

Testing the roles of competition and expansion in tetrapod evolution

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SUMMARY

Competitive replacement has probably played a minor role in the history of tetrapods. In an assessment of the origins of 840 families of amphibians, reptiles, birds, and mammals, fewer than 26%, and probably fewer than 13%, were identified as candidate competitive replacements (CCR's). This is the pool of families that shared their geographic area of origination and their broadscale adaptations with a pre-existing family, and is thus a maximum measure of families that might have competitively displaced another. Most tetrapod families arose by expansion of the ecospace and geographic areas previously occupied by other members of the clade Tetrapoda. The numbers of CCRs through time are roughly in proportion to numbers of originations, but particular peaks in CCRs occurred after mass extinctions. Pure expansions, with no possibility of competitive replacement, were prevalent during the Late Palaeozoic (radiation of early amphibian and reptile groups, and broadening of habitats occupied and diets) and during the mid Cretaceous (radiations of frogs, turtles, lizards, snakes, and birds).

1. INTRODUCTION

A classic view in evolution has been that many successful radiations of plant and animal groups in the past have been mediated by competitive interactions (Simpson 1953; Stebbins 1974; Stanley 1979; Maynard Smith 1983; Rosenzweig 1995). Newly successful groups are said to have outcompeted and displaced the previously established organisms, and hence to have demonstrated some progressive or advantageous feature. Classic examples include the supposed replacement of brachiopods by bivalves (Gould & Calloway 1980; Miller & Sepkoski 1988), mammal-like reptiles by archosaurs (Benton 1983; Charig 1984), cyclostome bryozoans by cheilostomes (Jackson & McKinney 1990; Lidgard *et al.* 1993), gymnosperms by angiosperms (Knoll 1984; DiMichele *et al.* 1987), and multituberculates by rodents (Krause 1986).

The pattern of radiation of tetrapods, and indeed of many other groups, suggests that it is unlikely that competitive replacement was paramount. In the case of tetrapods (figure 1), the clade has expanded from one family, and presumably one species, some time in the Devonian, to 360 families (Benton 1993*a*) and 23500 species (Wilson 1992) today. Such an expansion in diversity, lasting some 380 million years (Ma), suggests that many of the new taxa were moving into previously unoccupied ecospace. This is confirmed by studies of the broadscale ecological attributes of tetrapod families through time, which show (Benton 1990) that new diets and new habitats were added sporadically to their repertoire, and that each addition of ecospace was matched by an increase in familial diversity.

There is no question that competition, in which an

increase in abundance by one group harms another (MacArthur 1972), occurs in nature (Connell 1983; Schoener 1983; Branch 1984; Strong *et al.* 1984; Weiner 1995). There has, however, been a debate about the extent to which competition affects rates and patterns of speciation and morphological divergence (Connell 1980; Grant 1986; Benton 1987; Schluter 1988; Rosenzweig & McCord 1991; Masters & Rayner 1993).

Evidence for the role of competition in macroevolution has been provided by four observations. Experiments have shown (Schluter 1994) that character displacement is promoted by competition, leading to divergence during adaptive radiation. Second, there is evidence for escalation through evolutionary time (Vermeij 1987, 1994), in which modes of predation and modes of defence have changed as a result of biotic interaction. Third, there is some palaeontological evidence for plateaux in levels of global taxic richness, in which there appear to have been a stable number of families worldwide for long spans of time (Sepkoski 1984, 1996). These apparent equilibrium levels of familial richness would imply that life had filled all available ecospace, and new families could arise only by competitively replacing preexisting ones, but the evidence is simply that logistic (S-shaped) curves fit the diversification patterns better than straight lines or exponential curves (Benton 1995*a*). Fourth, the phenomenon of competitive release, in which the diversity of life rebounds explosively after an extinction event (Jablonski 1986; Miller & Sepkoski 1988; Sepkoski 1996), suggests that there have been particular patterns of species packing in the past, and that niches emptied by extinction may fill again in a partly predictable manner.

