a). The nature of the pattern being investigated will determine the extent to which cladistic pattern need be resolved; for some questions it may be necessary only to specify that two groups are sister-taxa, whereas for other questions a resolution of species interrelationships within the group may be required. Cladistic pattern is a prerequisite for macroevolutionary analysis because it: (1) identifies monophyletic groups (and strictly monophyletic groups are the subject matter of macroevolution), (2) specifies the branching sequences and thereby defines patterns of diversity, (3) specifies the sequence of evolutionary novelties characterizing each monophyletic group, thereby defining the pattern of character change, and (4) specifies the basis for defining geographic patterns. It is clear that major empirical advances in macroevolutionary analysis cannot take place in the absence of cladistic pattern; not only must cladistic patterns be elucidated in order to have something to explain at the outset, but only cladistic patterns can be used subsequently to test any explanatory hypothesis.

One final general comment about pattern should be made. Scientific explanations are concerned primarily with classes of events (patterns) rather than with the individual events themselves. Many contingent properties contribute to the uniqueness of any single event, and general explanations are not directed toward those unique contingent properties. Thus, explanations attempt to account for common, shared attributes of many individual events. In the past it has been common for those interested in macroevolutionary analysis to be concerned with explaining the "evolutionary history" of individual groups, particularly when the focus of that explanation has been the "adaptive" history of a group (see Eldredge and Cracraft, 1980: chapter 6; and below). An important point, often overlooked by those concerned with the histories of individual groups, is that unique aspects of history are defined by what is general (i.e., pattern shared with other groups). Consequently we must first have an idea of general pattern before we can identify these unique components; general pattern requires general explanations, whereas unique components require explanations of less universality. This seems to be a major principle of comparative biology (Croizat, Nelson, and Rosen, 1974; Eldredge and Cracraft, 1980; Nelson and Platnick, 1981; Lauder, 1981).

**Patterns of Diversity**

Macroevolutionary patterns are established over—but not defined by—geological time, and in most studies of macroevolution the data have been pa-
leontological. It should be emphasized, however, that macroevolutionary data need not be paleontological. A cladistic pattern of Recent taxa, especially when postulated relationships are mapped geographically, also constitutes macroevolutionary data of differential diversity and distribution of character change. Cladistic pattern reveals clades whose relative ages of origin can be established. And, if fossil taxa of known age are included in the analysis, or if congruent distribution patterns can be correlated with vicariance events of known age, then the absolute ages of origin of clades can be estimated. Although most macroevolutionary studies have ignored the wealth of pattern available from the Recent biota, this practice should change in the future.

Macroevolutionary patterns of diversity derived from paleontological data are established by the assumed times of origin (based on first appearance in the record), duration, and extinction (based on last appearance) of the individual species of the sample, by their cladistic relationships, by the distribution of shared evolutionary novelties (apomorphous characters), and by their spatial distribution. Some workers have correlated these parameters with certain patterns of diversity (for example, short duration with a pattern of radiation diversity). Such correlations may exist, but it is best to establish the diversity pattern on the basis of two factors, the cladistic pattern and the number of species in each clade being compared. Three major patterns of diversity have been discussed in the literature (Stanley, 1979; Eldredge and Cracraft, 1980:312–320).

Radiation diversity.—This pattern is described when a clade exhibits a significant increase in diversity through time (Fig. 1A). It has been standard for most workers to view this pattern as an “adaptive” radiation. Whether a specific pattern is “adaptive” by some objective criterion is independent of the pattern itself, and later in this paper it will be suggested that such patterns may arise entirely independently of the so-called “adaptive” characteristics of the component species (recently, others also have made similar suggestions: Stanley, 1979; Eldredge and Cracraft, 1980; Gould, 1980; Vrba, 1980). Likewise, it is essential to disengage the presence of a pattern of radiation from factors assumed to be correlated with, if not causal of, the pattern itself, such as high speciation rate or low extinction rate (see previously cited authors). Such factors may interact in very complex ways and yet produce the same pattern (see below).

Radiation diversity constitutes a major class of patterns in need of a general explanation. Indeed, if the geometry of phylogeny is pictured in cladistic terms, it is evident that radiations are much more common than generally recognized. If one eliminates the preconception of “adaptive” radiation, with its notion of a correlated phenotypic or ecological modality, and views radiation only in terms of relative diversity of sister-clades, then the numbers of radiations are astounding. And those numbers lead to a very important question for macroevolutionary analysis: Are there one or more deterministic explanations as to why sister-clades should so often vary in diversity? Possible answers to this question will be explored in subsequent sections.

Reduction diversity.—This pattern describes a relative reduction in diversity within an already established clade (Fig. 1B). Depending upon the time-scale employed, all clades exhibit reduction diversity on their way to becoming extinct (but it is not the intention here to apply this pattern to sudden “mass” extinction—sudden in a geological sense).

Like radiations, the ubiquity of reduction diversity patterns is obvious. An important problem for macroevolution, then, is the development of a theory sufficiently general to explain both patterns.

