

Palaeocommunity persistence despite environmental disruption: Carboniferous brachiopods from the North American Mid-continent

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A key question in paleoecology and macroevolution is whether assemblages of species (palaeocommunities) represent persistent entities that can endure over millions of years. Whilst it has often been presumed that any abrupt abiotic changes discernible in the geological record will lead to cascading extinction and community turnover, it has also been proposed that palaeocommunities persist for long time periods and regardless of environmental disruption. If palaeocommunities can and do remain stable entities despite disruption, what processes allow for such a scenario remains an open question. Potential options include the degree of change in the physical environment, which possibly only rarely exceeds the threshold required for community collapse, or due to 'Ecological Locking', where directional selection is constrained by ecological processes. We investigate these issues by analysing the detailed fossil record of Carboniferous brachiopod communities from the Mid-continent of North America. These highly diverse communities were subjected to frequent and geologically rapid phases of marine transgression and regression associated with climate change over approximately a 20-million-year period, a scenario where repeated community destruction and renewal would be expected as suitable habitat was lost and then subsequently re-established. By characterizing both the nature and scope of changes in these palaeocommunities over time, we firstly identify that brachiopod palaeocommunities were not stable throughout this interval, both in terms of taxonomic composition and the associated abundance of those taxa. Thus, there is no evidence of obdurate ecological stasis, as new discrete assemblages, statistically dissimilar from previous and subsequent iterations, form following each environmental disruption. However, at a higher ecological scale, stability is manifest, with diversity patterns stable across time and despite episodes of environmental change. In particular, we identify a form of qualified ecological stasis for both the different environments present during this interval and for the larger region as a whole. The individual taxa that comprise each palaeocommunity may differ over time, but there is a consistent number of species that can exist in any given assemblage, such that palaeocommunities remain functionally similar. This indicates that, whilst the individual taxa that come to form palaeocommunities arrive via the idiosyncrasies of recruitment, the overall diversity of the communities is set by some higher-level ecological rules. Specifically, the rules for taxon packing are seemingly constant in distinct environments, likely due to physiological controls that limit how many taxa can be maintained in an environmental setting and/or perhaps because the amount of space needed for any individual to develop into an adult is invariant across different taxa within the same clade. Further, these ecological rules allow for stability even in the face of constant disequilibrium, which aligns with patterns identified in the recovery of marine invertebrate communities from disruptive events in modern systems. Based on these results, we advocate for consideration of different hierarchical entities and scales when interpreting the ecological dynamics of fossil assemblages, as focusing exclusively on changes in taxon identity/abundance or diversity levels can lead to very different results.