



## **Biotic controls on Phanerozoic biodiversity**

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Positive species interactions such as competition, predation, and niche construction are fundamental to understand diversity accumulation and potential saturation effects in local and regional communities. Differential diversity analysis can be used to gauge the impact of such biotic controls on biodiversity. In the concept known as diversity partitioning, biodiversity is dissected into three components: alpha-diversity (local species richness), beta-diversity (differential diversity between localities), and gamma-diversity (overall species richness of the observed system). We applied this approach on the scale of geological formations as representation of roughly coeval, neighbouring habitats to test for species interactions controlling biodiversity in the geological past. Occurrence-data of non-colonial benthic marine macroinvertebrates were obtained from the Palaeobiology-Database from each geological formation with at least 25 collections (340 formations in total). These formational compilations were subsampled by randomly drawing 20 collections for 500 times. Average collection species richness (alpha), composite species richness (gamma-diversity) of the 25 collections and several measures for beta-diversity were calculated for each formation. Finally, all alpha- and beta-values were plotted against gamma-diversity. Our analysis reveals a strong and consistent positive correlation between alpha and gamma-diversity throughout the Phanerozoic. This suggests that local species richness is always contributing to overall diversity. In contrast, increases in beta-diversity drive changes in gamma-diversity only at low levels of gamma. This mode is most prevalent during the early to mid-Palaeozoic. Once a certain gamma level is reached, beta-diversity is relatively high but largely indifferent across the whole range of gamma. The acquisition of exceptionally high diversity values in marine formations during the Permian and particularly the post-Jurassic is clearly driven by adding more species to local habitats rather than higher levels of specialization of marine organisms to different habitats. A probable explanation is provided by the reorganization of marine ecosystems known as the “Mesozoic Marine Revolution”. It is characterized by intensified predation, infaunalisation, and a general expansion in ecospace utilization, jointly increasing the carrying capacity of marine ecosystems. We conclude that the general increase in positive interactions during the late Mesozoic unlocked species diversity in benthic marine communities.