Steady-state diversity.—This pattern characterizes a clade maintaining more or less the same amount of species diversity over a long period of time (Fig. 1C; Eldredge and Cracraft, 1980:321–323).
Judged from the fossil record, steady-state diversity is a common pattern shown by many clades.

Patterns of Character Change

Given the three patterns of change in diversity—radiation, reduction, steady-state—what patterns of character change might be possible within the context of each? Thus, in asking this question we are not concerned with establishing which pattern of character change is actually most often correlated with a particular diversity pattern, rather we only want to consider the extent of their potential congruence.

To answer the question above, one can use cladistic analysis to investigate whether there has been relatively little average phenotypic change accompanying speciation within a clade (the descendant species remaining relatively plesiomorphic for the characters investigated), or whether there has been substantial change (the descendant species being strongly apomorphic relative to their ancestors). It is important to realize that there must be some degree of change, otherwise one could not recognize that speciation has actually occurred (the methodological problems of speciation analysis are discussed by Eldredge and Cracraft [1980], Wiley [1981], and Cracraft [1982]). We can recognize four categories of character change—morphological, physiological, behavioral, and “genotypic”—and the degree of change for each can be placed on a plesiomorphic to apomorphic scale. Thus, using similar comparative methods, “genetic” characters also can be evaluated in terms of plesiomorphic or apomorphic change, and can be compared for their concordance with phenotypic change (Cracraft, 1981a, 1982).

It is apparent that virtually any pattern of character change is potentially compatible with the three patterns of diversity. To take one example, a radiation with little or no differentiation is characteristic of assemblages of closely related sibling species. There may be more behavioral or ecological change in this situation than morphological, but even so the degree of change may not be significant. Traditionally, radiations have been thought to be associated with increasingly more divergent morphologies accompanying speciation. A pattern of reduction diversity, on the other hand, could be characterized either by plesiomorphic or by apomorphic change during speciation. A pattern
of steady-state diversity has generally implied little change, and certainly such a clade could consist of a stable number of plesiomorphic species; but there appears to be no reason why a clade could not exhibit a uniform number of species through time and yet show diversification, with the species becoming increasingly apomorphic.

In summary, then, there is no a priori reason why each of the three diversity patterns must necessarily be characterized by a particular pattern of character change. An expectation of a causal relationship between these two types of pattern will have to come from an explanatory theory linking speciation with the degree of differentiation. The terms plesiomorphic and apomorphic apply to one or more unit characters, and species within clades may be apomorphic for quite different characters. Decisions as to which species are relatively more apomorphic are necessarily a matter of judgment and are best made with respect to comparable attributes.

If an analysis focuses on specific characters, change of these characters—whether of morphology, genotype, or behavior (and therefore of ecology)—is not likely to be random from one speciation episode to another. Trends will be apparent merely because a subset of all available characters will change and tend to become increasingly apomorphic through time. Systematic analyses have repeatedly shown this to be true, and the reason probably lies with the ways in which phenotypic variation is canalized developmentally and restricted by previous phyletic history to only a few potential pathways (Alberch, 1980; Oster and Alberch, 1982). Character trends will be common in clades undergoing taxonomic diversification, but it is not likely that any one character will exhibit a continuous sequence of change with each succeeding episode of speciation, nor that change in that character will be exhibited throughout the history of the clade. Rather, change of any particular character will, on average, be manifested only over a relatively small number of speciation events. Consequently, major long-term trends, so popular in discussions of macroevolution, will probably be relatively rare. Whatever their frequency, long-term trends can only be discovered once the cladistic relationships of the relevant species are understood, and it is important to note that very few discussions of long-term trends in the macroevolutionary literature are supported by the required phylogenetic data (see Vrba, 1980: 69, for an excellent example why many putative “trends” probably will be shown to be invalid).

EXPLANATIONS OF MACROEVOLUTIONARY CHANGE

Macroevolutionary change, it has been argued, consists of time-dependent variation in patterns of diversity and character change within and between monophyletic groups. In seeking to explain these patterns, it is well to remember that the subject of interest here is not the construction of a hypothesis to explain the diversity or pattern of change of a specific group (say, mammals or clams). Instead, we want to investigate the reasons why there are classes of patterns common to many groups of organisms. Evolutionary biologists have proposed two major kinds of explanations for macroevolutionary patterns, termed here “adaptationist” and “species selectionist.” It will be the purpose of this section to outline and evaluate these explanations.

Macroevolution and the Problem of Adaptation

Macroevolutionary phenomena became a subject for serious study through the efforts of Simpson (1944, 1953) and, to a lesser extent, Rensch (1947, 1960). Following in the Darwinian tradition of interpreting evolutionary change from a selectionist-adaptationist point of view (also referred to as transformationism: Eldredge, 1979; Eldredge and Cracraft, 1980), Simpson (1944, 1953) quite clearly is responsible for establishing the “adaptationist” explanation of macroevolution.
lutionary pattern as the dominant conception within contemporary evolutionary biology. Recent workers whose writings represent this school of thought include Stebbins (1950), Hecht (1965), Von Wahlert (1965), Van Valen (1973), and Bock (1965, 1979).

