

## **Dynamic redox and metazoan innovation in the Ediacaran**

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Dramatic perturbations of the carbon cycle appear to create the conditions for evolutionary diversification, such that variability in near surface oceanic oxygenation can promote morphologic evolution and novelty. Modern, low oxygen regions are heterogeneous and dynamic habitats that support low diversity, opportunistic, and non-skeletal metazoans. We note that several major radiation episodes, including the Ediacaran-Cambrian, follow protracted or repeating intervals (>1 million years) of persistent and dynamic shallow marine redox. We argue that such intervals create critical opportunities for the generation of evolutionary novelty, followed by innovation, and diversification.

A regionally heterogeneous redox landscape persisted in Ediacaran oceans, with ferruginous anoxic conditions and intermittently shallow oxic waters on productive ocean margins and oxygenation, at least episodically, in deeper waters. Multiple, but transient, episodes of widespread ocean oxygenation may have developed towards the Ediacaran-Cambrian transition but is possible that the entire Cambrian radiation occurred under at least fluctuating anoxic conditions.

Consistent with our model, most developmental and morphological innovations associated with the large bilaterian bodyplans that appeared in the Cambrian originated during the interval of low O<sub>2</sub>/unstable redox during the Ediacaran. Clades that appear in the Ediacaran and Cambrian Radiation bear skeletons but can be inferred to have developed from soft-bodied ancestors, and many key developmental novelties must also have preceded the late Neoproterozoic emergence of basal metazoan clades, including a gut, heart, central nervous system as well as clade-specific novelties. Assembly of phylogenetic data shows that prolonged and widespread anoxic intervals indeed promoted morphological novelty in soft-bodied benthos, which then provides the ancestral stock for subsequently skeletonised lineages to appear as innovations once oxic conditions became widespread and stable, so in turn promoting major evolutionary diversification.