Trends in Ecology & Evolution

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Review

Evaluating 'Plasticity-First' Evolution in Nature: Key Criteria and Empirical Approaches

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Many biologists are asking whether environmentally initiated phenotypic change (i.e., 'phenotypic plasticity') precedes, and even facilitates, evolutionary adaptation. However, this 'plasticity-first' hypothesis remains controversial, primarily because comprehensive tests from natural populations are generally lacking. We briefly describe the plasticity-first hypothesis and present much-needed key criteria to allow tests in diverse, natural systems. Furthermore, we offer a framework for how these criteria can be evaluated and discuss examples where the plasticity-first hypothesis has been investigated in natural populations. Our goal is to provide a means by which the role of plasticity in adaptive evolution can be assessed.

Trends

Phenotypic plasticity has long been proposed to precede and possibly facilitate adaptive evolution.

This 'plasticity-first hypothesis' is controversial because skeptics argue that it lacks compelling evidence from natural populations.

A chief difficulty with demonstrating plasticity-first evolution in natural populations is that, once a trait has evolved, its evolution cannot be studied *in situ*. To get around this difficulty, researchers can study extant lineages that act as ancestral-proxies to the lineage possessing the focal trait.

Using such an approach, key criteria of the plasticity-first hypothesis can be evaluated using a relatively simple experimental design.

Applying these criteria to various systems, the plasticity-first hypothesis has some empirical support. However, more studies are needed to conclusively determine the role of plasticity in adaptive evolution.

Need for a Predictive Framework

Among the enduring problems of evolutionary biology is explaining how complex, adaptive traits originate [1,2]. Although it is widely assumed that new traits arise solely from genetic factors [3], many researchers are asking whether environmentally initiated phenotypic change – in other words **phenotypic plasticity** (see Glossary) – precedes and facilitates adaptation [4–12].

This alternative route, dubbed the **plasticity-first hypothesis** [4,13], rests on the observation that phenotypic plasticity often produces developmental variants that can enhance fitness under stressful conditions [4,5,14]. If underlying genetic variation exists in the tendency or manner in which individuals produce such variants (as is often the case [15]), then selection can refine the trait from an initial, potentially suboptimal version through quantitative genetic changes over time; in other words **genetic accommodation** occurs [4]. Furthermore, depending on whether or not plasticity is favored [16], this selection can respectively promote either increased environmental sensitivity – which maintains the trait as a **polyphenism** (*sensu* [17]) or decreased environmental sensitivity – which can result in the constitutive expression of the trait; in other words **genetic assimilation** (*sensu* [18]). By 'jump-starting' phenotypic change in an adaptive direction [19], environmentally induced phenotypic change precedes, and promotes, the evolutionary origins of a complex, adaptive trait (Figure 1; Box 1).

When initiated by plasticity, refinement of a developmental variant into an adaptive trait (whether **novel** or not) does not require new genes. Instead, environmentally induced phenotypic change sets in motion an evolutionary sequence in which selection promotes adaptation by acting on existing genetic variation (e.g., [15,20–22]). In essence, such selection refines a trait through evolutionary adjustments in both the form and regulation of trait expression. The outcome of this process is an adaptive phenotype that, relative to its initial state, has been modified both in its

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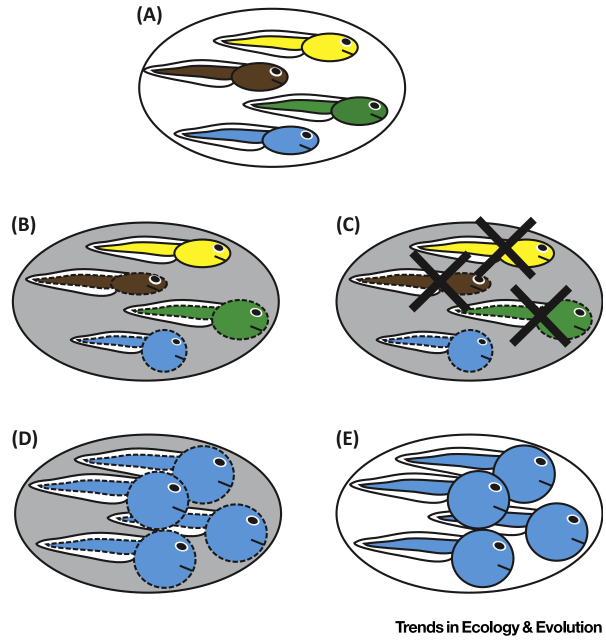