Inasmuch as this approach to macroevolutionary analysis has been characterized and criticized at length elsewhere (Eldredge and Cracraft, 1980:248–276), the present discussion focuses on examining adaptationists’ explanations of the specific macroevolutionary patterns described in the previous section.

The central organizing principle of the adaptationist approach to macroevolution is the concept of the adaptive zone: species or lineages move into unoccupied or new zones, lineages radiate within them, and characteristics of the zones are said to regulate the rate of evolution. The driving force for these evolutionary changes is the relentless adaptive imperative: natural selection resulting from organism-environment interactions.

As Simpson (1953:200–202) notes:

The definition of adaptive types has an arbitrary element . . . [and] . . . Adaptive types may be defined in part and in some cases in geographic or physical environmental terms, but it is essential to remember that what we are talking about here is not a geographic, physical, or even in the broadest sense environmental zone but an adaptive zone, representing a characteristic reaction and mutual relationship between environment and organism, a way of life and not a place where life is led.

By and large other workers have followed Simpson’s conception of an adaptive zone, viewing it as a way of life, and not as a specific physical manifestation of the environment. In virtually all discussions, adaptive zones are defined, operationally at least, in taxonomic terms (Simpson, 1953:204, 221–222, 225, and many others), even though the disclaimer is often made that zones are not to be defined solely by systematic relationships.

When speaking of evolution, Simpson (1953) generally means anagenetic, or phyletic, change. Speciation per se plays a relatively minor role in his world view of macroevolution; even though cladogenesis is obviously assumed to be involved in diversification, the main process is anagenesis (1953:380):

speciation is the process of differentiation within populations and of the rise of genetic isolation between populations formerly part of the same species. Subsequent divergence is not, strictly speaking, speciation but an aspect of phyletic evolution . . . . Speciation is the basic mechanism of the splitting of lineages, although it does not always or usually give rise to separate, significantly progressing and diverging lineages.

The adaptationist position toward macroevolutionary patterns, then, can be depicted as anagenesis within adaptive zones: “A basic evolutionary sequence, an element entering into most of the more complex evolutionary patterns, is the occupation by a group of organisms of an adaptive zone new to them, their subsequent diversification and phylogenetic change in that zone, and their eventual extinction in it . . .” (Simpson, 1953:206).

Diversification is said to take place by dividing a relatively wide adaptive zone into narrower and narrower zones (1953: 212 et seq.), and in the case of “adaptive radiations” also by the “. . . more or less simultaneous divergence of numerous lines all from much the same ancestral adaptive type into different, also diverging adaptive zones” (1953:223).

If one examines the adaptationist approach to macroevolution in terms of its logical components, it appears to resolve to the following: Taxa (species) have diversified and are observed to have different ways of life; these different ways of life are called adaptive zones; the mechanism bringing about this diversification is natural selection, which results in increasing adaptation. It would seem these “zones” are “adaptive” merely as a consequence of assuming they come to be occupied by a process known as “adaptation by natural selection.” In and of themselves, “adaptive zones” have no ontological status other than that in the mind of the investigator. Does the “penguin adaptive zone” (Simpson, 1953:204),
for example, have any reality other than the statement “it is what penguins are and do”? Defined and applied in this way—and all uses of “adaptive zone” are similar—the concept is a definitional tautology: penguins exist and their way of life constitutes a penguin adaptive zone, cats exist and their way of life constitutes a cat adaptive zone, and so forth. Moreover, the belief that evolution into, through, and out of these zones is driven by natural selection surely must be viewed as axiomatic (Cracraft, 1981a, b), and as such is clearly an untestable hypothesis when applied to historical situations.

Paradoxically, the logical structure of adaptationist thinking engenders a descriptive rather than explanatory view of macroevolutionary patterns. Radiations are characterized (described) as a change in the number and breadth of adaptive zones. But this constitutes the basic problem: as long as the zones and their width are defined in terms of the taxa themselves—and their hypothesized way of life—then the use of adaptive zones is little more than a restatement of the original pattern of diversification. Nothing is really explained, even when the process-level mechanisms of natural selection are included axiomatically.

The adaptationist position attempts to explain supraspecific (macroevolutionary) pattern with reference to within-population process phenomena, i.e., natural selection and adaptation (see Eldredge and Cracraft, 1980, chapter 6, for discussion). Simpson (1953:187, 198, 331), for example, invokes differential selection intensities as the causal agent for variable rates of evolution. Thus, he specifically views rates of evolution from the standpoint of anagenesis rather than cladogenesis (see especially 1953:336), even though the phenomena he seeks to study are patterns of taxonomic diversification.

