

## Invited Perspective

## The non-gradual nature of adaptive radiation

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## ABSTRACT

Adaptive radiation is a major source of biodiversity. Still, many aspects of this evolutionary process remain poorly understood. Our recent integrative examination of the cichlid adaptive radiation in African Lake Tanganyika provides new insights into the process of explosive diversification. The in-depth phylogenetic comparative analysis of nearly all species occurring in that lake permitted us to trace patterns of eco-morphological evolution throughout the phylogenetic history of the radiation and revealed that it occurred in a non-gradual manner, in the form of time-shifted bursts of accelerated evolution. The temporal pattern of divergence along different axes of morphological evolution provides empirical support for a scenario that potentially unifies two popular models of adaptive radiation, the “early burst model” and the “stages model”.

The phenomenon of adaptive radiation is arguably one of the most remarkable evolutionary processes and the likely source of much of the biodiversity on Earth (Schluter, 2000; Simpson, 1953). This rapid – and nearly simultaneous – ecological diversification of a single ancestral lineage into a set of novel species has received sustained attention over the past decades, yet understanding *how* adaptive radiations unfold remains an open question (Gavrilets and Losos, 2009; Schluter, 2000).

George G. Simpson (Simpson, 1953) laid the foundation for the view that adaptive radiation is not a gradual process but characterized by an evolutionary burst, usually near its onset. This idea has subsequently been conceptualized in a popular mathematical model for adaptive radiation, known as the “early burst model” (see e.g., Gavrilets and Losos, 2009). The main driver of such an early burst is considered excess “ecological opportunity”, which opens when a new environment with unoccupied ecological niches is colonized (e.g., a newly formed island or lake); after the extinction of competitors freeing previously occupied niches; or after the evolution of a novel trait that allows a lineage to invade under- or unutilized niche space. Accordingly, evolutionary rates should initially be high in an adaptive radiation as species invade unoccupied adaptive zones. Over time, however, as niches become filled, ecological opportunity should decrease and, hence, evolutionary rates should slow down. What Simpson, in his seminal book (Simpson, 1953), also emphasized is that diversification may continue in subgroups of a radiation in “renewed bursts as new adaptive levels are reached in succession” (Simpson, 1953, p. 229). This view was in turn incorporated into the so-called “stages model” (Streelman and Danley, 2003), which predicts that adaptive radiations should proceed along different and

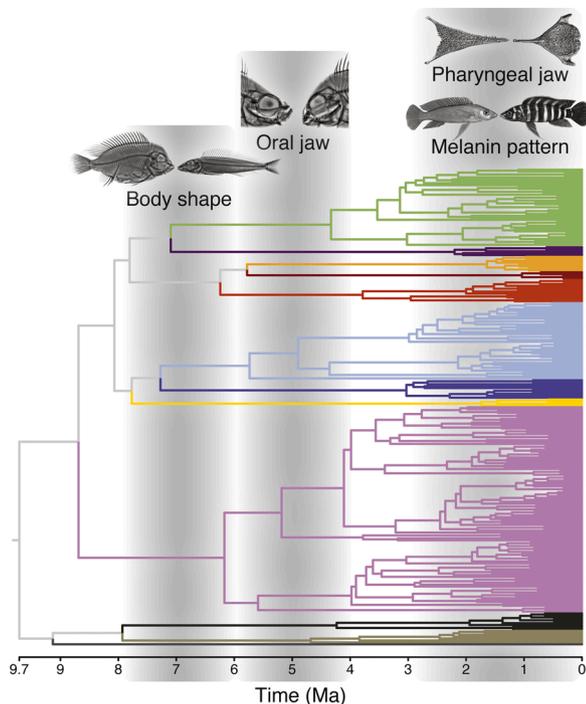
time-shifted axes of diversification: a first stage characterized by diversification along the macro-habitat axes; a second stage of trophic specialization; and a third stage involving diversification along the signaling axes, that is, with respect to traits related to communication.