Figure 1. An Idealized Representation of How Plasticity-First Evolution Leads to a Novel, Adaptive, Complex Trait. (A) A genetically variable population (here, different-colored tadpoles represent different genotypes) (B) experiences a novel environment (shading), which immediately induces novel developmental variants (dashed lines). However, different genotypes vary in the manner in which they respond (or indeed, if they respond at all). (C) Selection acts on this formerly cryptic genetic variation (revealed by the change in environment) by disfavoring those genotypes that produce phenotypes that are poorly adapted in the new environment (here, the round-bodied phenotype is favored, whereas all others are disfavored, as indicated by the 'X'). (D) This selection also leads to the adaptive refinement of the favored phenotype (depicted here by the enlargement of the blue tadpole). If the ancestral phenotype (i.e., narrow-bodied tadpole) is still maintained in the ancestral environment (see A), then the result is a novel polyphenism. (E) However, selection might instead favor the loss of plasticity (i.e., genetic assimilation), resulting in a novel phenotype that is now produced constitutively, even when the population experiences the ancestral environment (indicated here by the loss of shading and dashed lines). Note that observations from natural systems likely will not be as clear-cut as the process described here. Furthermore, although we have shown how a plasticity-first process promotes novelty, this process could also explain the evolution of traits that are not novel (e.g., body size).

morphological and physiological attributes as well as in its environmental sensitivity. Of course, other evolutionary forces (e.g., genetic drift, mutation) could alter the degree of plasticity. However, the plasticity-first hypothesis assumes that any such change occurred via genetic accommodation, which (by definition) is driven by selection.

Although lab studies have demonstrated that the plasticity-first hypothesis can promote adaptation (e.g., [18,23–25]), and there are suggestive field studies (e.g., [26–30], reviewed in [31]), whether plasticity, followed by genetic accommodation, has actually contributed to the evolution of any complex trait in any natural population is controversial [32–35]. Part of the difficulty is that the key criteria of the plasticity-first hypothesis have not been made clear. However, if as stated in two recent prominent reviews: 'what remains to be done is to generate creative approaches to collecting empirical data from natural populations to test predictions. . .' [11], and if 'the best way to elevate the prominence of genuinely interesting phenomena such as phenotypic plasticity... is to strengthen the evidence for their importance' [35], then these criteria and predictions must be made clear and rigorously tested.

We describe here key criteria for testing the plasticity-first hypothesis. We also present a general framework in which these criteria could be evaluated in natural populations, and we discuss case

Glossary

Cryptic genetic variation: genetic variation that normally has little or no effect on phenotypic variation except under atypical conditions.

Genetic accommodation: a mechanism of evolution wherein a phenotype, generated by either a mutation or environmental change, is refined into an adaptive phenotype through selection driving quantitative genetic changes. Accommodation can also promote either increased or decreased environmental sensitivity of the focal phenotype; when environmentally induced phenotypes lose environmental sensitivity, they undergo 'genetic assimilation'.

Genetic assimilation: an extreme form of 'genetic accommodation' that occurs when selection causes environmentally induced (i.e., plastic) phenotypes to lose their environmental sensitivity over evolutionary time.

Novel trait: broadly, any major developmental innovation; sometimes defined as a body part that is neither homologous to any body part in the ancestral lineage nor serially homologous to any other body part of the same organism; a difficult concept to define.

Phenotypic accommodation: the maintenance of a novel, induced trait or phenotype that is an automatic consequence of multidimensional adaptive physiological, morphological, and/or behavioral plasticity in the face of a developmental change.

Phenotypic plasticity: the ability of an organism to alter its behavior, morphology, and/or physiology in response to changes in environmental conditions; sometimes used synonymously with developmental plasticity.

Plasticity-first hypothesis: a mechanism of adaptive evolution in which environmental perturbation leads, via phenotypic plasticity, to developmental reorganization (via, e.g., altered gene expression) and uncovers 'cryptic genetic variation' for, and ultimately production of, a novel developmental variant (i.e., trait) that immediately undergoes 'phenotypic accommodation' and is subsequently refined through 'genetic accommodation' some definitions include cases in which mutation initiates trait origin (not discussed here; see Box 1).