Within the adaptationist world view of macroevolution, the driving force for evolutionary change is directional natural selection. Species transform through time, more or less gradually; thus, within-
species change is directly translated into between-species change. This interpretation of the history of life is directly falsified, however, if two conditions prevail: (a) if species can be defined as discrete entities through time, and (b) if those species exhibit long-term phenotypic stasis. Given our present knowledge of the fossil record, these two conditions seem to be upheld (Eldredge and Gould, 1972; Gould and Eldredge, 1977; Stanley, 1979). Although this pattern leaves the exact mechanics of character transformation unexplained, it would seem to render superfluous recent attempts by population geneticists to rationalize an adaptationist-transformationist view of macroevolutionary pattern with the results of theoretical and experimental population genetics. Nevertheless, in an attempt to cover all bases, these workers are quick to claim that long-term stasis is “consistent with” or can be “explained by” known mechanisms of population genetics (e.g., stabilizing selection). Yet, until population genetics can develop a predictable theory telling us when populations will exhibit long-term stasis versus when they will change, or why species maintain stasis in the face of environmental change, or how phenotypic change is related to genotypic change, or in what way genotypic change is related to reproductive disjunction—until such questions are addressed by a predictive theory, it may not be unreasonable for biologists to question the “explanatory” power of population genetics.

Species Selection and Macroevolution

The concept of species selection, as originally formulated (Stanley, 1975:648), was analogized to natural selection: one clade is favored over another if the former includes species that survive for longer periods (thus increasing their chances for speciation) or if there is a tendency for them to speciate at a higher rate. Stanley further suggested (1975:648) that “differential survival [of species] is in response to the basic agents of nonacciden-
tial extinction: predation, competition, and habitat alteration.” The rate of large-scale evolution, it was postulated (p. 649), is due primarily to the rate of speciation but also to “the intensity of species selection.”

Species selection, in Stanley’s view (1975, 1979, 1982), encompasses the deterministic causes of species extinction (1979:197–205), and even though large-scale evolution is ascribed primarily to variance in speciation rate, he presents very little discussion about speciation rate-controls, simply relating rate to “adaptive radiation,” “adaptive innovation,” or to characteristics of “adaptive zones.”

Whereas Stanley characterizes species selection in terms of the selective mortality (extinction) of species, Gould and Eldredge (1977:139–140) define it in a totally anomalous fashion: punctuated equilibrium + Wright’s rule = species selection. It seems obvious that combining a “punctuated equilibrine” mode of speciation with the assumption that morphologies produced at speciation events are “random” with respect to the overall trend within a clade (“Wright’s rule”) is insufficient to constitute a “speciation theory of macroevolution.” Neither punctuated equilibrium nor Wright’s rule is necessary or sufficient to describe the differential success of one clade compared to another. A concept of species as discretely defined taxonomic units is required, however. And, it makes little difference whether morphological change is “random”: in fact, seen from the standpoint of individual characters, change is demonstrably nonrandom. Despite this definitional and conceptual problem in their view of species selection, Gould and Eldredge (1977:143–144) identify high speciation and resistance to extinction as the reasons for success of a clade. No mechanisms were proposed for the rate-control of speciation, but resistance to extinction was attributed to large population size, large environmental range, and superior competitive ability. In a later paper, Gould (1980:126) alters the above conception of species selection and adopts a position close to that of Stanley: species selection as differential extinction. Gould (1982:94) has further modified his conception of species selection, suggesting the concept be restricted to differential survival as a result of species-level properties that enhance the rate of speciation or decrease the rate of extinction.

Eldredge and Cracraft (1980: chapter 6) depict species selection not so much in terms of species mortality—although occasionally that view surfaces (e.g., p. 273)—as they do a pattern of species survival, and that pattern is as much a function of speciation as extinction (the latter is said to be coupled to the ecological characteristics of species: eurytopes are postulated to have low extinction rates, stenotopcs high). Eldredge (1979) and Vrba (1980) have advanced the idea that stenotopcs are more susceptible to geographic isolation than are more widely distributed eurytopes, thus the former should speciate more rapidly. Vrba’s perception of species selection tends to be similar to that of Eldredge and Cracraft (1980) and not Gould and Eldredge (1977): species selection is a pattern of species survival, not a process of species extinction (see especially Vrba, 1980:79–80, and also Stanley, 1982:471).

What can be concluded from this short summary of opinions on species selection? Namely, that species selection—like natural selection as a within-population phenomenon—is typically used in two distinct ways: (a) as a pattern of differential survival of species within or between clades, or (b) as a process invoking the reasons for selective mortality (extinction) of some species relative to others. Which is to be preferred? A good argument can be made for dropping the term altogether, because no clear consensus is likely to develop and continued confusion over the concept will do little to promote our understanding of macroevolution; such a suggestion probably will not be widely accepted, however. “Natural selection” was coined for a “process”: certain individuals survive and re-
produce because they are said to possess characteristics that place them at an advantage relative to individuals not having those characteristics. One might argue, accordingly, that species selection should be defined in an analogous way: some species are selected because they are characterized by intrinsic or extrinsic properties, which operate either to increase the probability of speciation or decrease the probability of extinction (this is similar, I think, to what Gould, 1982, recommends). If this view of species selection is accepted, then the second definition—selective extinction of species—should be dropped. By incorporating both differential speciation and extinction into a concept of species selection, the focus is not only on the observed systematic pattern but also the relative roles of speciation and extinction rates in producing that pattern. But in accepting this view, one inescapable conclusion follows: species selection per se is a pattern of differential species survival within and among clades and not a process or cause of that pattern. The “processes” producing the pattern are variations in the rates of speciation and extinction. Because species selection, like natural selection, is a pattern of differential survivorship, as such it cannot be considered a theory of macroevolution because to express species selection as a “cause” is merely tautological: it is a truism that differential survivorship must be the result of an interaction between speciation and extinction. A theory of macroevolution, therefore, will arise only from a deterministic explanation for common patterns of diversity in terms of speciation and extinction rates. Such a deterministic theory, however, does not imply that the rate-controls of speciation and extinction must reside only in the intrinsic properties of species within clades. Although this must be partially true, external controls can also greatly influence the pattern of differential species survival. Indeed, it will be suggested below that these external controls on rates may be far more important than the intrinsic ones. Accordingly, to define species selection in terms of species-level properties (as Gould, 1982, apparently does) may obscure the analysis of some highly deterministic, external causes of macroevolutionary pattern. Species selection, therefore, is best thought of only in terms of a pattern of differential species survival.

