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SUPPRESSED SPECIATION RATES AND COMPOSITIONAL CHANGES IN PALEOZOIC FAUNAS

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ABSTRACT

Shifts in the taxonomic composition of Paleozoic communities are commomly ascribed to selective extinctions. Suppression of realized speciation rates owing to shrinkage of available adaptive space (lowering of potential niche number), even though unselective, results in differential diversity losses, the greatest losses being sustained by clades with the highest speciation and extinction rates (the high–turnover caldes). The resulting compositional shifts apear to be selective. Foreclosures of speciation opportunities probably play an important and perhaps in some cases a dominant role in taxonomic shifts during the Paleozoic.

Key Words: Evolution, Communities, Paleozoic.

RESUMEN

Normalmente, las desviaciones en la composición taxonómica de cumunidades paleozoicas se atribuyen a extinciones selectivas. Sin embargo, reducciones de los ritmos de especiación adquiridos, debidas a la disminución del espacio adapatativo disponible (descenso del número de nichos potenciales), tienen como consecuencia, aunque dicha disminución no sea selectiva, pérdidas diferenciales de diversidad. Las mayores pérdidas las soportan los clados con mayores ritmos de especiación y extinción (los clados de alto cambio). Así, las derivas de composición resultantes parecen ser selectivas. Las anulaciones de las oportunidades de especiación probablemente juegan un papel importante, y quizás en algunos casos dominante, en las derivas taxonómicas durante el Paleozoico.

Palabras clave: Evolución, Comunidades, Paleozoico

INTRODUCTION

The increase, decrease or stability of numbers of species within a clade depends upon the rates of speciation and extinction. The same is true of the number of species within the biosphere. Within ecological units that are not closed, such as biotic provinces or communities, the effects of immigration and emigration of species must also be taken into account. General diversity reductions due to extinction, for example, could be made up within a community if surviving species expanded their ranges ecologically or geographically and immigrated into the community to replace the species that were lost. Even though no intracommunity diversity change had occurred, however, the pattern of the compositional changes within the communities (in this example an increase in intercommunity similarity) should be detectable in the fossil record. Indded, the contrast berween changes in species composition and diversity in entire world or provincial faunas and those within communities might provide important evidence in evaluating macroevolutionary events.

Shifts in the quality of species within marine communitities also seems to be related to macroevolutionary rates. Over the long term, clades with relatively low turnover rates (low speciation and extinction rates) appear to increase their diversities at the expense of clades with relatively high turnover rates (see Sepkoski, 1984; Van Valen, 1985; Valentine, 1990). Thus there is a shift among dominant marine clades from those with high turnover rates (trilobites) to those with somewhat lower turnover rates (articulate brachiopods, crinoids) during the Paleozoic, and to those with still lower rates (gastropods, bivalves) during the Mesozoic and Cenozoic (Valentine, Tiffney and Sepkoski, 1991). Furthermore, within each of these clades, the early groups tend to have higher turnover rates than the later forms. As a result of such trends, the composition of Paleozoic marine communities was significantly altered.

The greatest compositional turnovers tend to accompany times of major extinctions. It has been sugested that some of the major Paleozoic extinctions result from a suppression of speciation rates rather than an increase in extinction rates. It is the purpose of this

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paper to evaluate the effects of supressed speciation rates on clades of different turnover potentials, and to assess their significance in Paleozoic community evolution.

MACROEVOLUTIONARY MODEL OF AN ADAPTIVE ZONE

Macroevolution involves an interplay between speciation and extinction. The common association of changes in faunal composition with high levels of extinction has focused attention on high resistance to extinction as a major aspect of clade success. It is useful also to consider what may happen when extinction rates are held more or less constant, so that any macroevolutionary changes that occur are owing to variation in speciation rates. A context within which such situations may be considered is provided by a model of the macroevolution of a clade envolving within a closed environment (an adaptive zone) that has finite resources and therfore a limited capacity for species diversity (Walker and Valentine, 1984). In this model it is assumed that the clade has an inherent speciation potential, but that the realized speciation rate is a function of species diversity within the clade; as the environment begins to «fill up» with species, the opportunities for speciation decline and the rate of species origination falls. The species extinction rate, however, is based on the rate and magnitude of environmental change and is not sensitive to the species diversity of the clade. If this extinction rate is higher than the inherent speciation rate, the clade quickly disappears. However if the initial speciation rate is higher than the extinction rate, then the clade will diversify. As species numbers increase the realized rate of species origination begins to fall, and it eventually drops to the level of the extinction rate; at this point, the two rates being equal, a species equilibrium diversity is established. The clade may have a high or low turnover rate depending (in this model) upon the extinction rate.