The role of competition in group originations and

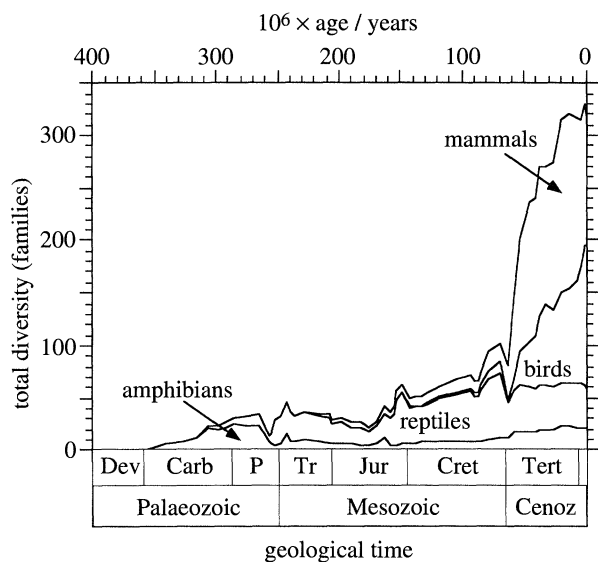


Figure 1. Diversification of tetrapods through time, showing patterns of familial richness since the Devonian. Separate curves are indicated for groups traditionally classed as amphibians, reptiles, birds, and mammals; the data are represented cumulatively. Data are from *The fossil record 2* (Benton 1993*a*), and are based on all 840 non-singleton families of tetrapods. A total of 194 singleton families were excluded, those that are currently based on single specimens or single species from single localities. Such singleton families represent point occurrences in time and space, and they cannot be assessed effectively in calculations of diversification or extinction metrics. Abbreviations: Carb, Carboniferous; Cenoz, Cenozoic; Cret, Cretaceous; Dev, Devonian; Jur, Jurassic; P, Permian; Tert, Tertiary; Tr, Triassic.

radiations is unclear. There are a number of models of clade radiations by competitive replacement and by expansion (Gould & Calloway 1980; Marshall *et al.* 1982; Benton 1987, 1990, 1991, 1996; Rosenzweig & McCord 1991; Lidgard *et al.* 1993; Masters & Rayner 1993; Heard & Hauser 1995; Rayner & Masters 1995; Sepkoski 1996). Reviews, such as these, of postulated examples of competitive replacement have shown that few of them involved direct competition, in which members of one clade regularly and persistently deprived members of another clade of a resource, and finally drove them to extinction. Commoner than these may be models that involve a lesser role for competition, such as incumbent replacement (Rosenzweig & McCord 1991), in which an existing clade maintains its position because of its incumbency, and is replaced by a new group only after the impact of an external perturbation.

2. TESTING THE PREVALENCE OF COMPETITIVE REPLACEMENT

Insights into the role of competitive replacement in the origin and radiation of clades may be obtained by studies of particular examples. From time to time, a census of case studies may give an indication of the frequency of competition and expansion in a sample of studied cases, but there is no guarantee that the sample is comprehensive or random. An alternative to the case-study census method (Connell 1983; Schoener

1983) is the comprehensive approach, in which an attempt is made to assess every case within a prescribed part of the evolutionary tree of life.

The clade Tetrapoda (amphibians, reptiles, birds, mammals) was selected for study here because many examples of postulated competitive replacement involve tetrapods. In addition, the clade is diverse, containing 1034 families with a fossil record (Benton 1993*a*), those families are mainly monophyletic as a result of cladistic revision, their ecologies and habitats may be assessed in a broad way, and independent tests suggest that the tetrapod fossil record is adequate for macroevolutionary studies. This last point is further elaborated.

The quality of the tetrapod fossil record has been tested by cross-comparison of phylogenetic data obtained from the independent sources of stratigraphy, morphological cladistic reconstruction, and molecular phylogeny reconstruction (Benton 1994, 1995*b*; Benton & Hitchin 1996; Benton & Storrs 1994, 1996). It has been established that macroevolutionary patterns derived from data on fossil tetrapod temporal distributions have not been substantially altered by recent major changes in knowledge (Maxwell & Benton 1990), and that new collecting and systematic revision have filled cladistically predicted gaps in the fossil record, leading to a 5% improvement in knowledge over the past 26 years (Benton & Storrs 1994, 1996). A further important finding was that the stratigraphic order of appearance of fossils matches the order of branching in cladograms of tetrapods (Norell & Novacek 1992), confirming the adequacy of stratigraphic and cladistic data. Further, the continental tetrapod fossil record is as complete, at family level, as is that of (marine) echinoderms (Benton & Simms 1995) and fishes (Benton & Hitchin 1996).

