

Extinction, Biotic Replacements, and Clade Interactions

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INTRODUCTION

During the history of life, major groups of plants and animals have waxed and waned; once-dominant groups have disappeared, and others have risen to take their place. Faunal and floral replacements, or biotic replacements, are a pervasive feature in the long-term evolution of all groups, and they are often seen as punctuation marks in the narrative history of a particular group, ecological realm, or geographic area. Many individual examples have been studied in a general way, and two or three cases have been examined in great detail by paleobiologists. However, little effort has been made to generalise about the role of biotic replacements in the diversification of life, nor to examine the processes that cause them. Indeed, a general attitude has been to assume that they were all broadly competitive, part of the supposed progress of life from primitive to advanced forms. Further, such replacement phenomena have been linked with mass extinction events only in an ad hoc way, and there is no clear view about the broader relationships of the two in a general theory of macroevolution.

There are some fundamental questions to be asked about biotic replacements:

1. Do they exist as discrete events, or are they artefacts of our rather clouded perception of the ecology of major changes in the past?
2. If they exist, how do we define them and categorise them?
3. What is their role in the history of life? Are they unusual rarities, disturbing a more normal, gradual kind of piecemeal species-by-species replacement over time; or are they a key feature?
4. What causes biotic replacements of different kinds; how do they relate to macroevolutionary models of competition and opportunism; and how do they relate to extinctions and mass extinctions?
5. How should they be studied in order to develop testable models of patterns and processes?

EXAMPLES

Many biotic replacements have been identified and studied in one way or another (summarised in Benton, 1987). Some of the better-known examples are:

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1. progymnosperms vs. pteridosperms	U. Dev. – L. Carb.	20-50 Myr
2. gymnosperms vs. angiosperms	L. Cretaceous	10-50
3. Cambrian vs. Paleozoic invertebrates	U. Camb. - U. Ord	40-80
4. Paleozoic vs. 'modern' invertebrates	Perm. - Trias.	10-90
5. brachiopods vs. bivalves	Paleozoic	50-330
6. hybodonts vs. modern sharks	U. Jur. – L. Cret.	40-70
7. holosteans vs. teleosts	Jur. – Cret.	40-140
8. mammal-like reptiles vs. archosaurs	Triassic	5-40
9. dinosaurs vs. mammals	U. Cret.	1-30
10. multituberculates vs. placentals	L. Tertiary	10-60
11. perissodactyls vs. artiodactyls	U. Tertiary	5-35
12. Great American Interchange	U. Tertiary	1-6

This list illustrates some of the taxic and stratigraphic ranges of the well-known examples of biotic replacement, as well as the category level of the groups involved (mainly orders to phyla), and the total durations (1-50 Myr for minimum duration estimates, and 6-320 Myr for maximum estimates).

TERMINOLOGY AND SCALE

Biotic replacements have been termed ecological or evolutionary relays (Simpson, 1953; Newell, 1963), but these terms contain an implication about the processes involved. The terms faunal and floral replacement refer specifically to the zoological and botanical realms respectively, so that a general equivalent term is proposed here, namely *biotic replacement*, which has no connotations of the processes involved. Terms that explicitly indicate the hypothetical processes are introduced later.

Biotic replacements may be divided into two broad categories, depending upon whether there was a major shift in the geographic distribution of the replacing group(s) or not. In turn, each of these two categories may be further subdivided according to whether extinctions took place or not (Fig. 1):

1. *in situ radiations* (global or smaller-scale), in which there was no substantial change in geographic distribution; the groups involved both/all existed worldwide, or in the same regions(s):
 - a. *replacement radiation*, where one group, or set of groups, dies out, and the replacing group(s) radiate into vacated ecospace;
 - b. *expansion radiation*, where there are no extinctions involved, and the new group(s) radiate into new ecospace;
2. *invasion radiations*, where the new groups have entered the area because of the destruction of a barrier' or because of transport:
 - a. replacement radiation, where extinctions occur and the invaders radiate into vacated ecospace;
 - b. expansion radiation, where the invaders occupy previously untenanted ecospace; includes *insinuation* (Marshall, 1981), where the invading species find niches that do not seriously affect the species already present.

The scale of biotic replacements is an important topic. As noted in the examples above, the taxa involved typically range from orders to phyla, and the duration of replacements from 1-330 Myr. Biotic replacements may be discerned at all distances of observation of the history of life, from the global scale involving virtually all marine animals -the

