


Extending microevolutionary theory to a macroevolutionary theory of complex adaptations

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Received January 7, 2022

Accepted January 19, 2022

Over the last two decades of the 20th century, the macroevolutionary theory was transformed. Held at the outset of that period, the 1980 Chicago colloquium “Macroevolution: Pattern and Process” became notorious for its heated debates about punctuated equilibria and the adequacy of “Neo-Darwinism.” The debates were so intense that the proceedings were never published (Futuyma 2015). Punctuated equilibria may have dominated the debate but advocates of that theory were not the only workers who found Neo-Darwinism inadequate to explain macroevolution. What seemed missing, especially to morphologists, were the processes, both developmental and evolutionary, that could explain complex adaptations. Even those willing to accept, on principle, that gradual allelic substitution is a model for evolutionary change and that adaptation is due to natural selection, might still wonder whether that was enough to explain complex adaptations. What seemed missing was articulated by Gould in his promise of a new theory (1980, p. 129): “... the new theory will restore to biology a concept of organism. In an exceedingly curious and unconscious bit of irony, strict selectionism... debased what had been a mainstay of biology—the organism as an integrated entity exerting constraint over its history”. That view of organisms as integrated was indeed a mainstay of morphology; as Weidenreich (1941, p.323) put it, “It is an entirely inconceivable idea that each morphological unit should have developed independently from all others and from the body as a whole, as an isolated and incidental variation, subsequently tested as to its feasibility for the organism...”

Defending the theory, Charlesworth, Slatkin, and Lande responded that “...the concept of organism, including constraints of history, development and architecture, which Gould (1980)

This article is the introduction to the virtual issue, “Extending microevolutionary theory to a macroevolutionary theory of complex adaptations”: [https://onlinelibrary.wiley.com/doi/toc/10.1111/\(ISSN\)1558-5646.microevolutionarytheory](https://onlinelibrary.wiley.com/doi/toc/10.1111/(ISSN)1558-5646.microevolutionarytheory)

seeks to restore to evolutionary biology, has always been an integral part of the neo-Darwinian theory” (Charlesworth et al. 1982, p. 480). That appreciation of constraints was evident in their explanation for parallel trends, “Correlated evolution of a set of characters in parallel in different lineages may arise either through functional interactions between the characters (i.e., selective constraints) or through genetic and developmental constraints reflected in the pattern of genetic variation and correlations among characters” (pp. 490–491). But even if these ideas could be found in, or read into, Neo-Darwinism, the explicit, mathematical extension of the microevolutionary theory to a macroevolutionary theory of complex adaptations had just begun.

The purpose of this special issue is to highlight a selection of works published in *Evolution* that were seminal in the development of that theory, and the foundational papers in that development, leading to recent empirical studies of macroevolutionary patterns. Six papers in this issue focus on studies of variability and integration, three of which predate the formulation of a multivariate theory of phenotypic evolution (Bader and Hall 1960; Berg 1960; Gould and Garwood 1969). What is evident in all three is the idea that the (phenotypic) correlations among traits can be explained by function and/or development. Cheverud’s pioneering study (1982) similarly examined developmental and functional causes of correlations, but within a quantitative-genetic framework and a theory predicting that functionally and developmentally related characters would be co-inherited, facilitating adaptive evolution. Wagner and Altenberg’s (1996) Perspective “Complex adaptations and the evolution of evolvability” articulates the main ideas motivating current interest in modularity, that a modular organization of functionally related traits improves the ability to generate selectively useful variation, limiting the interference between the adaptation of different functions. The most recent work, concludes that a non-linear genotype-phenotype map leads to discrepancies between predicted and observed responses to selection (Milocco and

Salazar-Ciudad 2020). The selected works also represent the diversity of evolutionary biology, especially contemporary work in the field; containing work by women as first authors, from four continents.

Six papers are selected as foundational works in the extension of microevolutionary to macroevolutionary theory. The earliest (Lande 1976) begins with Simpson's concept of the adaptive landscape, and models a single trait under stabilizing selection and random genetic drift; the next, also by Lande, extends the multivariate quantitative-genetic theory to explain a well-known trend, brain: body allometry (Lande 1979). Burger (1986) introduces a corridor/ridge model for the evolution of functionally coupled traits, concluding that the structure of covariation among traits may cause populations to evolve towards a more remote optimum (presuming that extinction cannot occur). Zeng (1988) examines the long-term consequences of multivariate stabilizing and directional selection, showing that short-term responses differ qualitatively from long-term responses. Hansen and Martins (1996) approach the extension of microevolutionary theory from a different perspective, grounded in a phylogenetic approach to comparative biology (Felsenstein 1985), deriving the interspecific covariance structure from evolutionary models. The final work in this section is more empirical, advancing and testing the hypotheses that divergence will be strongly biased along the axis of greatest genetic variation (\mathbf{g}_{\max}), that the evolutionary rate would be proportional to the angle between the direction of evolution and \mathbf{g}_{\max} , and that the effect of that bias will decay over time (Schluter 1996).

Six recent empirical studies were selected to represent contemporary approaches to the evolutionary origins of morphological integration, classic topics of macroevolutionary theory, and an increase in the diversity of evolutionary biologists. Jamniczky and Hallgrímsson (2009) compare covariance structures of natural populations of rodents and laboratory-bred mice, showing that its structure is conservative in natural populations but highly variable across mutant strains of laboratory mice. Rossoni et al. (2019) analyze an adaptive radiation and the evolutionary dynamics of morphological integration. Two studies analyze evolutionary trends, one testing a hypothesis of a directional trend in recessing bivalve scallop shell shape (Sherratt et al. 2016) and the other, using time-series from the fossil record, analyzes the direction of evolutionary change relative to \mathbf{g}_{\max} (Renaud et al. 2021). Martínez-Abadías et al. (2012) analyze genetic integration to examine how it deflects the evolutionary response to selection for localized shape changes (Martínez-Abadías et al. 2012). The sixth examines evolutionary allometry and the impact of size on evolutionary rates (Friedman et al. 2019).

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Handling Editor: T. Chapman