MACROEVOLUTIONARY PATTERNS AND RATES OF SPECIATION AND EXTINCTION

Viewed over their entire history, all clades begin with a single ancestral species and end when the last descendant species ceases to exist. All such clades, therefore, will show radiation and reduction diversity patterns, and they may also exhibit some steady-state diversity. Extant clades can be characterized by one or more of the three patterns, depending upon their past history of diversity.

Each pattern of diversity is unambiguously associated with certain relative rates of speciation and extinction. Radiation diversity occurs when the speciation rate (S) exceeds the extinction rate (E), reduction diversity when E is greater than S, and steady-state diversity when S and E are approximately equal. However, when trying to assess empirically the contributions of speciation and extinction to these patterns of diversity, their relative contribution is not always sufficient, because each pattern—when examined over a discrete time interval—is a function of the initial rates of speciation and extinction, the difference in their magnitude, and the initial diversity of the clade. Moreover, the history of most clades is one of changing diversity, and five major large-scale patterns seem especially common (see Sepkoski, 1981:38, for pictorial representations of these patterns): (a) radiation followed by a steady-state of moderate to high diversity (Fig. 1C; examples: Holothuroidea, Steleroidea, Polychaeta), (b) radiation followed by reduction and eventual extinction (Fig. 2A; examples: Conodontophora, Graptolithina, Trilobita), (c) radiation followed by reduction and then by radiation again
(Fig. 2B; examples: Echinoidea, Ostracoda), (d) radiation followed by a mass extinction followed again by a re-radiation (Fig. 2C; examples: Crinoidea, Anthozoa, Stenolaemata), and (e) very slight radiation followed by long-term steady-state of very low diversity (Fig. 2D; examples: Priapulida, Pterobranchia, Cephalochordata).

The description of each pattern, or combinations of them within a clade, depends upon the level at which phylogenetic relationships are resolved, and the extent of that resolution is entirely responsible for the appellation—radiation, reduction, steady-state—given to any particular pattern (Cracraft, 1981a).

A pattern of radiation diversity is produced when, for any time interval, speciation rate (S) exceeds extinction rate (E). A radiation can originate or be maintained as a result of three obvious changes in the rate-functions of S and E (Table 1): S increases, E remains constant (1a); S remains constant, E decreases (1b); and S increases, E decreases (1c). But, as long as S exceeds E, a radiation pattern will result even if S and E are both decreasing through time (1d) or both increasing (1e); and, if the initial rate of S far exceeds E, a radiation pattern will continue to develop under conditions of S remaining constant and E increasing (1f), until such time E exceeds S. Finally, a clade will continue to radiate if S and E remain constant, as long as S is greater.

A pattern of reduction diversity obtains when E is greater than S. Three obvious interactions of S and E produce reduction diversity (Table 1): S decreases, E increases (2a); S remains constant, E increases (2b); and S decreases, E remains constant (2c). As long as E is greater than S, reduction diversity will take place even if both S and E are decreasing (2d) or both increasing (2e). If E were much higher than S initially, then E could remain constant and S increase and still maintain a reduction diversity pattern, until S exceeds E. And, both S and E could remain constant, but with E greater than S, and thereby maintain reduction diversity.

Finally, steady-state diversity is maintained if S approximates E, no matter whether those rates are constant (Table 1, 3a), decreasing (3b), or increasing (3c).
A THEORY FOR MACROEVOLUTIONARY CHANGE

The Rate-Control of Speciation

It is postulated here that there are two principal regulators of the rate of speciation, one intrinsic, the other extrinsic. Intrinsic mechanisms include the degree of morphogenetic complexity expressed within a species, which determines the susceptibility of that species to a break in its reproductive cohesion (Wiley and Brooks, 1982), but they can also embrace ecological characteristics influencing that cohesion (e.g., Vrba, 1980; Eldredge and Cracraft, 1980; Jablonski, in press). Extrinsic mechanisms include changes in environmental complexity to which a species or group of species is exposed; these changes determine the frequency that populations will encounter geological and/or climatic barriers, thus resulting in geographic isolation and subsequent differentiation. Intrinsic mechanisms are primary: in the absence of internal complexity, no amount of environmental complexity can lead to speciation; in the absence of environmental complexity, the accumulation of internal complexity will lead to speciation, no doubt slowly, but nevertheless inevitably.