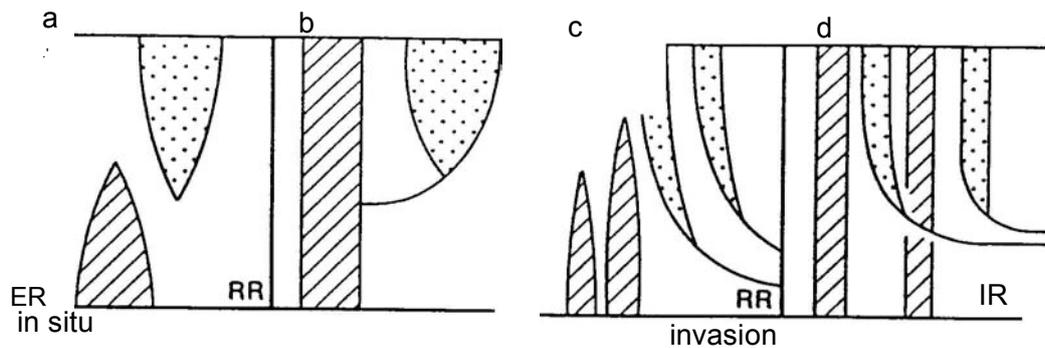


Figure 1. The main kinds of biotic radiations, those involving no geographic shift (a, b), and those involving invasion (c, d). In both cases, the radiation may be a replacement radiation (RR), or an expansion radiation (ER). In the case of an invasion, an expansion radiation has been called an insinuation radiation (IR), after Marshall (1981), since immigrating taxa *insinuate* into the faunas without necessarily causing extinction.

"evolutionary faunas" of Sepkoski (1984) - to geographically restricted events involving selected species, such as the genera of mammals involved in the Great American Interchange. It is likely that these different scales of biotic replacement do not form a restricted set of discrete levels, each displaying different patterns. Rather, the scaling may be more fractal in nature. That is, however close or however distant the observer is from the great multidimensional phylogenetic tree of all living things over the past four billion years, the patterns of branching, extinction, and replacement would show similar degrees of complexity. There are upper and lower limits to the scaling; namely, all organisms that have ever lived on earth at the upper limit, and individual organisms at the lower limit but similar scale limits apply to the more familiar physical examples of fractal phenomena (for example, the complexity of the coastline of Britain, or turbulent water). The nature of the scaling of *patterns* of biotic replacement does not, of course, necessarily imply a continuity in the *processes* involved (see later).

In the present study, the examples of biotic replacements are at suprageneric level (generally orders to phyla), and they span millions of years (1-330 Myr; mainly in the range 20-50 Myr). An important issue that can fundamentally distort our view of biotic replacements is the phylogenetic status of the taxa involved. This will be discussed first, before the patterns and processes of such replacements are addressed.

THE PROBLEMS OF PARAPHYLY

The taxa involved in postulated biotic replacements must be monophyletic. Indeed, this is doubtless true for the majority of cases noted above, and for many other well-known examples. However, monophyly of the taxa under study must be established before any attempts at macroevolutionary study can be made. This has probably been accepted as an implicit rule over the years, but it has only been expressed explicitly with the full development of cladistic techniques (e.g., Cracraft, 1981; Patterson & Smith, 1987; Smith & Patterson, 1988; Benton, 1988, 1989; Fortey, 1989). This issue was brought to the notice of many people by Patterson and Smith's (1987) survey of parts of the Sepkoski (1982) data set that has been widely used: they found that up to 75% of the families of echinoderms and fishes in this listing were "invalid" for one reason or another, most being non-monophyletic.

Monophyletic taxa, those that contain all the descendants from a single common ancestor, have natural boundaries. In other words, a monophyletic group, or clade, is

phylogenetically defined by the possession of one or more unique derived characters, and its termination is precisely defined by the extinction of the included species, a real event or sequence of events.

Non-monophyletic taxa include polyphyletic groups, those that arose from more than one ancestor, and paraphyletic groups, those that contain only some of the descendants of the common ancestor, the other descendants having been removed to another group by systematists. The termination of the group then is not natural. Fortunately, polyphyletic groups have nearly always been avoided in evolutionary studies, but the same is not true of paraphyletic groups. A well-known paraphyletic group is the Class Reptilia as it is generally understood. It includes all of the animals that evolved from a single common ancestor in the Carboniferous, except for the hairy reptiles (Class Mammalia), and the feathered reptiles (Class Aves, the birds). These latter two groups are in themselves monophyletic, but their extraction from the Class Reptilia renders it incomplete. This can be further emphasised in two ways.

Firstly, although the Classes Mammalia and Aves are both monophyletic, having evolved from a single common ancestor, there is debate at present about where the line between 'reptile' and mammal and 'reptile' and bird should be drawn. Wherever the line is drawn, the Classes Mammalia and Aves will always be monophyletic, but the 'Class Reptilia' remains paraphyletic, and it shrinks and expands according to the systematist's whim.

The second, related, aspect that illustrates the uselessness of paraphyletic groups for macroevolutionary study can be illustrated with the 'Class Reptilia'. Suppose one were to plot rates of evolution for the group over the entire span of its existence. These show initially relatively rapid evolutionary rates, with new groups appearing, but after the Triassic and Jurassic periods, the rates appear to stagnate (Benton, 1988). Is this a valid observation or not? The answer is no, since the stagnation in rates is simply an artefact of the extraction of mammals and birds from the evolving lineages. Systematists are manipulating the macroevolutionary findings when they create paraphyletic groups. The solution is to study rates of evolution in the appropriate monophyletic group, in this case the 'Superclass' Amniota (i.e., reptiles + birds + mammals).