3. THE TEST

A study was made of all families of tetrapods (amphibians, reptiles, birds, and mammals) which have a fossil record. There are 1034 such families noted in the latest comprehensive compilation of data (Benton 1993*b*; Milner 1993; Stucky & McKenna 1993; Unwin 1993). Many of these families (194) are based on point occurrences, frequently single species, or even single specimens, from a single locality. Such singleton family records were excluded from the study as they are either too poorly known, or have a higher chance of being spurious than multi-species families. Alternatively, if these singleton families truly had such restricted distributions, they probably did not figure in competitive replacements.

A search was made across all 840 non-singleton families of tetrapods (figure 1) for cases in which biotic interaction might have occurred. The first requirement for competition is that species within a pair of families could have met each other: thus overlaps of pairs of families in time, space, and ecology were sought first. Minimum overlaps spanned one stratigraphic stage (mean duration, 6 Ma), and the true duration of overlap could have been less than that. The duration of overlaps, however, was often much more than one

Table 1. *Geographic and ecological categories used in the analysis of tetrapod families*

(Each of the 840 non-singleton tetrapod families was assigned to one category of each geographic and ecological attribute. Families were assigned to the most appropriate categories, based on consideration of all species in the family, and taking account, as far as possible, of changing body sizes and diets during growth.)

1. Geographic assignments: South America, Central America (including Caribbean), North America, Europe, Africa, Asia, Australasia, Pacific islands, Indian Ocean islands Antarctica.
2. Body size: small (snout-vent length (SV) < 150 mm), medium (150 mm < SV < 1.5 m), large (SV > 1.5 m).
3. Diet: carnivores (insects, fishes, tetrapods, molluscs, eggs), omnivores, herbivores (browsers, grazers, grain-eaters, gnawers fruit-eaters, nectar-drinkers).
4. Habitat: predominantly terrestrial, freshwater, marine, arboreal, aerial, subterranean.

stage in length, and some exceeded five or six (durations of 30–40 Ma). Such lengthy overlaps could be said to imply impossibly slow rates of evolution, during which the postulated competitive advantage of one group over another would be disappearingly minute. However, all overlaps, however lengthy, were retained in this analysis, to allow for the possibility that competitive replacement began some time after the origin of a family.

In addition, allowance was made for possible missing fossils. Cases in which families shared some part of their geographic ranges and ecologies were sought with spacings of 0, 1 and 2 stratigraphic stages between the time of extinction of one and the time of origination of the other. These additional pairs of families gave a measure of maximum candidate competitive replacements (ccrs). Future collecting may either fill some of these gaps, and demonstrate that the cautious approach adopted here was appropriate, or the gaps may remain resolutely empty, and then these non-overlap ccrs will be excluded from consideration for competition.

Ecological categories were deliberately made broad (table 1) to maximize the ccr values. Hence, only three size categories are employed. This allows for potential wide size variations among species within a family, and for size changes during growth. Ecological categories were determined by reference to a broad range of palaeontological and zoological literature. The category determination for each family includes all ecological assignments for species within the family. Clearly such assignments are subject to error, especially where a family lacks living members. However, the breadth of the categories (e.g. freshwater fish-eater, terrestrial browser, arboreal insectivore) is perhaps appropriate to the ability of vertebrate palaeontologists to interpret diets from teeth and habitats from enclosing sediments.

Geographic categories are also broad, being at the level of modern continents, even though, at times in the past, many of these were not coherent land masses. Hence, assignment of two families to 'Asia' means that they may be judged as ccrs, but in reality Siberia,

India, and parts of China were long separate, and many contemporaneous 'Asian' families never met. This broad view of geography, however, allows the best chance of finding all ccrs, even if most of them are later excluded after close study.

4. RESULTS

The numbers of overlaps and ccrs vary through time (figure 2) roughly in proportion to the numbers of originations. Highest incidences correspond to times of overall diversification, particularly during the Late Permian to Late Triassic, and the Late Cretaceous to Early Tertiary intervals. The overlaps and ccrs lag the onset of diversification in both cases because they indicate the replacement of first-wave families by second-wave families that arose later during the radiation. In both cases, the elevated occurrences of ccrs follow important mass extinctions, those at the Permo-Triassic and Cretaceous-Tertiary boundaries.

