

## The evolutionary links between fixed and variable traits

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This paper discusses the evolutionary relations between fixed and varying traits. The first puzzle is, how did the fixed traits become fixed? In one scenario, after speciation establishes the independence of the daughter gene-pools, selection canalizes different traits in different species. In each clade, some still-variable traits coevolve with the canalized trait. This embeds the canalized trait in a network of interactions with other traits so that continued successful function depends upon that trait remaining canalized. Clade-specific constraints result because the canalized trait cannot now be changed without incurring costs too high to be paid in the fitness contributions of the other traits, and because the canalized trait is clade-specific. In another scenario, colonization of a new habitat, or evolution of a new stage in the life cycle, produces some 'temporarily neutral traits' that had been useful in the old habitat or life cycle. Those traits are then free to evolve for other purposes; some of them become incorporated in structures serving other functions than their ancestral homologues. The process is irreversible, for they cannot evolve back to their previous structures and functions without an unacceptable fitness cost. The second major puzzle is, do the fixed traits affect the further evolution of the traits that remain genetically variable, thus producing clade-specific patterns of response to selection? The impact of discontinuous growth on the expression of genetic variation in size-related traits in arthropods suggests that the answer is yes. Comparative, phylogenetic analysis of the impact of prior fixations on patterns of variation may also yield insights; potential problems are discussed.

**Key words:** canalization, phylogenetic constraint.

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