Some paleobiologists and evolutionists have argued in favor of using some paraphyletic groups in macroevolutionary studies (e.g. Van Valen, 1978, 1985; Charig, 1982; Sepkoski, 1984, 1987). Reasons include:

1) the groups are well-known and traditional; 2) the groups may be well defined in ecological and adaptive terms, and it is sensible to exclude members of the clade that have adopted entirely different lifestyles (for example, birds are strictly members of the 'Infraclass' Dinosauria, since they arose from theropod dinosaurs, so we cannot be so dogmatic as to say that the dinosaurs have never died out); 3) the groups are more accurate surrogates of species than are monophyletic higher taxa; and 4) in large-scale studies, the effects of summing paraphyla will cancel out, so the detail is unimportant.

The first argument is not relevant to the present discussion: there is no harm at all in talking about reptiles, since everyone knows what is meant, but the group can be avoided in macroevolutionary studies. The second argument might seem to carry more weight. However, it is not clear how such groups are to be recognised (Smith & Patterson, 1988), and they probably introduce circularities into evolutionary studies. If the termination of a paraphyletic group corresponds with a mass extinction event or to a stratigraphic boundary, as is usually the case, then statistical analysis of the stratigraphic distributions of such families is bound to emphasise the events and boundaries. We must use phylogenetic (cladistic) criteria only in defining taxa for evolutionary studies, since only then can they be used to test for extinctions and other events. As for the dinosaurs, all 20 or so major families of dinosaurs are monophyletic, and they have all died out. Birds are included in the Dinosauria, and they have survived. There was indeed a major extinction of several

clades of dinosaurs towards the end of the Cretaceous period. The third argument, that paraphyla are the best higher-level representatives of species in macroevolution, is hard to sustain in view of evidence that extinctions of paraphyla often correspond to gaps in the fossil record, rather than to any real species-level events (Smith & Patterson, 1988). The fourth argument, that summing paraphyla will tend to cancel out any errors introduced, is probably also incorrect since the terminations of such unnatural groups often correspond with mass extinction events or major environmental shifts, and errors introduced will tend to be systematic and to reinforce the circularities just noted.

All cases of global, or other in situ, replacements must be demonstrated to involve pairs of clades. Invasion replacements, such as the Great American Interchange, involve at first sight two polyphyletic groups, the edentates, notoungulates, litopterns, and rodents of South America, and the horses, elephants, and carnivores of North America. If this is the appropriate scale of analysis, then that would be the case. However, this famous invasion was not a single event: the swapping of species took several million years, and the interactions are more appropriately considered at the species level. Hence, the taxa are monophyletic.

In conclusion of this section, detailed phylogenetic analyses are a necessary prelude of macroevolutionary studies in order to establish monophyletic groups so that: 1) the earliest representatives of groups can be determined truly to belong to them (avoiding the problems of "ancestor hunting"; Benton, 1988); and 2) true terminations and patterns of decline are determined, not the artificial cut-offs of paraphyletic groups.

HOW TO RECOGNISE A BIOTIC REPLACEMENT

Several general observations of patterns from the fossil record are necessary in order to identify a biotic replacement: 1) two or more clades must be involved; 2) the 'before' and 'after' clades must occupy demonstrably similar adaptive zones (ie., sets of niches); and 3) there must be an approximate coincidence in timing of the decline and/or disappearance of the 'before' clade(s) and the radiation of the 'after' clade(s), according to a variety of patterns:

- i. both over a long time;
- ii. both rapidly;
- iii. rapid decline/ extinction of one and long-term radiation of the other;
- iv. long-term decline of one, and rapid radiation of the other.

In order to determine these basic facts, the fossil record in question has to be adequate; and in particular it ought to possess these qualities: 1) accurate stratigraphic dating throughout; 2) abundant finds of fossils throughout the time-span in question; 3) fossils that may be identified readily to their clades, so that there is no confusion between the 'before' and 'after' taxa; 4) fossils and sediments that give detailed information on ecology and adaptations; 5) clear geological evidence for geographic shifts over time, if an invasion radiation is suspected; and 6) a strongly founded cladistic phylogeny of the taxa of interest.

A well-studied example, the Great American Interchange of the past 6 million years (Marshall, 1981; Marshall et al., 1982; Stehli & Webb, 1985), appears to fulfil these criteria (Fig.2).

1. **Dating of the sediments** containing mammal remains from the last 6 Myr in South America is reasonably good: six geological formations have been determined, each containing a distinctive fauna of mammals, and there are a variety of radiometric dates and magnetostratigraphic indicators for most of these formations (Marshall et al., 1983, 1984).

