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Testing Hypotheses of Early Tetrapod Diversity and Biogeography

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The Carboniferous and early Permian were critical intervals in the diversification of early four-limbed vertebrates (tetrapods), yet the major patterns of diversity and biogeography during this time remain unresolved. Previous analyses suggest that global tetrapod diversity rose continuously across this interval and that habitat fragmentation following the 'Carboniferous Rainforest Collapse' (CRC) drove increased endemism among communities. However, this work failed to adequately account for spatial and temporal biases in sampling. We reassessed patterns of early tetrapod diversity and biogeography using innovative quantitative methods including, for the first time, spatially-explicit neutral model simulations. We first documented patterns of species richness by applying cutting-edge sampling-standardisation methods to a new global species-level dataset created within the Paleobiology Database. We then assessed global patterns of biogeographic connectedness through time by integrating our occurrence dataset with phylogenetic information and performing network analysis. Our results suggest that species richness initially increased into the late Carboniferous, then decreased substantially across the Carboniferous/Permian boundary and slowly recovered in the early Permian. Our biogeographic analysis does not support the hypothesis that the CRC drove endemism; instead, we find evidence for increased cosmopolitanism in the early Permian, suggesting that this event promoted species dispersal. These findings indicate that while the CRC did not adversely affect the global distribution of tetrapod communities, the changing environment may have played a role in reducing diversity in the earliest Permian. Estimates of sample coverage show that variation in sampling intensity strongly affects our ability to decipher genuine patterns of diversity change during this interval. To further examine this phenomenon, we are using spatially-explicit neutral model (SENM) simulations to demonstrate how empirical patterns of sampling can control observed (=raw) richness estimates. Our SENM simulations of species richness generated using plausible parameters of population density and dispersal can be sampled in the same spatially and temporally explicit manner as the real-world samples were collected. Preliminary results from simulations focusing on tetrapod communities on homogeneous landscapes (i.e. excluding habitat fragmentation or environmental change) suggest that simulated species richness is remarkably similar to the observed (=raw) richness estimates inferred from the fossil record This finding implies that uncorrected fossil data does not accurately reflect large-scale patterns of diversity through time and stresses the importance of using methods of sampling standardisation for analyses of diversity. Subsequent, more complex, simulations will focus on introducing habitat fragmentation to specifically test proposed hypotheses of early tetrapod evolution across the Carboniferous/Permian boundary. Together with our analyses of diversity and biogeography these simulations will enable us to perform the most rigorous exploration of early tetrapod diversity achieved to date.