How many species exist at equilibrium diversity depends upon only a few factors: the number of resources (visualized as the number of niches in the model), and the ratio of the inherent speciation rate to the extinction rate. If the biology of the clade is such that the inherent speciation rate is quite high, then for a given extinction rate, diversification will drive the equilibrium species diversity higher than if the inherent speciation rate is low. Similarly, if the extinction rate is low, a given inherent speciation rate will drive the equilibrium diversity higher than if the extinction rate is high. A logistic equation specifies the curve of increasing diversity. If this equation is solved for a species equilibrium condition, the proportion of «empty niches» at equilibrium is simply the extinction rate divided by the inherent speciation rate, and the proportion of «full niches» at equilibrium is the reciprocal of this (Figure 1). The absolute number of full or of empty niches depends upon the size and complexity of the adaptive zone that is being modeled, and upon any conditions that permit or restrict specialization on resources within the zone; in other words, on the number of niches, full or empty, that are available to the clade in question.

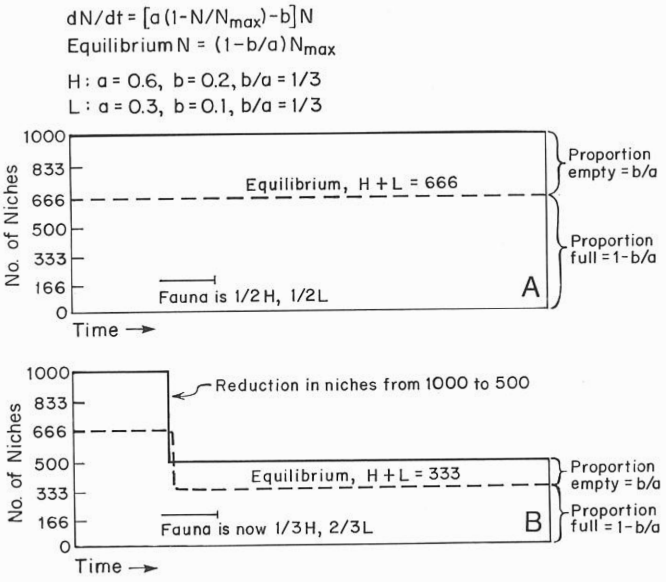

Figure 1. Effect of halving the available space (niche number) on species diversity in two clades,one (**H**) with a turnover rate twice as high as the other (**L**). A, Adaptative space at 1,000 niches, **H** and **L** equally represented. B, adaptative space shrinks abruptly to 50 niches; **H**, with twice the extinction rate, is now only half as diverse as **L. N**, number of species; **N max**, total niches available; **a**, inherent speciation rate; **b**, species extinction rate. (Equations from Walker and Valentine, 1984).

So long as the extinction rate is greater than zero, the adaptive zone cannot be «full» of species (unless the speciation rate is infinitely large and speciation therefore instantaneous). Estimates of inherent speciation rates and of species extinction rates have been made for a number of marine invertebrate clades (Stanley, 1979; Walker, 1984) and they suggest that, while some clades maintain a higher occupation density in their adaptive zones than do others, about one third of potentially occupied niches are in fact empty (Walker and Valentine, 1984). This may be an overestimate, owing to the difficulty of determining the operationally inherent rates of speciation of clades, but the conclusion is still that there usually are resources available to support significant numbers of additional species. If species diversity is kept below the equilibrium level, perhaps in an environment that is subjected to numerous shocks, then there will be even more empty niches than at equilibrium. On the other hand, if an adaptive zone shrinks, say in an environment that is deteriorating so that the number of potential niches is lowered, then the extinction rate would of course rise, the species diversity would fall, and it is possible that the standing diversity would exceed the declining equilibrium diversity for a time. It seems unrealistic to expect that the equilibrium diversity, which should itself vary almost constantly in a world as variable as ours, would ever be attained for long; the equilibrium is best regarded as a shifting datum level towards which the factors that raise or lower diversity will tend.