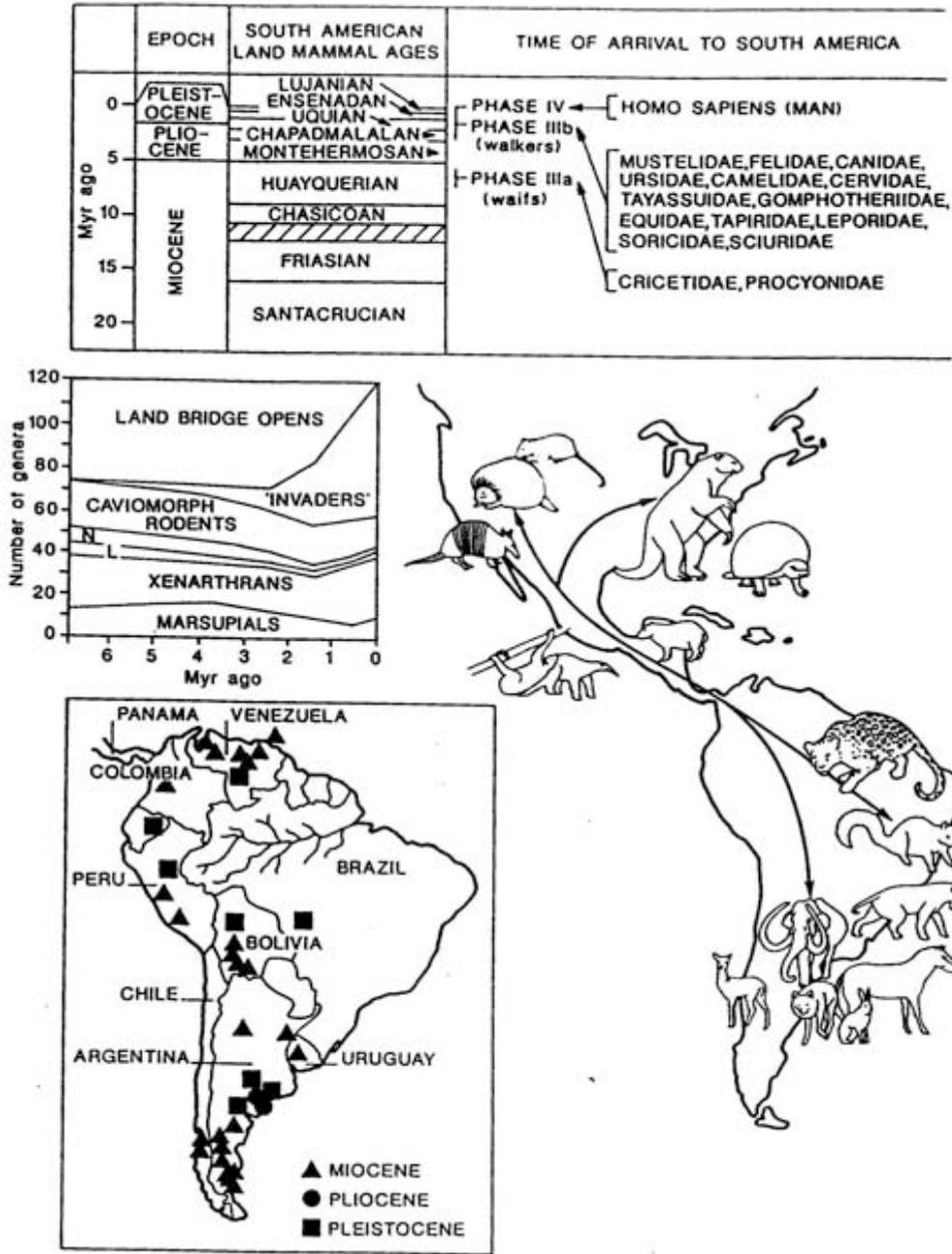


Figure 2. The Great American Interchange, showing some of its major characteristics. The stratigraphic timescale (a) is detailed, and well dated in parts: the interchange itself involves three phases of immigration (termed IIIa, IIIb, and IV). A typical pattern of generic diversity of mammals in South American over the past 6 Myr (b) shows that the North American 'invaders' mainly insinuated, since there is relatively little extinction among the native South American forms (shown shaded). Terrestrial faunas with mammals of Miocene, Pliocene, and Pleistocene age are known from various parts of South America, particularly Argentina (c). The passage of South American mammals into Central and North America and of North American mammals into South America was roughly evenly balanced (d), although the picture looks very different today because of subsequent extinctions. (Based on Marshall 1981, and other sources.)

2. **Fossils are abundant** in all of the formations. Each of the six formations has yielded 72-120 genera (mean 87.8), representing 30-39 families (mean 34.3). Living totals are 75 genera and 35 families, so that the Pliocene and Pleistocene fossil record of mammals would appear to be rather complete compared to the present day, unless past diversities were strikingly higher than they are today (they were in fact higher in the Pleistocene, particularly at the generic level).

3. **The fossils are readily identifiable** to species, genus, and family. Even isolated jaws and teeth, the commonest fragmentary fossils, may be so identified, because of the great variation seen in mammalian teeth, their rich contained phylogenetic information, and the enormous experience of mammalian paleontology. In many cases, of course, the mammalian remains in question are virtually complete, to the extent of preservation of hair in some later Pleistocene examples!

4. **The ecology and adaptations may be determined** to a considerable extent. since the teeth and bones give a great deal of specific information on diets and modes of locomotion, since most taxa have closely related living relatives, and since the associated sediments and fossils give extensive information on the habitats.

