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Parallel genotypic adaptation: when evolution repeats itself

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Abstract

Until recently, parallel genotypic adaptation was considered unlikely because phenotypic differences were thought to be controlled by many genes. There is increasing evidence, however, that phenotypic variation sometimes has a simple genetic basis and that parallel adaptation at the genotypic level may be more frequent than previously believed. Here, we review evidence for parallel genotypic adaptation derived from a survey of the experimental evolution, phylogenetic, and quantitative genetic literature. The most convincing evidence of parallel genotypic adaptation comes from artificial selection experiments involving microbial populations. In some experiments, up to half of the nucleotide substitutions found in independent lineages under uniform selection are the same. Phylogenetic studies provide a means for studying parallel genotypic adaptation in non-experimental systems, but conclusive evidence may be difficult to obtain because homoplasy can arise for other reasons. Nonetheless, phylogenetic approaches have provided evidence of parallel genotypic adaptation across all taxonomic levels, not just microbes. Quantitative genetic approaches also suggest parallel genotypic evolution across both closely and distantly related taxa, but it is important to note that this approach cannot distinguish between parallel changes at homologous loci versus convergent changes at closely linked non-homologous loci. The finding that parallel genotypic adaptation appears to be frequent and occurs at all taxonomic levels has important implications for phylogenetic and evolutionary studies. With respect to phylogenetic analyses, parallel genotypic changes, if common, may result in faulty estimates of phylogenetic relationships. From an evolutionary perspective, the occurrence of parallel genotypic adaptation provides increasing support for determinism in evolution and may provide a partial explanation for how species with low levels of gene flow are held together.

Introduction

Homoplasy, or the recurrence of similarity in distinct evolutionary lineages, occurs frequently in nature. Such similarities have been documented at practically every level of biological organization, from nucleotide/amino acid sequences (Stewart, Schilling & Wilson 1987) to large scale deletions (Downie & Palmer, 1992), whole genome duplications (Soltis & Soltis, 1991), and the acquisition of complex phenotypic characters such as succulent, spiny stems in the Euphorbiaceae and Cactaceae. There is even evidence of the repeated origin of animal and plant species (Soltis & Soltis, 1991; Rundle et al., 2000; reviewed in Levin, 2001). This list includes examples of both molecular and morphological homoplasy, which are generally thought to be the result of distinct evolutionary processes. Because it is unlikely that complex phenotypes would arise repeatedly via a stochastic process, morphological homoplasy is widely regarded to be the result of selection. In contrast, nucleotide

sequences are limited in the number of ways that they can evolve, thus most instances of molecular homoplasy have been interpreted as the chance fixation of independently arising variants in diverging lineages (Doolittle, 1994; Wells, 1996).

Although morphological homoplasy is generally viewed as being driven by natural selection, many evolutionary biologists assume that the phenotypes of interest result from unique genetic changes. In some cases, they are clearly right: The evolution of spines in euphorbs and cacti results from the modification of non-homologous structures. In cases where homology is plausible, this view is perhaps best explained by the traditional acceptance of Fisher's infinitesimal model, in which quantitative traits are assumed to be controlled by an effectively infinite number of genes, each of very small effect (Fisher, 1930). Under this view, there should be numerous paths from any one phenotype to another. Thus, the likelihood that two lineages would independently accumulate changes at the same subset of underlying loci would be low. It has become increasingly clear, however, that continuous patterns of variation may sometimes be explained by the existence of a few major quantitative trait loci (QTLs) (Tanksley, 1993). Under this so-called oligogenic model of inheritance, the number of pathways from one phenotype to another is considerably more limited, increasing the likelihood that parallel phenotypic changes have a common genetic basis.

In organisms where connections between genotype and phenotype have been made, there is emerging evidence that molecular homoplasy is sometimes driven by natural selection. Unfortunately, our understanding of the genetic basis of all but the simplest traits in the simplest organisms is woefully incomplete. Thus, it is difficult to say with any certainty whether or not some of the more complex instances of morphological homoplasy have a common genetic basis. Here, we review the best examples of selection driving different lineages to the same phenotype through the fixation of independent changes at homologous loci. This pattern of evolution has several important implications. With respect to phylogeny reconstruction, it is widely recognized that homoplasy, regardless of the cause, can lead to inaccurate conclusions regarding the evolutionary history of taxa. Parallel selection responses at the genotypic level also suggest that adaptation may be a more deterministic process than previously believed, with genetic background effects and historical contingency playing a lesser role. If parallel changes prove to be common, they may provide a mechanism by which populations of a species can evolve collectively. Furthermore, such changes may increase the likelihood of the recurrent origin of taxa by allowing geographically isolated populations of the same species to independently invade a novel, unoccupied habitat.

Definitions

Historically, taxonomists have divided phenotypic homoplasy into two categories, parallelism and convergence. Parallel evolution is defined as 'the independent occurrence of similar changes in groups with a common ancestry and *because* they had a common ancestry' (Simpson, 1961, p. 103). In contrast, 'convergence is the development of similar characteristics separately in two or more lineages without a common ancestry pertinent to the similarity but involving adaptation to similar ecological status' (Simpson, 1961, pp. 78–79). As noted above, selection is believed to be the primary evolutionary force causing the recurrence in both situations.

The advent of DNA and protein sequencing necessitated a more precise definition of these terms. Molecular evolutionary biologists use parallelism and convergence in an analogous yet distinct manner. Nucleotide or protein sequence changes from the same ancestral state to the same derived state are called parallel changes, whereas changes from different ancestral states to a common derived state are considered convergent changes (Zhang & Kumar, 1997; Figure 1). Because our goal is to make an explicit connection between evolution at the phenotypic and genotypic levels, we need an operational definition that bridges the phenotypic and molecular views. Thus, we define parallel genotypic adaptation as the independent evolution of homologous loci to fulfill the same function in two or more lineages. Note that these changes need not be identical, just functionally equivalent. Under this definition, changes at non-homologous loci resulting in the same phenotype would be considered convergent (e.g., Chen Devries & Cheng, 1997), and fall outside the scope of this review.