A general theory for the accumulation of populational complexity, and its importance for speciation, has been proposed by Wiley and Brooks (1982), and will not be considered in detail here. Instead, attention is directed towards describing a general theory for the evolution of environmental complexity and describing its potential for explaining macroevolutionary patterns.

The origin of new taxonomic units (species) takes place generally through allopatric disjunction (Mayr, 1963; Grant, 1971; Bush, 1975; White, 1978). There are, at present, inadequate systematic and biogeographic studies to assert that parapatric or sympatric modes of differentiation are of widespread occurrence (one exception being polyploidy within some plant groups). Accordingly, the key to speciation is geographic disjunction, and this can come about in two ways: (a) vicariance of widespread taxa by geological and/or climatic barriers that arise within the distributions of those taxa, and (b) by long-distance dispersal of an ancestral population across an already established barrier. The theory advanced here is neutral with respect to the frequency of these modes of disjunction; instead, it is merely a theory for the evolution of environmental complexity, which in turn should be directly proportional to the numbers of populations that can eventually become isolated.

The lithosphere can be considered an open thermodynamic system, exchanging matter and energy across its boundaries with the underlying mantle (Cracraft, in prep.). Prigogine and colleagues (Prigogine, 1962, 1978, 1980; Prigogine et al., 1972) have proposed that the general behavior of open thermodynamic systems can be described by

<table>
<thead>
<tr>
<th>Table 1. Possible relationships between macroevolutionary patterns and changes in speciation and extinction rates.</th>
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<tbody>
<tr>
<td>Macropattern pattern</td>
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<tr>
<td>----------------------</td>
</tr>
<tr>
<td>1. Radiation diversity</td>
</tr>
<tr>
<td>($S &gt; E$)</td>
</tr>
<tr>
<td>a. Increases</td>
</tr>
<tr>
<td>b. Constant</td>
</tr>
<tr>
<td>c. Increases</td>
</tr>
<tr>
<td>d. Decreases</td>
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<tr>
<td>e. Increases</td>
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<tr>
<td>f. Constant</td>
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<tr>
<td>g. Constant</td>
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<tr>
<td>2. Reduction diversity</td>
</tr>
<tr>
<td>($S &lt; E$)</td>
</tr>
<tr>
<td>a. Decreases</td>
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<tr>
<td>b. Constant</td>
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<tr>
<td>c. Decreases</td>
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<tr>
<td>d. Decreases</td>
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<tr>
<td>e. Increases</td>
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<tr>
<td>f. Constant</td>
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<tr>
<td>g. Constant</td>
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<tr>
<td>3. Steady-state diversity</td>
</tr>
<tr>
<td>($S = E$)</td>
</tr>
<tr>
<td>a. Constant</td>
</tr>
<tr>
<td>b. Decreases</td>
</tr>
<tr>
<td>c. Increases</td>
</tr>
</tbody>
</table>
structures, which are located far from equilibrium, and which in that configuration dissipate minimum entropy (entropy can be viewed as that energy not available to do work, and thus is a measure of disorder or energy dissipation). If these steady-states are perturbed, and accumulate complexity and increase in entropy, then under some circumstances they may rapidly transform to new steady-state levels (see, in particular, Johnson, 1981; Mercer, 1981; Wiley and Brooks, 1982; for a general discussion). Individual organisms (Prigogine and Waime, 1946), species (Wiley and Brooks, 1982), and ecodemes (Johnson, 1981) have been postulated to be dissipative structures. Elsewhere, the suggestion will be made that lithospheric plates are also dissipative structures (Cracraft, in prep.) and that the thermodynamic behavior of the lithosphere can be described by

\[ dS_t = dS_s + dS_e + dS_c + dS_w \]  
(2)

where \( dS_t \) is the total change in entropy produced within the lithosphere, \( dS_e \) the entropy exchanged with the underlying mantle, and the components of entropy production representing the irreversible processes within the lithosphere including \( dS_s \), the entropy produced at plate separations or axes of rifting, \( dS_c \), the entropy produced at plate boundary convergences, and \( dS_w \), the entropy produced within the confines of the plates themselves (see Cracraft, in prep., for a more complete discussion). As a general theory, expression (2) reduces plate tectonic behavior, and the evolution of the earth’s crust, to the second law of thermodynamics. In order to relate the above to the rate-control of speciation, it is only necessary to show that one or more of the terms in the expression can be expanded to account for the complexity of the environment. It is proposed that this can be accomplished by the expression (Cracraft, in prep.):

\[ dS_w = dS_{it} + dS_{lm} + dS_{tb} \]  
(3)

where \( dS_{it} \) is the change in entropy of the terrestrial environments, \( dS_{lm} \) of the con-
tinal margin environments, and $dS_{tb}$ of the ocean basin environments. These environments contain most, if not all, of the known biotic diversity, and expression (3) can be taken to apply either to the entire lithosphere or only to small portions of it (see Fig. 3, and Cracraft, in prep., for examples).

