

SCALE, BIOFACIES STASIS, AND FAUNAL RECURRENCE: COMPARATIVE STUDIES

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Patterns in ecology are highly dependent upon the scale of observation. Historically, ecologists invoked causal mechanisms involving community organization to explain ordered patterns seen at some levels of resolution on ecological time scales. Most now use random patterns observed at larger scales to argue that communities are random associations of species that happen to share similar environmental tolerances. At the ecologically coarse scales of resolution seen in much of the fossil record we identify three different temporal scales at which such random or ordered patterns are observed. These scales are: the 10^5 year scale of periods of accelerated faunal turnover (increased immigration, extinction, and evolution), the 10^6 year scale of Ecological-Evolutionary Subunits (EESU), and the 10^7 year scale of Ecological-Evolutionary Units (EEU). The fossil record suggests that different patterns can be observed at these different temporal scales.

Studies of the Middle Devonian Hamilton-Tully EESU have traced ten distinct biofacies through five depositional sequences and about 15 small scale cycles, constituting 5-6 million years, with the following tentative results: 1) For each biofacies, the general faunal list, dominant and rare taxa, and species richness values are similar throughout. Some 60-80% of species lineages occur in samples of a particular biofacies from its lowest to highest occurrence. In particular, most rare stenotopic species (those confined to a single biofacies) recur with considerable fidelity with each cycle. 2) This similarity suggests faunal tracking, in which species assemblages migrated laterally, following shifting environments; such a pattern is confirmed in some cases by lateral tracing of a single facies within depositional sequences. 3) Most species occur in more than one biofacies, although typically with dramatically different relative abundances. Hence, the biofacies are best considered as parts of continuous faunal gradients rather than discrete biotic communities. 4) Entire gradients are relatively constant within the 5-6 my duration of the interval, and radically different from those in EESUs immediately above and below. 5) Faunal stability is not absolute. Slight differences exist in relative abundance and membership, such that recurring assemblages should not be construed as the same community, in a true biological sense, but rather as the same community type or biofacies. 6) Several ecological epiboles, in which normally rare species become abundant in one or more cycles, and their inverse, outages, occur in the Hamilton. 7) Environmental change, as evidenced by sedimentary cycles occurs during this time interval. 8) Interestingly, as documented nearly a century ago by Henry Shaler Williams, there is evidence for a longer recurrence of some parts of the biofacies at stratigraphically higher horizons following extended periods of outage. This seems to imply retention of certain biofacies characteristics even over faunal turnover events. The general pattern on this scale is of broad faunal stability in the face of a changing environment, although often faunal turnover events correlate with large scale environmental changes. Studies of molluscan evolution in Pliocene East African Rift lake deposits show similar patterns of faunal stability in a less diverse fauna (30 as opposed to 150 species) and a much narrower range of biofacies.

Conversely, faunal turnover events, both those marking the boundaries of the Hamilton-Tully EESU and in African Rift Lakes, involve relatively short (within single small scale cycles) intervals of local extinction, species evolution, and immigration where species appear to be mixing and matching in much more random patterns than within EESUs. Thus, in the fossil record we can see random movements at some time scales, but also see lasting close associations of species on longer time scales.