5. **The geography is relatively well established.** The present location of finds is close to their ancient distribution since the time of interest is within only the past 6 Myr. Independent geological evidence documents the major stages in the opening of the Central American land bridge. Most of the relevant fossil faunas are, unfortunately, from Argentina alone (Marshall 1981), at the southern end of the distribution of most groups, so the geographic story for the whole of South America is unknown.

6. **The phylogenies are essentially cladistic.** Most of the groups have been revised recently, and cladograms developed. The status of the families and orders as clades is now mainly established, although there may be dispute in the cases of some genera, and in placing the families and orders into the framework of a broader cladogram of all mammals.

THE ROLE OF BIOTIC REPLACEMENTS

If the taxa of interest in a macroevolutionary study are all monophyletic, then it is axiomatic that all radiations of new taxa, at whatever scale, must involve either an expansion radiation into new ecospace or a replacement radiation or biotic replacement. The only other way that evolution could proceed in order to avoid this inevitability would be if there were extensive lineage swapping between supraspecific clades, and no clearcut replacement of one by the other. However, this does not appear to be the case, or at least not after a branching event has taken place, so that all clade radiations that are not into previously unoccupied ecospace are to be treated as biotic replacements.

The role of biotic replacements in the history of life may be assessed by the analysis of substantial parts of the fossil record. While it would be best to attempt to compare all parts of the history of plants and animals in order to determine how common and how significant biotic replacements have been, this would represent an enormous undertaking. In part, it might prove impossible, especially where the fossil record is poor, or where the systematic basis for classification is not demonstrably cladistic. Hence, the fossil record of tetrapods has been selected as a test case.

This fossil record is better than most in terms of its cladistic resolution, since vertebrate paleontologists have applied such techniques for a number of years now, and since the taxa lend themselves particularly well to detailed character-based phylogenetic analysis. These arguments are developed more fully elsewhere (Benton, 1988, 1989).

A preliminary analysis of data on families of tetrapods from the Devonian to the Triassic shows that expansion radiations dominated in 'normal' times (ratio, 3:1), while replacement radiations dominated in mass extinction times (ratio, 1:2). This question will be further investigated (Benton, in prep.).

THE CAUSES OF BIOTIC REPLACEMENTS

Is Competition the Cause?

It has already been noted that the tacit assumption by many that major biotic replacements in the past have been mediated broadly by competition, in a way like scaled-up individual/individual or species/species interactions, may be incorrect (Gould & Calloway, 1980; Benton, 1983a, b, 1986, 1987; Gould, 1985, 1988). There are a number of levels of assumptions in many of the story-like accounts of biotic replacements that have gained currency, and these ought to be teased apart.

Firstly, the pattern of replacement must be appropriate for competition to be invoked as the guiding principle. True long-term competition would produce a double-wedge pattern of replacement, in which taxon A (the loser) declines progressively over a measurable geological time span (say, 1-100 Myr in typical postulated examples), while taxon B (the winner) increases in diversity at an equivalent rate. The double-wedge pattern is distinguished from the mass-extinction pattern (Fig. 3) in which taxon A declines and disappears *before* the radiation of taxon B. Typically, the extinction of taxon A will appear to be a rapid event, but it need not be.

After establishing that the fossil record shows a double-wedge pattern for any particular case, the paleobiologist must determine whether the taxa are interacting. This may not always be the case on closer inspection. A rather ludicrous example is the matching double-wedge pattern of the decline of the ichthyosaurs and the rise of the angiosperms which lasted for much of the Cretaceous period, a time span of 70-80 Myr. In this case, it is obvious that the decline of a group of dolphin-like marine reptiles could not have been caused by the rise of flowering plants. But, in other quoted cases, the evidence is more subtle. For example, a rapid look at the Great American Interchange appears to show a gradual increase in dominance of 'North American' -type mammals in South America after 3-4 Myr ago, and a matching decline in numbers of endemic forms. However, in specific cases, the competition argument is hard to make since many of the animals had very different lifestyles and would not have competed. For example, the endemic giant ground sloths and the invading elephants had very different diets and modes of feeding, and it is unlikely that they would have competed for any particular resource. Other evidence indeed confirms (Marshall, 1981; Marshall et al., 1982) that the two groups lived side by side for 2-3 Myr before both died out at the same time in the late Pleistocene.