High rates of origination, however, do not always lead to high numbers of ccrs, particularly during episodes of apparently unrestrained expansion into new ecospace, as happened during the Late Palaeozoic (initial radiations of amphibians and reptiles into new terrestrial habitats, and diversification of diets from

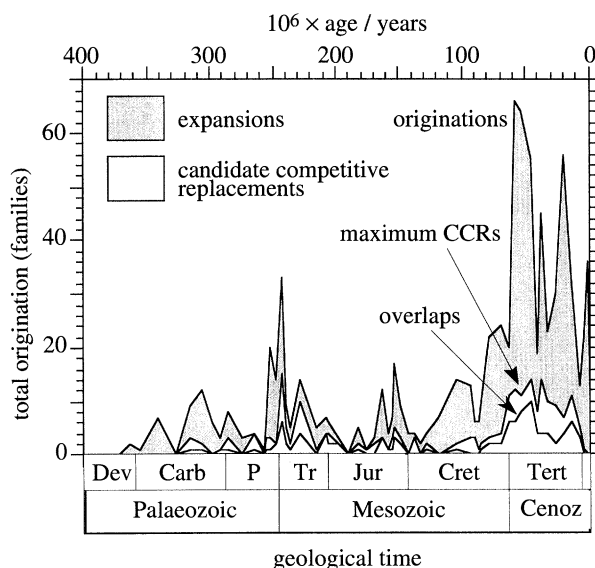


Figure 2. Distribution in time of originations of tetrapods of all habitats, showing also the occurrences of overlaps and of maximum candidate competitive replacements (ccrs). ccrs were identified by comparison of pairs of families. First, stratigraphic range charts were plotted for each combination of body size, diet, and habitat, and maximum geographic ranges of each family were noted. Then, the point of origin of each of the 840 families was scrutinised to determine whether it was a ccr or an expansion. ccr cases were subdivided into overlaps, where the stratigraphic range of the family overlapped another family, and situations where the family apparently originated at the precise time of extinction of another (gap 0), or after a gap of one or two (gap 1, 2) stratigraphic stages. Overlaps give evidence that the two families could have encountered each other, while the gap 0, 1 and 2 cases allow for possible incompleteness of the fossil record. ccrs are plotted as overlaps and maximum ccrs (the sum of all overlaps and gap 0, 1 and 2 cases).

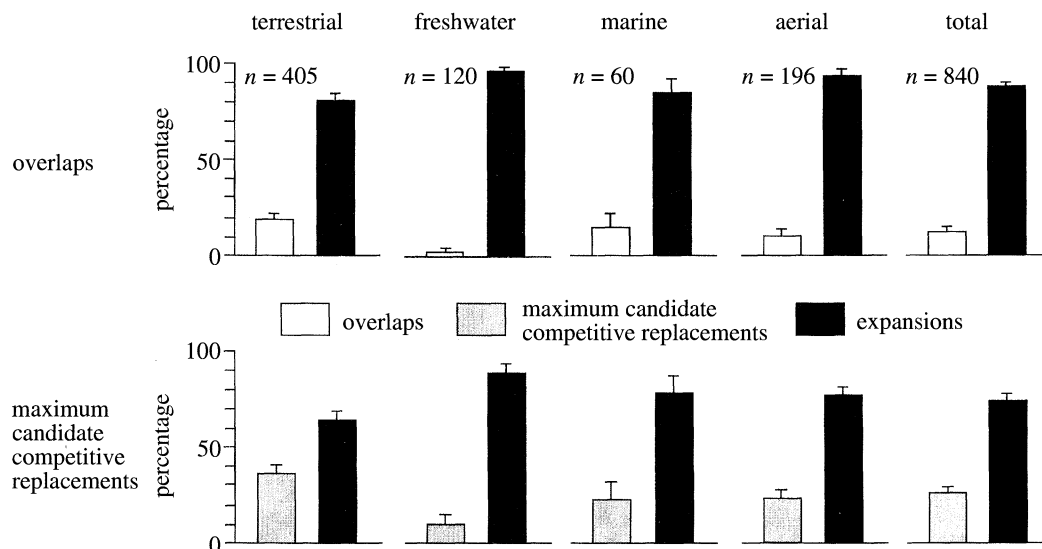


Figure 3. Comparison of the numbers of familial originations of tetrapods in principal habitat groupings divided into overlaps (blank), maximum ccrs (stipple), and expansions (black). Families classed as subterranean ($n = 27$) and arboreal ($n = 32$) are excluded because sample sizes were so small. Error bars were calculated according to an approximation formula for errors based on a binomial probability distribution (Raup 1991). Abbreviation: n is sample size.

