Peer Community In
Evolutionary Biology

Genetic adaptation counters phenotypic plasticity in experimental evolution

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Huang Y, Agrawal AF (2016) Experimental Evolution of Gene Expression and Plasticity in Alternative Selective Regimes. bioRxiv, ver. 1, peer-reviewed and recommended by Peer Community in Evolutionary Biology.
https://doi.org/10.1371/journal.pgen.1006336

Submitted: 20 December 2016, Recommended: 20 December 2016

Cite this recommendation as:

Chevin, L.-M. and Bedhomme, S. (2017) Genetic adaptation counters phenotypic plasticity in experimental evolution. *Peer Community in Evolutionary Biology*, 100015. 10.24072/pci.evolbiol.100015

Published: 20 December 2016

How do phenotypic plasticity and adaptive evolution interact in a novel or changing environment? Does evolution by natural selection generally reinforce initially plastic phenotypic responses, or does it instead oppose them? And to what extent does evolution of a trait involve evolution of its plasticity? These questions have lied at the heart of research on phenotypic evolution in heterogeneous environments ever since it was realized that the environment is likely to affect the expression of many (perhaps most) characters of an individual. Importantly, this broad definition of phenotypic plasticity as change in the average phenotype of a given genotype in response to its environment of development (or expression) does not involve any statement about the adaptiveness of the plastic changes. Theory on the evolution of plasticity has devoted much effort to understanding how reaction norm should evolve under different regimes of environmental change in space and time, and depending on genetic constraints on reaction norm shapes. However on an empirically ground, the questions above have mostly been addressed for individual traits, often chosen a priori for their likeliness to exhibit adaptive plasticity, and we still lack more systematic answers. These can be provided by so-called 'phenomic' approaches, where a large number of traits are tracked without prior information on their biological or ecological function. A problem is that the number of phenotypic characters that can be measured in an organism is virtually infinite (and to some extent arbitrary), and that scaling issues makes it difficult to compare different sets of traits. Gene-expression levels offer a partial solution to this dilemma, as they can be considered as a very large number of traits (one per typed gene) that can be measured easily and uniformly (fold change in the number of reads in RNAseq). As for any traits, expression levels of different genes may be genetically correlated, to an extent that depends on their regulation mechanism: cis-regulatory sequences that only affect expression of neighboring genes are likely to cause independent gene expression, while more systematic modifiers of expression (e.g. trans-regulators such as transcription factors) may cause correlated genetic responses of the expression of many genes. Huang and Agrawal [1] have studied plasticity and evolution of gene expression level in young larvae of populations of *Drosophila melanogaster* that have evolved for about 130 generations under either a constant environment (salt or cadmium), or an environment that is heterogeneous in time or space (combining salt and cadmium). They report a wealth of results, of which we summarize the most striking here. First, among genes that (i) were initially highly plastic and (ii) evolved significant divergence in expression levels between constant environment treatments, the evolved divergence is predominantly in the opposite direction to the initial plastic response. This suggests that either plasticity was initially maladaptive, or the selective pressure changed during the evolutionary process (see below). This somewhat unexpected result strikingly mirrors that from a study published last year in Nature [2], where the same pattern was found for responses of guppies to the presence of predators. However, Huang and Agrawal [1] went beyond this study by deciphering the underlying mechanisms in several interesting ways. First, they showed that change in gene expression often occurred at genes close to SNPs with differentiated frequencies across treatments (but not at genes with differentiated SNPs in their coding sequences), suggesting that cis-regulatory sequences are involved. This is also suggested by the fact that changes in gene expression are mostly caused by the increased expression of only one allele at polymorphic loci, and is a first step towards investigating the genetic underpinnings of (co)variation in gene expression levels. Another interesting set of findings concerns evolution of plasticity in treatments with variable environments. To compare the gene-expression plasticity that evolved in these treatments to an expectation, the authors considered that the expression levels in populations maintained for a long time under constant salt or cadmium had reached an optimum. The differences between these expression levels were thus assumed to predict the level of plasticity that should evolve in a heterogeneous environment (with both cadmium and salt) under perfect environmental predictability. The authors showed that plasticity did evolve more in the expected direction in heterogeneous than in constant environments, resulting in better adapted final expression levels across environments. Taken collectively, these results provide an unprecedented set of patterns that are greatly informative on how plasticity and evolution interact in constant versus changing environments. But of course, interpretations in terms of adaptive versus maladaptive plasticity are more challenging, as the authors themselves admit. Even though environmentally determined gene expression is the basic mechanism underlying the phenotypic plasticity of most traits, it is extremely difficult to relate to more integrated phenotypes for which we can understand the selection pressures, especially in multicellular organisms. The authors have recently investigated evolutionary change of quantitative traits in these selected lines, so it might be possible to establish links between reaction norms for macroscopic traits to those for gene expression levels. Such an approach would also involve tracking gene expression throughout life, rather than only in young larvae as done here, thus putting phenotypic complexity back in the picture also for expression levels. Another difficulty is that a plastic response that was originally adaptive may be replaced by an opposite evolutionary response in the long run, without having to invoke initially maladaptive plasticity. For instance, the authors mention the possibility that a generic stress response is initially triggered by cadmium, but is eventually unnecessary and costly after evolution of genetic mechanisms for cadmium detoxification (a case of so-called genetic accommodation). In any case, this study by Huang and Agrawal [1], together with the one by Ghalambor *et al.* last year [2], reports novel and unexpected results, which are likely to stimulate researchers interested in plasticity and evolution in heterogeneous environments for the years to come.

References:

[1] Huang Y, Agrawal AF. 2016. Experimental Evolution of Gene Expression and Plasticity in Alternative Selective Regimes. PLoS Genetics 12:e1006336. doi: [10.1371/journal.pgen.1006336](https://doi.org/10.1371/journal.pgen.1006336)

[2] Ghalambor CK, Hoke KL, Ruell EW, Fischer EK, Reznick DN, Hughes KA. 2015. Non-adaptive plasticity potentiates rapid adaptive evolution of gene expression in nature. Nature 525: 372-375. doi: [10.1038/nature15256](https://doi.org/10.1038/nature15256)

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