Thirdly, and most importantly, even if a double-wedge pattern is established, and the two taxa appear to have had near-identical ecologies and to have interacted, competition

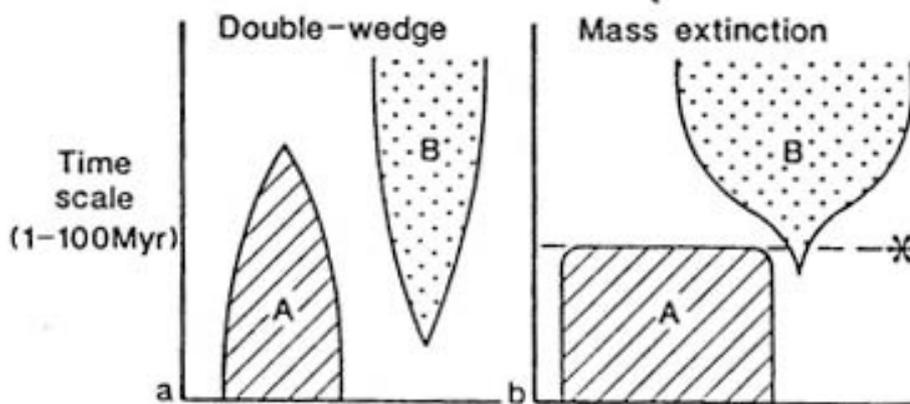


Figure 3. Two distinctive patterns of biotic replacement: (a) the double-wedge pattern (Gould & Calloway, 1980), in which group B waxes, while group A wanes; and (b) the mass extinction pattern, in which group B radiates only after the extinction of group A (the extinction event is indicated by a dashed horizontal line and an asterisk). (After Benton, 1987.)

may not be the only, or even the most likely explanation. Connell (1980) presented a set of three criteria that must be satisfied in order to demonstrate that competition has caused a particular replacement pattern: 1) divergence in adaptation or mode of life must have occurred; 2) competition must be demonstrated between living members of the taxa involved, and its evolutionary effects must be shown; and, 3) the divergence must have a genetic basis. These criteria apply especially to ecological studies, where competition is cited as the likely cause of changes in adaptations or distribution for living taxa. These criteria are too stringent for application to most macroevolutionary examples, where there may be no closely related living representatives, so that competition in action and genetic coding cannot be assessed (criteria (2) and (3)).

Many ecologists would argue that it is futile even to contemplate testing theories of competition in the distant past. This is strictly correct. It is impossible to apply the critical tests cited by Connell (1980) to any fossil example, and indeed it has proved very hard to do so for modern examples. However, competition has been so all-pervasive in paleo-biological writings, and in many well-known macroevolutionary theories (reviewed, Benton, 1987), that some effort must be made to put the subject on a firmer footing. The criteria of Connell (1980) for the demonstration of the role of competition in evolution must be weakened substantially in order to have any applicability to typical paleontological examples: 1) evidence of a double-wedge pattern of biotic replacement; 2) evidence of the likelihood of competition, based on similarities of postulated adaptations, and coincidence of timing and geography; and 3) probability of a genetic basis for the key competitive characters of the taxa involved. Satisfactory tests of all of these points can only be said to point to the *possibility* of competition applying in particular paleontological examples; it can never be seen as an adequate proof. This is an opposite viewpoint to the common assumption of pervasive competition in macroevolution, and it emphasises that the burden of proof rests with those proposing competition, rather than with those criticising it.

Alternatives to Competition

Double-wedge patterns of biotic replacement could be produced by a variety of causes, as reviewed by Benton (1987):

1. **Differential response to predation.** Many marine examples in particular have been investigated in which the relative fates of two or more similar groups appear to have been determined by predator pressure. For example, the evolution of bivalves appears to have been profoundly influenced by the appearance of new kinds of predators at different times. Bivalves that live buried in soft sediment, the endobyssate bivalves, dwindled in importance from the late Paleozoic onwards. This has been ascribed (Stanley, 1977) to increasing predation. A second, better known, burst of new predators arose in the late Mesozoic - voracious crabs, teleost fishes, and carnivorous snails - and these seem to have further reduced the importance of endobyssate bivalves (Stanley, 1977; Vermeij, 1977). The most abundant modern bivalves are those that have reduced the chances of predation by living in rock crevices, by growing thick or spiny shells, by living in the intertidal zone, or by being able to swim fast (the scallops).

2. **Differential environmental response.** Many double-wedge replacement patterns may be caused by the differential response of two clades to a major change in the physical or biotic environment. Changes in climate, sea level, topography, geography, and other physical phenomena can profoundly alter the relative survivorship of different groups. Changes in the distribution of plants, or in the major groups present, could produce a double-wedge pattern among dominant herbivores. A well-known example is the so-called 'competitive' model for the replacement of dinosaurs by mammals (e.g., Sloan et al., 1986) in which the decline of the dinosaurs and the rise of the mammals, at the end of the Cretaceous period, is explained by cooling atmospheres and the spread of temperate

floras. Differential response to predation (1) is a special case of differential environmental response (2).

3. **Chance.** As already noted, a double-wedge pattern may arise wholly by chance, in that there is no causal connection between the two clades, or between them and a specific causative factor. In paleontological cases where competition or differential response to predation or to environmental change is posited, the pattern might always have arisen by chance.

The non-competitive models for double-wedge patterns of biotic replacement which have just been outlined would loosely be called competition by many researchers – the 'diffuse competition' of Van Valen (1980). However, it is not competition in the strict sense, which must involve a limiting resource, and damage to one group produced by the success of another.