fish-only to others, such as insects, tetrapods, and plants), the mid Cretaceous (radiations of frogs, turtles, lizards, snakes, and birds), and the Late Tertiary and Quaternary (radiations of perching birds, marsupials, bats and rodents). Indeed, very few ccrs were identified during the last 10 Ma of tetrapod evolution.

In tetrapod evolution as a whole, and for individual principal habitats, competitive replacement played a minor role (figure 3). The frequency of family-range overlaps ranges from 0% (arboreal families) to $19 \pm 3.8\%$ (terrestrial families), and the proportion of maximum ccrs ranges from 0% (arboreal families) to $36 \pm 4.7\%$ (terrestrial families). Figures for all 840 tetrapod families are $13 \pm 2.3\%$ overlaps (106 families) and $26 \pm 3\%$ maximum ccrs (220 families). All of these ccrs are listed in Benton (1996).

A comprehensive census of the modes of origin of all 840 non-singleton families of tetrapods shows that biotic interaction might have played a role in 13%, or at most 26% of cases. These particular cases (Benton 1996) are worthy of individual study.

5. DISCUSSION

The importance, or lack of importance, of competition in evolution has been a much-disputed topic. The conflict has been more than a question of establishing a minor evolutionary principle, because both viewpoints are symbolic of wider debates in biology. Proponents of the importance of competition include ecologists, population geneticists, palaeobiologists, and evolutionary modellers who favour an equilibrium approach to diversity, including ideas of global and regional carrying capacities, and the key role of the biotic environment in guiding evolution (Van Valen 1980; Rosenzweig 1995; Sepkoski 1996). Those who argue strongly against the importance of competition include ecologists and modellers who see

no evidence for equilibrium in nature and palaeontologists brought up in a geological background who focus on the importance of the physical environment in directing principal evolutionary change (Gould & Calloway 1980; Strong *et al.* 1984; Benton 1987). It may be impossible to test the overall importance of competition in directing evolution. Attention has focused on reconsidering individual case studies, and seeking evidence of true evolutionary change induced by competition, rather than short-term changes that do not involve selection (Weiner 1995). In addition, the broader question of the role of competition has been assessed by making censuses of hundreds of published field and laboratory studies (Connell 1983; Schoener 1983). These censuses are indicative of general patterns, but they could be biased by the range of organisms selected for study over the years. Perhaps evidence for competitive replacements has been suppressed or enhanced by the choice of case studies.

The present study is crude, but it has employed a comprehensive approach. Every tetrapod family with a fossil record has been scrutinised, and the decisions have been made by one person using one set of decision rules. Future work may increase the proportions of overlaps and ccrs as a result of extensions to stratigraphic and geographic ranges of families. However, it is more likely that the proportions will diminish as a result of refinement of the crude ecological and geographic divisions used here. Bear in mind that the number of ecological categories investigated here (table 1) was at most 216 (three size classes \times 11 diet classes \times six habitat classes). Most of the cells of this three-dimensional ecological data table have no entries (e.g. large arboreal mollusc-eaters; small marine seed-eaters; medium subterranean fish-eaters), so the effective number of ecological categories, into which all 840 families were shoe-horned, was 65. Further, the geographic distributions of the tetrapod families were

represented by ten continent-scale divisions. For some speciose families, this is probably the correct scale, but for many it is too crude, and overestimates the possibilities of families having had the opportunity to meet and interact (there is a wide climatic range through Africa or Asia, and many tetrapod families do not have continent-wide geographic distributions).

The present comprehensive assessment refers only to tetrapods, and it cannot be said whether the finding here of the apparently minor role of competitive replacement of families is typical. Perhaps tetrapods experienced a greater or lesser degree of competitive interaction during their evolution than some other groups, and comparative tests could be fruitful. For tetrapods at least, three-quarters, or seven-eighths, of diversification took place as unrestrained expansion in the absence of biotic interaction.

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