MACROEVOLUTION DRIVEN BY SPECIATION RATES

The empirically determined long–term superiority of low–turnover clades over high–turnover clades of marine invertebrates (Valentine, Tiffney and Sepkoski, 1991) is usually explained as owing chiefly to the superior extinction–resistance of the low–turnover clades. Of course if a high–turnover clade has a far lower inherent extinction-to-speciation ratio than a low–turnover clade it should have the advantage, but there is reason to believe that this ratio is rather similar for many clades (Stanley, 1979, 1990). Low–turnover clades do not have to rely upon high speciation rates to maintain their presence in an adaptive zone because they resisit extinction, while high–turnover clades, easy prey to extinction factors, risk being eliminated altogether during times of generally elevated extinctions (see Sepkoski, 1984; Van Valen, 1985; Valentine, 1989, 1990). However, there is evidence that a lowering of origination rates rather than a raising of extinction rates may often have been a major contributor to diversity declines within clades. Van Valen (1985) and Gilinsky and Bambach (1987) have shown that at the family level, extinction rates are less variable than origination rates. It is possible, though perhaps unlikely, that such family–level variations could occur without corresponding species–level rate changes. However, there is some empirical evidence suggesting that suppression of speciation may contribute importantly to even major extinction events; for example McGhee (1988) has concluded from fossil evidence of brachiopods and other invertebrates that a decline in speciation rates played a major role in the Frasnian–Fammenian extinction.

In the macroevolutionary model reviewed previously, speciation rates are suppressed as opportunities (number of open niches) decline. Opportunities are reduced as clades become inreasingly diverse, but this of itself would not lead to extinction. Opportunities may also be reduced for one clade when another clade succeeds in occupying niches and appropriating resources available to both. This niche preemption would result in a shift in relative diversity between the clades in question but should not of itself raise the extinction rate of the fauna. Finally, opportunities are reduced when the adaptive zone «shrinks» so that fewer niches are available. Such shrinkage would result in a lowering of the absolute number of species at the equilibrium diversity level, so that some extinction must occur. However, it is possible that there would not be an extinction «spike» at the species level if the shrinking was slow, or if a lag between the lowering of the equilibrium level and the fall of diversity to this new level were sufficiently long. At any rate, the first question to ask is whether high or low turnover clades would be affected differently.

What are the consequences for fast and slow turnover clades if the shrinkage is the result of a cataclysm that can be considered as geologically instantaneous? Take an example of clades that are equally represented in an adaptive zone, one of which has twice the turnover rate (half the extinction resistance) of the other. It is assumed that the shrinkage falls equally upon occupied and unoccupied niches, that is, in the portion that they are represented, and that it is unselective with respect to the clades present. If the extinction rate/speciation rate ratio were 1:3 for each clade, and the zone originally contained 1000 niches, at equilibrium the zone would contain 666 species, 333 species of each clade (Figure 1). A sudden change that cut the species capacity of the environment by half, to 500, would create an equilibrium level of 333 species, but as the extinction resistance of the low turnover clade (**L**) is twice that of the high turnover clade (**H**), we expect in the model that **H** loses twice as many species as **L**, so that now the zone contains 222 species of **L** but only 111 species of **H**. If the shrinkage did not affect the two clades in these proportions, then it would be selective; in affecting each in accordance with the clades inherent resistance to extinction, it is unselective. As there are no available niches except those opened by background extinction, which is twice as high for **H** than for **L**, clade **H** will not ordinarily be able to increase its proportional representation; it can never recoup its losses unless it is unrealistically lucky or unless something else occurs that favors it disproportionately.