The Role of Competition in Biotic Replacement

Many of the problems with the study of the role of competition in the study of biotic replacement have been engendered by the use of value-laden terminology, or imprecise terminology. The basic patterns of biotic replacements have been noted above, but some further comments on the assumptions implied by commonly-used terms should be noted here.

The portion of a biotic replacement in which competition is demonstrated, or more commonly assumed, is the radiation phase of the 'successful' group. This radiation is usually called an *adaptive radiation*, which immediately implies the possession of a feature, or set of features (*key adaptations*), that ensured success. Hence, for 'adaptive radiation', read 'radiation in which the group out-competed another and succeeded because of its special feature(s)'. Cracraft (1985) has already rightly suggested that adaptive radiations should be known simply as *radiations*. The term key adaptation involves so many assumptions about process that it should be avoided altogether if possible. It will be used in the following list of models of competition-induced biotic replacements because it is a traditional part of such models. However, as Kemp (1985) has pointed out, it is most unlikely that any radiation was based on the possession of a single character; organisms are much too complex for that.

There is not a single model for a competitive replacement, but at least five, as Benton (1987) noted (Fig. 4):

1. Clade B possesses a key adaptation which allows it to compete successfully with, and replace, clade A. Clade B has demonstrated the competitive superiority conferred upon it by the key adaptation, by causing the extinction of clade A.

2. There is a mass extinction event, and survivors of clade B (with its key adaptation) compete successfully in the disturbed post-extinction ecosystems with the survivors of 'clade A (which lack the key adaptation) and clade B prevails. Again, clade B has demonstrated its competitive superiority.

3. There is a mass extinction event and clade B resists extinction. Clade A lacks the ability to resist extinction, and it dies out. Clade B has demonstrated its competitive superiority in terms of its ability to resist extinction. That ability may or may not be related to the possession of a key adaptation that mediates the radiation of clade B after the crisis time has passed. Adaptations that favor groups in times of mass extinction stress may be different from those that favour survival in normal selection regimes (Jablonski, 1986).

4. There is a mass extinction event during which many A and B organisms die out, and, by chance, only a few B organisms survive. They evolve into clade B, and they have a key adaptation that ensures a successful radiation. Clade B has not demonstrated its competitive superiority over clade A.

5. There is a mass extinction event during which all or most of clade A, and most of clade B die out by chance. The survivors of clade B radiate, but there is no particular key

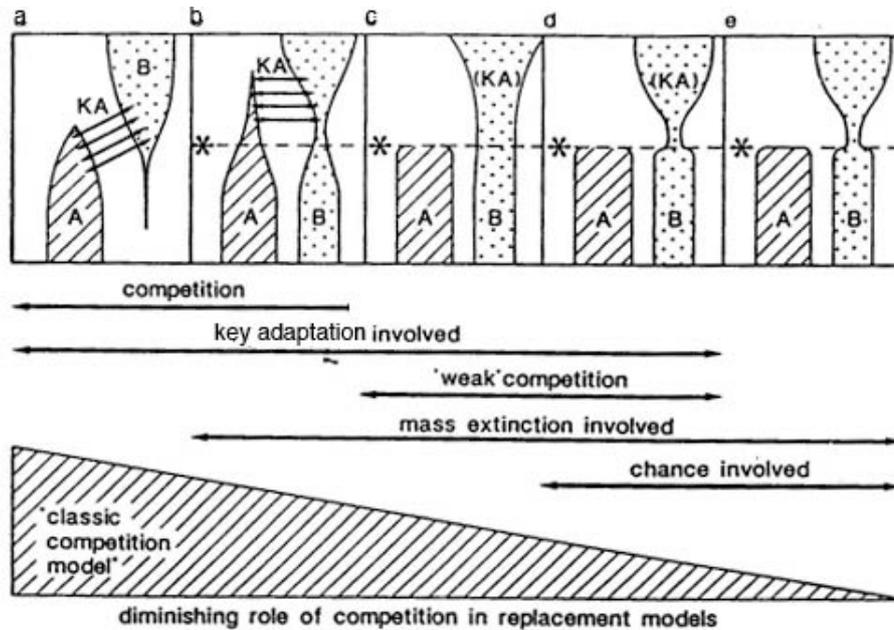


Figure 4. The role of competition, key adaptations, and mass extinction (opportunism) in five models of biotic replacement. The role of competition diminishes from left to right, from a strong, directly-competitive model of replacement (a) to an opportunistic model, in which group B has no particular competitive advantage over group A (e). The intermediate cases involve direct competition after a mass extinction event (b), and competitive advantages in group B which prevent it from becoming extinct (c), or which aid it in its recovery after being depleted (d). In the four models that do not involve strong competition throughout (b-e), an extinction event is an essential trigger (shown by dashed line and asterisk).

adaptation that ensures the success of that radiation. This is a stochastic model for a radiation, and any postulated key adaptations are imaginary.

