



Early dinosaur radiation: testing macroevolutionary models through diversification rate shift analyses of an early Mesozoic amniotan supertree

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The early radiation of dinosaurs has been traditionally explained through a “competitive model”, which attributes dinosaur success to their superiority in a drawn-out process involving inter-specific competition, or a more accepted “opportunistic model”, which states that dinosaur radiation occurred in an empty ecospace cleared by two successive Late Triassic extinctions. Following the “opportunistic model”, it would be expected that dinosaurs acquired diversification shifts only after the Late Triassic extinctions. Conversely, in the “competitive model” diversification shifts would be expected during the evanescence of their competitors. With the aim to test how these models fit to current phylogenetic reconstructions, a diversification rate analysis was performed on an amniotan supertree of 690 taxa. We found that the early dinosaur phylogeny significantly departs from a stochastic branching model ($p < 0.001$) and a significant branching shift is located at the base of Dinosauria ($p < 0.05$). This result is in agreement with the high diversity of early dinosaurs observed in the Ischigualasto Formation (early Late Triassic), clearly supporting that the dinosaur radiation started before the end-Ischigualastian extinction (middle Late Triassic). Ischigualastian continental assemblages were dominated by rhynchosaurs and traversodontids, and crurotarsans were common faunistic elements, indicating that the early radiation of dinosaurs firstly took place into a crowded-ecospace. However, branching patterns are not homogenous within Dinosauria: diversification shifts for Theropoda occurred at Ischigualastian and Hettangian-Sinemurian times (Early Jurassic), but in the case of Sauropodomorpha and Ornithischia the shifts took place in the Coloradian (latest Late Triassic), immediately after the end-Ischigualastian extinction. Together with herbivorous dinosaurs another six significant/conspicuous branching shifts are also recorded among Coloradian amniotan clades (e.g., mammaliomorphs, crocodylomorphs, pterosaurs), indicating that this stage of diversification was also experienced by another amniotan lineages. Accordingly, the early radiation of dinosaurs started during the Ischigualastian in a crowded-ecospace, showing different patterns within the group later in the Triassic, within a macroevolutionary scenario that does not completely fit with none of the two traditional models.

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