PATTERNS OF DIVERSITY ON THE PALEOZOIC SHELF: IMPLICATIONS FOR CONTROLS ON CLADE HISTORY

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Global diversity often is treated as a barometer of evolutionary success of clades without reference to their occurrence in ecological or biogeographical space. But global diversity is a composite of various spatial scales: alpha diversity, the number of taxa co-occurring in local communities; beta diversity, the distinction in taxonomic composition among local communities; and gamma diversity, the distinction, or degree of endemism, among geographic provinces, It has been argued by some workers that global diversity correlates strongly with alpha (and beta) diversity but by others that provinciality is the principal control of global patterns. The distinction is important, implicating either ecological processes ("adaptation") or physical geography ("contingency") as the major factor in expansion of clades.

We have examined the ecological half of this problem with a data base comprising 505 fossil assemblages sampled from Paleozoic strata of Laurentian North America. On the basis of associated sedimentary characteristics, each assemblage has been assigned to one of six environmental categories, ranging from onshore peritidal situations to offshore basinal conditions. For each taxonomic order and class, average numbers of genera in each category have been determined for each of 18 time units. These average alpha diversities have been contoured on time-environment diagrams and compared to patterns of global diversity.

Three major generalizations are derived from these diagrams: 1. Major groups tend to be environmentally conservative, maintaining their life zones of maximum and minimum alpha diversity over vast stretches of time.

- 2. Onshore-offshore shifts are most common during early expansion or late contraction of groups, when their global diversity is rapidly waxing or (more slowly) waning.
- 3. Maxima and minima in global diversity within the groups through time, with few exceptions, are reflected in alpha diversity as fluctuations within the environments of maximum richness and/or as variations in the range of environments occupied.

The last observation indicates a tight link between local ecology and global diversity, although the direction of causation is not unambiguous: alpha diversity could be reflecting only the global pool from which species can be recruited into local communities. However, in view of the onshore-offshore shifts during early and late histories of clades we conclude that local ecology is the dominant factor in controlling global diversity, and provinciality is secondary.