Digest: Macroevolutionary pattern from microevolutionary processes

Laura E. Hunter[1,2]

[1]*Department of Organismal Biology and Anatomy, University of Chicago, Chicago, Illinois 60637*

[2]*E-mail: laurahunter@uchicago.edu*

How can we bridge the gap between studies concerning microevolution and those concerning macroevolution? Taverne et al. provide a framework for how to study both intraspecific and interspecific variations simultaneously through their examination of how craniomandibular skeletal and muscle shape responds to ecological pressures in *Podarcis* lizards.

The challenge of bridging the gap between microevolution and macroevolution has endured throughout the history of biology, so much so that G.G. Simpson (1944) referred to it in his seminal 1944 work *Tempo and Mode in Evolution* as an "old but still vital problem" (pp. 97). Simpson himself chose to address this old challenge by applying the genetic concept of adaptive landscapes (Wright 1932) to phenotypic data. In Simpson's description, the adaptive landscape concept imagines an n-dimensional space in which $n - 1$ dimensions correspond to phenotypic characters and the last dimension corresponds to the fitness of an organism at any coordinate location in the $n - 1$-dimension trait space (for a review, see Simpson 1944; Arnold et al. 2001). This can be most easily visualized in three dimensions, in which the x- and y-coordinates of an organism convey its character states for the traits on the x- and y-axes and the z-axis conveys the fitness at each x-y coordinate (Fig. 1A).

The adaptive landscapes concept is a powerful tool for modeling and understanding evolution due to its ability to aid in predicting macroevolutionary patterns from microevolutionary processes like selection and drift (Arnold et al. 2001). Despite this, the theoretical underpinnings of the concept have been mostly neglected entirely or applied separately to intraspecific or interspecific data, with little effort to apply them to both simultaneously. Although they do not employ the language of adaptive landscapes explicitly, Taverne et al. (2021) reveal that two species of *Podarcis* lizards inhabit similar adaptive landscapes. Their analyses of 16 populations of lizards from island and mainland sites revealed similar patterns of intraspecific and interspecific variations in head shape and jaw musculature in response to similar ecological conditions. This finding implicates the microevolutionary processes that influence intraspecific populations of *Podarcis* lizards (ecological pressures associated with diet) in dictating macroevolutionary patterns across the genus, and, by doing so, Taverne et al. (2021) provide an empirical example of how adaptive landscapes transcend the gap between microevolution and macroevolution (Arnold et al. 2001).

In their Discussion section, Taverne et al. (2021) consider the bipartite nature of evolution as both deterministic (e.g., selection) and stochastic (e.g., contingency) and address the implications and limitations of focusing their study on two species of the same genus. In particular, they focus on the hypothesis that convergence is more likely to occur among closely related organisms due to the diminished role of contingency among taxa that only recently diverged (i.e., greater shared evolutionary time limits the number of stochastic differences that can accumulate in unique lineages; Fig. 1B). This hypothesis—and, in fact, the general endeavor of understanding the simultaneous deterministic and stochastic elements of evolution—has been studied and modeled through "replay" experiments and phylogenetic comparative analyses (e.g., Hansen 1997; Blount et al. 2018). Like the adaptive landscape concept, however, these experiments are typically limited to studying these phenomena at the population level (microevolution), species level (macroevolution), or the family/order/etc. level ("mega-evolution" *sensu*

Figure 1. Example of adaptive landscape and the process of phenotypic evolution in hypsodont equid taxa (sensu Simpson 1944; Hansen, 1997). (A) Visualization of an adaptive landscape of equid taxa as a topographical map. Horizontal axis corresponds to tooth crown height, and vertical axis corresponds to mandibular ramus height. Darker colors correspond to higher levels of fitness. (B) Visualization of tooth crown height evolution across four taxa. Top: Two-dimensional graph of fitness against crown height in two adaptive landscapes, which impact the trees below. Bottom: Four taxa in the traditional phylogenetic arrangement (left), evolution of crown height among these four taxa over time in the case of a flat adaptive landscape (middle), evolution of crown height among these four taxa over time in the case of a flat adaptive landscape (below red dashed line), and after two fitness hills (as seen in A) emerge in response to changed ecological pressures (above red dashed line). Note that jitter in the lines of these lineages corresponds to stochasticity in evolution and that more closely related taxa more readily phenotypically converge.

Simpson 1944) without consideration of how these levels interact or differ.

Although Taverne et al. (2021) rightly acknowledge that two species of the same genus are a small sample inadequate for examining these questions at higher levels of biological integration, they provide a crucial middle step by bridging the first gap between microevolution and macroevolution. In addition, it is crucial to note that they do so by examining anatomical features with an incredible level of abstraction. By focusing on craniomandibular skeletal shape and muscular size, Taverne et al. (2021) have made their study replicable for any researchers studying taxa within the subphylum Vertebrata and have created for themselves and others an opportunity to study evolutionary patterns and adaptive landscapes at multiple levels of hierarchical biological integration simultaneously.

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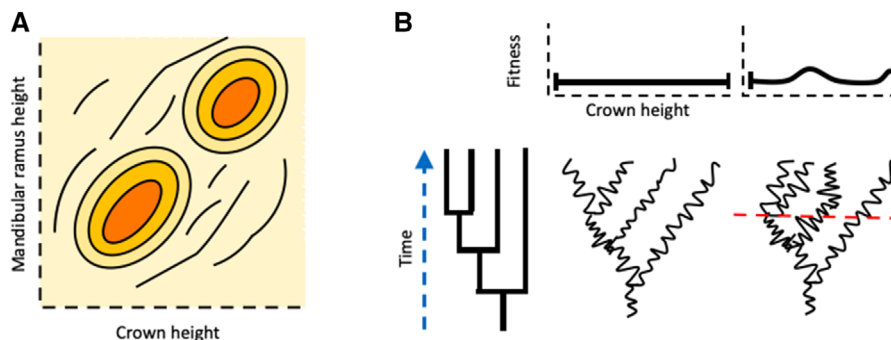
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