It is proposed that the components of $dS_w$ be measured, or estimated, using the well-known relationship between entropy and information content (Gatlinc, 1972; Kubat and Zeman, 1975). Thus, $dS_{itb}$, $dS_{im}$, and $dS_{tb}$ can be estimated by measures of the information content, or complexity, of the terrestrial, marginal, and ocean basin environments. Their relative contribution to $dS_w$ will depend solely upon the area, and tectonic regime, being considered (e.g., Fig. 3). The use of information theory to measure complexity is not new; ecologists have adopted similar methods to relate differences in local habitat complexity to variation in species diversity within those habitats (MacArthur and MacArthur, 1961; MacArthur et al., 1962, 1966). The use of information theory proposed here, in order to relate it to speciation rates, need only be applied to "global" areas, of hundreds of square miles or more. Thus, $dS_{itb}$, $dS_{im}$, and $dS_{tb}$ are estimates of the changes in environmental complexity through a specified period of time.

The hypothesis, therefore, is that rate of speciation is directly proportional to the evolutionary history of lithospheric complexity (information content) for a given interval of space and time. The greater the environmental complexity, the greater the number of geological and climatic barriers will develop to promote geographic isolation and differentiation. Others, of course, have suggested a correlation between environmental complexity and speciation (e.g., Simpson, 1964; Bakker, 1977); the present hypothesis differs in providing a formal theory positing a causal mechanism regulating changes in the rate-function of speciation.

Eldredge (1979), Vrba (1980), and Eldredge and Cracraft (1980) have hypothesized that stenotopic species are likely to speciate more rapidly than do eurytopes, and Vrba (1980), in particular, has implicated this as a possible explanation for some macroevolutionary patterns. Although some evidence exists for a correlation between relative stenotopy and increased diversity (see Vrba, 1980), a causal connection between the ecological characteristics of species and the rate at which they speciate has not been firmly established (but see Jablonski, in press, for a possible example). Thus, it is not yet known to what extent these patterns of increased diversity might be related to increased internal complexity, greater environmental complexity, greater environmental favorableness (see below), or some combination of these. Moreover, it seems likely that stenotopic species would be more susceptible to extinction than eurytopes, thus the relationship between stenotopy and increased diversity is confounded further. It is unlikely that differences in ecological characteristics, by themselves, will be able to explain most macroevolutionary patterns, and the possibility that these differences are effects, not causes, of species diversity gradients among clades will have to be considered and investigated.

The Rate-Control of Extinction

Unlike speciation rate, a case has not yet been made for a relationship between internal complexity and the rate of extinction. Species of relatively little complexity—e.g., those exhibiting minimal phenotypic variation spatially (e.g., monotypic, widespread species)—are common, and there is no evidence to suggest they become extinct at a significantly different rate than do those of greater complexity.

Environmental factors are by far the major influence on extinction rate. As an extension of the hypothesis that plate motions constitute the external regulator of speciation rate, the theory also claims that plate tectonic events effect a primary control on extinction rates through (1) the
mechanical elimination or modification of habitats and their biotas, and (2) control over patterns of climatic change, which shifts the physical characteristics of an environment to such a degree that the physiological tolerances of species within that environment are exceeded.

The physical effects of plate tectonic activity—continental drift, volcanism, sea level changes, for example—on the extinction of biotas has been documented and discussed extensively (Valentine and Moores, 1970, 1972; Valentine, 1971, 1973; Schoof, 1974; Bakker, 1977; Hallam, 1981; Axelrod, 1981). And, it has long been surmised that plate tectonic events can have major effects on climates through modification of continental arrangements, ocean circulation patterns, continental relief, or the development of polar ice caps (Hamilton, 1968; Cox, 1968; Crowell and Frakes, 1970; Frakes and Kemp, 1972, 1973; Robinson, 1973). Nevertheless, a predictive hypothesis relating climatic regimes and extinction rates has been difficult to achieve. One attempt will be published elsewhere and is summarized briefly here.

Each species has a physiological capability to exist only within the limits of a specific environmental regime, and when environmental conditions are perturbed beyond the tolerances of individuals of that species, populations can become extinct. Moreover, it seems clear that some environmental regimes lie far outside the tolerances of many different kinds of organisms. These simple observations lead to a hypothesis: the likelihood of extinction is inversely proportional to the degree of environmental favorableness to which a species is subjected.

As used here, the concept of “favorableness” is not to be equated with the ideas of “stability,” “constancy,” or “equability.” I suggest relative favorableness be measured instead as a function of mean annual temperature, mean annual range of temperature, and mean annual rainfall and its annual dispersion relative to the physiological tolerances of most living organisms. In terms of actual climatic regimes, highly favorable environments can be characterized by a high mean annual temperature (23–28°C), low mean annual range of temperature (less than 10°C), and high annual rainfall (generally 200–250 cm, or more) dispersed evenly throughout the year.