What happens if niche shrinkage is slow and gradual? The same result occurs, only more slowly; each niche lost has twice the chance of having been occupied by **H** as by **L**, for **L** resists extinction twice as well, and the superior speciation rate of **H** is of no help in maintaining its diversity, for there are no more available niches than those resulting from background extinctions. The sudden niche reductions would produce a large extinction «spike» –a 50% species extinction– and generic, familial and other extinction spikes appropiate to the distribution of species in taxa at each higher rank. In the real world, environmental change so dramatic as to shrink by half the capacity of the environment to support species would surely entail extinctions beyond those due simply to the lowered species capacity of the environment, and therefore the extinction spike would be even higher than suggested by the model. A gradual niche reduction, on the other hand, would produce elevated extinction levels appropiate to the rate of niche shrinkage and to taxonomic level, but these would result in extinction «plateaus» rather than spikes. Presumably the rate of niche shrinkage, no matter how slow, would produce extinctions that are additive with the ordinary «background» extinctions that arise from other causes –from rates of change in the quality (rather than the quantity) of the niches.

In the fossil record, the niche shrinkage would register according to an interplay between the event and the taphonomic processes that determined its stratigraphic resolution. Sudden shrinkage would create a spike of last appearances, smeared backwards in time from the actual extinction event (Signor and Lipps, 1982). The extinction would appear to be selective, because although the extinctions were proportional to inherent resistances as they had always been, there would be a selective loss of taxa on higher levels involving the fast–turnover clades, because their ability to maintain their diversities by virtue of their rapid speciation potentials would be lost, their speciation opportunities being foreclosed by the shrinkage. Slow niche shrinkage, while producing an elevated disapearance rate at the specific or generic levels, appropriately smeared back in time from the actual onset of the event, might engender little or no increase in disappearance rates at higher taxonomic levels, which although greatly reduced in species could retain some representation in the fauna. Nevertheless the reduced **H** clades would now be at a greater risk of extinction than previously and all other things being equal would be disproportionately eliminated in time.

It has been argued previously that **H** clades, with their lower extinction resistance, should tend to become reduced relative to **L** clades during the episodic fluctuations in extinction intensities that are registered in curves of taxonomic disappearance (for separate approaches to this problem see Van Valen, 1985; Valentine, 1990). This result occurs in part because during inclement times the less extinction–resistant clades may be entirely eliminated from many adaptive subzones, re-entry to which is relatively difficult. The more extinction-resistant clades are more likely to maintain at least some representation in most subzones and despite their low speciation rates they may spread to become dominants before re-invasion by more rapid–turnover clades can occur. When adaptive space (niche number) is expanding rather than shrinking, the **H** clades will be able to colonize «empty niches» faster than the **L** clades and will accordingly dominate the accompanying diversification. However, the **L** clades will not be eliminated, and if adaptive space stabilizes they will eventually dominate. Clearly, there is a fundamental assymmetry between increase and decrease in diversity; clades may test the high side of diversity without penalty, but to test the low side –extinction– greatly lowers the ability to recoup even if the extinction is only local, and of course definitively ends clade history when general.

SUMMARY AND CONCLUSIONS

Suppressed speciation, as opposed to increased extinction, appears to be quite effective at promoting the ddifferential diversity of **L** and **H** clades, and should be able to operate without regard to the structure of adaptive zones, that is, to the presence or size of subzones, although subdivision of zones would certainly favor the **L** clades as described previosly. Assuming that the suppression of speciation does not affect **L** and **H** clades differentially, and that there are no associated changes in extinction rates that affect them differntially (that is, that affect inherent rate differences between the clades), the only method of achieving lowered speciation rates is to reduce the size adaptive space, that is, to reduce the number of adaptive opportunities available to the fauna. Such reduction places high turnover clades at a distinct macroevolutionary disadvantage, other things being equal. The factors that underlie reductions in available adaptive space are numerous, and can involve a reduction of provinces, and/or of comunity biotopes within provinces, and/or of habitats within communities, or a reduction in the ability of species to subdivide adaptive space (see Valentine, 1973 for a review). These are very different factors from those that create extinctions through increased species extinction rates, whether catastrophic or episodic.

Diversity reductions owing to suppressed speciation, if of much magnitude and rapidity, should be expresed as extinction peaks at supraspecific levels in the fossil record, and entail concomitant shifts in the composition of the faunas involved. These shifts should favor the rise of slow–turnover linages within clades and of slow–turnover clades within the faunas. These expectations appear to be met in a qualitative way by Paleozoic faunas. As diversity reductions owing to suppressed speciation involve shifts in the structure of biogeographic and ecological units, it should be possible to assess the importance of this process in biotic history as our operational resolution of the fossil record improves.

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