The early burst and the stages models of adaptive radiation have typically been treated separately (e.g., Harmon et al., 2010; Streelman and Danley, 2003). However, in a recent study (Ronco et al., 2021), we showed that the diversification of the cichlid fishes in Lake Tanganyika – a textbook example of adaptive radiation – followed Simpson’s concept of a “stages scenario” initiated by an “early burst” (Fig. 1), potentially providing a framework that unifies two popular models of adaptive radiation.

The adaptive radiation of cichlid fishes in Lake Tanganyika comprises 12 phylogenetic sub-lineages, so called tribes, which, together contain around 250 endemic species. A new phylogenetic hypothesis based on whole-genome sequences of nearly all cichlid species occurring in this lake (Ronco et al., 2021), which was time-calibrated with a recently established timeline of cichlid evolution (Matschiner et al., 2020), reveals that this cichlid radiation commenced around 9.7 million years ago (Ma), coinciding with an early period in the formation of Lake Tanganyika. Further, molecular ecological information (stable carbon and nitrogen isotope signatures obtained from muscle tissue) and extensive phenotyping of several morphological features (body shape, oral jaw morphology, lower pharyngeal jaw shape, and melanin pigmentation pattern), allowed, for the first time, to quantify the ecological and morphological diversity of an entire massive cichlid adaptive radiation (Ronco et al., 2021). Tracing morphospace expansion

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**Fig. 1.** The adaptive radiation of cichlid fishes in African Lake Tanganyika unfolded around 9.7 million years ago (Ma) and gave rise to around 250 species grouped into 12 phylogenetic sub-lineages (i.e., tribes, represented with different colours). A comparative eco-morphological analysis across this radiation (Ronco et al., 2021) revealed that diversification was non-gradual, but proceeded in trait-specific bursts of accelerated morphological evolution: an early burst occurred for body shape, followed by rapid diversification of oral jaw morphology, and finally by divergence in the lower pharyngeal jaw apparatus and in melanin pigmentation patterns.

of these multivariate phenotypic traits through the phylogenetic history of the radiation revealed that these traits did not evolve in a gradual way, but in the form of time-shifted bursts of accelerated evolution across a multidimensional adaptive landscape. The first burst – timed 6 to 8 Ma – concerned body shape evolution, suggesting that macrohabitat divergence was the first axes of diversification in Tanganyikan cichlids. After this “early burst” in body shape, a second burst of morphological evolution occurred between 4 and 6 Ma, this time involving the oral jaw, a trait related to foraging and food uptake (Fryer and Iles, 1972). Finally, in the last two million years, overlapping signals of accelerated morphological evolution and rapid morphospace expansion are evident in two traits – the lower pharyngeal jaw bone and melanin-based pigmentation patterns. While the pigmentation pattern represents a trait putatively involved in communication (which might or might not be driven by sexual selection), the lower pharyngeal jaw bone is part of an important trophic trait complex used for food processing in cichlids, the pharyngeal jaw apparatus (Fryer and Iles, 1972; Liem, 1973).

Together, these three bursts of morphological evolution provide empirical support for an early burst scenario that, over time, transitioned into stage-like pulses of diversification. However, in contrast to the classic stages model, trophic adaptations were not restricted to only the second stage of the cichlid adaptive radiation in Lake Tanganyika. The temporal separation of morphological evolution in oral and pharyngeal jaws suggests that these two trophic structures evolved largely independently, once more emphasizing the importance of the pharyngeal jaw apparatus in cichlid evolution.

Advances in genome sequencing now allow to use large sequencing data sets to infer robust phylogenies. These will ultimately strengthen phylogenetic comparative approaches that provide exciting opportunities to examine temporal patterns of diversification across multiple – and perhaps less well-known cases of – adaptive radiation. A comparison across radiations will then permit to conclusively assess if multidimensional bursts are a general feature of adaptive radiations or if such consecutive bursts are characteristic for massive radiations such as the one of cichlid fishes in Lake Tanganyika.

### Declaration of Competing Interest

All authors declare no conflict of interest.

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