Temperature and moisture regimes are the primary parameters establishing the limits of physiological tolerances of organisms. The above measures of “highest” favorableness seem to define that climatic regime, for terrestrial environments, which is the most favorable for the greatest variety of organisms, both plant and animal. Deviations from these mean temperature and moisture values, or increases in their variability, are likely to subject an increasing number of species to environmental fluctuations sufficient to cause severe physiological stress, or possibly extinction.

Consequently, it is proposed that the extinction rate of populations differentiating within, or dispersing into, environments of less favorableness will be greater than it would be in more favorable environments.

This hypothesis does not deny the possibility of other deterministic explanations for extinction at an ecological level, such as predation or competition with other species. It merely proposes that large-scale gradients in diversity, within and among clades, are less likely to be controlled by processes operating at a local ecological scale. And only large-scale gradients in extinction seem applicable to the problem of understanding macroevolutionary pattern.

DISCUSSION

Under the viewpoint adopted here, the most important question of macroevolutionary analysis is: How do we explain patterns of diversity shared among monophyletic groups? The question of the origin and distribution of characters or character-complexes is a problem best
examined within the context of diversity patterns, specifically as those patterns relate to the mechanisms of cladogenesis. Thus, the origin of evolutionary novelties is not a major problem for macroevolutionary analysis but rather for developmental genetics at the level of individual organisms, or perhaps for those interested in character change during the process of diversification.

The major purpose of this paper has been to emphasize the external control of the rate of speciation and extinction with respect to their importance for explaining macroevolutionary (diversity) patterns. If the contribution of the external controls can be assessed, it will help determine the relative importance of “internal” factors—such as morphogenetic complexity within species—in regulating the rate of speciation and thus diversity patterns.

The hypotheses proposed herein—that speciation rate is regulated by environmental complexity, and extinction rate by environmental favorableness—permit a number of predictions about macroevolutionary patterns, including the following:

1. Clades in geographically more complex environments should speciate more rapidly than those in less complex environments. If this is true, then at least some of the differences between sister-clades having very disparate diversities are not due to “traditional” explanations such as the expression of different key “adaptations” or different “adaptive zones,” but merely to being distributed in environments of different complexity. The prediction should hold unless the clades are distributed in environments of variable favorableness, or unless they are characterized by contrasting amounts of internal complexity.

2. If two clades are distributed in areas of comparable complexity, then that clade inhabiting the area of highest favorableness should have the highest diversity. Examining clades of varying diversity but which occupy areas of comparable complexity and favorableness should provide a test for the importance of internal complexity: all things being equal, the most diverse clade should have the most complex species.

3. In clades distributed in areas undergoing a climatic change, extinction rates should be lower when changes are toward more favorable environments than in those situations when change is toward less favorable environments. This prediction is based on the assumption that as favorableness increases, more and more species of a biota will remain within their physiological tolerances. This may not be the case, however, since it is well documented that less favorable environments exhibit greater annual variation in temperature and moisture conditions (see data and graphs in Bailey and Axelrod, 1969; and Wolfe, 1978, 1979), and thus species in less favorable environments may be able to tolerate a greater degree of change (see also Janzen, 1967).

4. Given the above, patterns of radiation diversity should result from an increase in environmental complexity, favorableness, internal complexity, or some combination. By comparing radiations in which one or more of these variables can be taken to be constant, the relative importance of each can be estimated.

5. A pattern of reduction diversity usually should be attributed to a deterioration in environmental favorableness. Because environmental complexity degrades only over very long times, only very long-lived clades would be expected to show a relationship between reduction diversity and a decrease in environmental complexity. With respect to internal complexity, a substantial portion of the component species of a clade would have to become less complex in order to produce a reduction diversity pattern. It is not immediately apparent what might cause this.

6. A pattern of steady-state diversity in a clade of moderate to high diversity would be expected to result from environments of moderate complexity and moderate favorableness. Speciation must be sufficient to replace extinctions, but extinction must also be high enough to dampen a pattern of radiation.

7. A pattern of steady-state diversity in clades of very low diversity would be predicted to be caused by low internal complexity among the species, or by such clades inhabiting environments of very low complexity and moderate favorableness. Environments of very high complexity and very low favorableness might maintain a steady-state of low diversity, but probably not for long periods of time; with high extinction rates, a clade would be expected to become extinct by chance alone.

Finally, virtually all recent discussions of macroevolutionary pattern have focused almost exclusively on “trends” (in particular, see Gould, 1982; for an exception, see Eldredge and Cracraft, 1980). It should be clear from the foregoing that “trends” are independent of a particular pattern of diversity. Moreover, it is likely that long-term trends are actually less important than the quantity of previous discussion would seem to imply. All characters undergoing phylogenetic
transformation by definition exhibit trends; this means that trends are indeed ubiquitous, but the vast majority clearly span only a small number of cladogenetic events. Trends would appear to be the "by-products" of diversification and of less general interest than the pattern of diversification itself.

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