Most cases of biotic replacement have been assumed to be type 1, that is, fully competitive. However, study of a number of well-known examples (Benton, 1987) has shown that many do not even show a double-wedge pattern, and those that do could just as plausibly be the result of differential environmental response and the conquest of new adaptive space. Examples where simple type 1 competition might apply include the major replacements of plant groups, cheilostome bryozoans with intrazoidal budding by those with zooidal budding (Lidgard, 1986), and multituberculates by rodents (Krause, 1986). However, certain paleobotanists (e.g., DiMichele et al., 1987) argue that large-scale competition in plant evolution is unimportant, and that major floral replacements have more to do with differential responses to stressful changes in the physical environment. Similar arguments might apply to the other two 'competitive' examples.

The Problems of Invoking Large-scale Competition

There are many fundamental problems in postulating competition in a simplistic way as the cause of major biotic replacements. These are noted only briefly here since they have been discussed more extensively by Gould & Calloway (1980), Gould (1985, 1988), Benton (1986, 1987), and others.

1. **Confusion of pattern and mechanism.** In the non-analytical, or 'story-telling', mode of narrative in paleontology, the word 'competition' has often been used as a kind of shorthand for 'patterns of change' or 'trends'. Instead of saying simply that, for example, the mammal-like reptiles declined over time, and the dinosaurs radiated and replaced

them in the late Triassic, certain paleontologists have stated that the two groups competed, and the dinosaurs won. As already discussed, these two sentences are not equivalent, and the latter involves a large number of hypotheses that must be tested at all levels. In fact, this case, like many others, appears to fail even the most basic of tests, since there is no evidence even for a double-wedge pattern of replacement, let alone direct aggressive competition between the two clades.

2. **Over-simplification.** The prevalent confusion of pattern and mechanism just noted is related to the problem of over-simplification of ecological and evolutionary concepts. To imagine that major clades can wax and wane because of the possession or absence of a particular key adaptation is surely simplistic in the extreme. The search for the specific feature of dinosaurs that enabled them to vanquish the mammal-like reptiles, small and large, carnivore and herbivore, globally distributed and endemic, is likely to end in failure. Indeed, in this, and many other particular examples, there is strong evidence for the involvement of a complex of biotic, abiotic, and stochastic factors in the replacement.

3. **Lack of proof.** Competition cannot be treated as the null model against which all other proposals are to be tested. Part of the narrative attitude in paleontology has been that the fossil record tells us the story of a progressive march from the primeval slime to the haughty intelligence of humans today: progress and competition are implicit. This view is seriously flawed (Gould, 1985; Benton, 1987).

4. **Incorrect scaling of concepts.** The postulate that biotic replacements were caused by competition involves a major scaling-up of the concepts of ecology. There are several serious problems with this notion. First, of course, is the question of whether an ecological interaction that takes place between individuals, or species, over periods of years, and in restricted areas, can truly be expanded to apply to supraspecific clade interactions, over periods of millions of years, and often in a global context. Ecological competition can cause the death of individual organisms and the local extinction of species. It could also, arguably, cause global species extinction. shifts in geographic distribution, changes of habits, and genetic changes in the characters of a species. However, even these modest attempts to scale up the postulated effects of observable competition at the present day, have met with considerable criticism (reviewed, Strong et al., 1984; Price et al., 1984; Benton, 1987). It is not clear how local small-scale ecological phenomena can be scaled up even further to the paleontological cases of major biotic replacements. The second problem of scaling concerns the interpretation of 'adaptations of higher taxa'. How does a key adaptation work at supraspecific levels? Do families and orders possess monolithic adaptations that can be compared at clade level, or do all individuals in a clade have an equivalent advantage over all (or most) individuals in another? Surely, as Gould and Calloway (1980) pointed out, the advantageous adaptation might be significant in the first members of a clade, but it is inconceivable that the same feature would continue to provide the same measure of success in interactions between later members of the 'competing' lineages. The third problem of scaling concerns the time scales involved. Major biotic replacements typically spanned times of 1-50 Myr (see above), and hence many millions of generations. Dawkins (1982) and others have noted that it is impossible to imagine how a competitive advantage could be maintained for so long, and still express itself as one group slowly replacing another. The level of genetic advantage per generation would be statistically nil.

CONCLUSIONS

1. Biotic radiations have occurred frequently in the past. They should be divided into expansion radiations, those in which the radiating taxon moves into previously unoccupied adaptive space, and replacement radiations, in which the new group replaces a pre-existing one. Radiations also involve geographic factors, and a distinction should be

made between those that involve no geographic shift, and those that involve invasion.

2. A test example, based on terrestrial tetrapods, suggests that most biotic radiations are expansion radiations, but replacement radiations dominate after episodes of mass extinction.

3. The simple competitive key adaptation model is not the only cause of biotic replacement, and indeed it may only rarely be the cause. A variety of other models, some of them weakly competitive, some of them non-competitive, apply in studied examples.

4. The notion of competition in macroevolution is problematic at various levels: it is hard to demonstrate, and it has been inappropriately scaled in many formulations.

5. The role of mass extinctions in triggering episodes of replacement radiations needs to be investigated further. Certainly, the study of individual radiations should continue, but more general analyses may throw light on broader patterns underlying the long-term diversification of life, and the continual turnover of taxa that has occurred through geological time.

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