The evolution of adaptive phenotypic plasticity stabilizes populations against environmental fluctuations

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Introduction

Environmental fluctuations are ubiquitous in nature. Populations have evolved a wide range of strategies to cope with environmental change, including periodic migration (Winger et al., 2019), bet-hedging (Beaumont et al., 2009), adaptive tracking (Barrett and Schluter, 2008), and phenotypic plasticity (Ghalambor et al., 2007). The particular mechanisms that evolve in response to environmental fluctuations profoundly influence subsequent evolution.

Here, we summarize our recently published study using digital evolution experiments to investigate the evolutionary consequences of adaptive phenotypic plasticity (Lalejini et al., 2021). Phenotypic plasticity is the capacity for a single genotype to produce alternate phenotypes depending on environmental conditions (West-Eberhard, 2003). Such plasticity is controlled by genes whose expression is coupled to one or more environmental signals, which may be either biotic or abiotic.

Phenotypic plasticity's effect on evolutionary change has long interested evolutionary biologists because of its role in generating phenotypic variance (Gibert et al., 2019). However, the effects of plasticity on adaptive evolution have been disputed, as few studies have been able to observe both the *de novo* evolution of plasticity and subsequent evolutionary change in natural populations (Ghalambor et al., 2007; Wund, 2012; Forsman, 2015; Ghalambor et al., 2015; Hendry, 2016). Adaptive plasticity has been predicted to both promote and constrain evolutionary change depending on the genetic and environmental contexts (*e.g.*, Lalejini et al. 2021, Figure 1).

In (Lalejini et al., 2021), we used populations of self-replicating computer programs ("digital organisms") to investigate the evolutionary consequences of adaptive plasticity in a cyclically changing environment. We examined the evolutionary histories of both adaptively plastic and non-plastic populations of digital organisms in order to ask: (1) Does adaptive plasticity promote or constrain evolutionary change? (2) Are plastic populations better able to evolve and then maintain novel traits? And, (3) how does adaptive plasticity affect the potential for maladaptive alleles to accumulate in evolving genomes? Note that this study does not focus on *how* phenotypic plasticity evolves initially (see Clune et al., 2007; Lalejini and Ofria, 2016), but instead, we focus on how plasticity influences subsequent evolutionary dynamics after it evolves.

Experimental results

We conducted three evolution experiments using the Avida Digital Evolution Platform (Ofria et al., 2009) in order to examine the effects of adaptive plasticity on subsequent genomic and phenotypic change, the capacity to evolve and then maintain novel traits, and the accumulation of deleterious alleles. We divided each experiment into two phases. In the first phase, we preconditioned sets of founder organisms with differing plastic or non-plastic adaptations, and in phase two, we examined the subsequent evolution of populations founded with organisms from phase one (Lalejini et al., 2021, Figure 2). For each experiment, we compared the evolutionary outcomes of populations evolved under three treatments: (1) a PLASTIC treatment where the environment fluctuates, and digital organisms can sense the current environmental state; (2) a NON-PLASTIC treatment where the environment fluctuates, but organisms can not sense the current environment; and (3) a STATIC control where organisms evolve in a constant environment. See (Lalejini et al., 2021, Section 2) for complete methods.

Adaptive plasticity slows evolutionary change in fluctuating environments

In our first experiment, we tested whether the evolution of adaptive plasticity constrained or promoted subsequent evolution, comparing the number of selective sweeps as well as the frequency of both genotypic and phenotypic changes along lineages evolved under each treatment. We found strong evidence that adaptive plasticity slows evolutionary change in fluctuating environments (Lalejini et al., 2021, Figures 3, 4). PLASTIC populations where adaptive plasticity evolved underwent fewer total selective sweeps and fewer total genetic and phenotypic changes relative to NON-PLASTIC populations evolving under identical environmental conditions. NON-PLASTIC populations relied on *de novo* mutations to adapt to each environmental fluctuation, which repeatedly drive the fixation of mutations that align an organism's phenotype to the new conditions. PLASTIC populations, however, could use sensing mechanisms to dynamically align their phenotype with the environment.

Adaptive plasticity improves novel function retention in fluctuating environments

While adaptive plasticity constrains the rate of evolution in fluctuating environments, it is unclear how this dynamic influences the evolution of novel functions. Based on relative rates of evolutionary change, we might expect NON-PLASTIC populations to be able to evolve more novel functions than PLASTIC or STATIC populations. But how much of the evolutionary change in NON-PLASTIC populations is useful for exploring novel regions of the fitness landscape versus continuously revisiting the same regions?

In our second experiment, we compared the capacity for novel functions to evolve during phase two of each treatment (Figure 1). We found that organisms evolved under PLASTIC and STATIC conditions performed a greater number of novel functions than those evolved under the NON-PLASTIC treatment. This result, however, was not due to PLASTIC and STATIC populations *discovering* more novel functions. Instead, the evolutionary stability of PLASTIC and STATIC populations allowed for better retention of any evolved novel functions. Indeed, lineages evolved under NON-PLASTIC conditions exhibited a substantially greater number of loss-of-novel-function mutations than lineages evolved under PLASTIC or STATIC conditions.

Lineages with plasticity express fewer deleterious functions in fluctuating environments

Plasticity allows for genetic variation to accumulate in unexpressed genomic regions, which can lead to the fixation of deleterious alleles in PLASTIC populations. However, in our previous experiment, we observed higher rates of novel function loss in NON-PLASTIC lineages, indicating that they may be more susceptible to deleterious mutations. In our third experiment, we investigated whether the evolution of adaptive plasticity can increase the incidence of deleterious function performance. We found that the lineages of organisms evolved under the NON-PLASTIC treatment exhibited both greater totals and higher rates of deleterious function acquisition than that of PLASTIC lineages (Lalejini et al., 2021, Figure 8).

Conclusion

In general, we found that the evolution of adaptive phenotypic plasticity shifted evolutionary dynamics to be more similar to that of populations evolving in a static environment than to non-plastic populations evolving in an identical fluctuating environment. Our work lays the groundwork

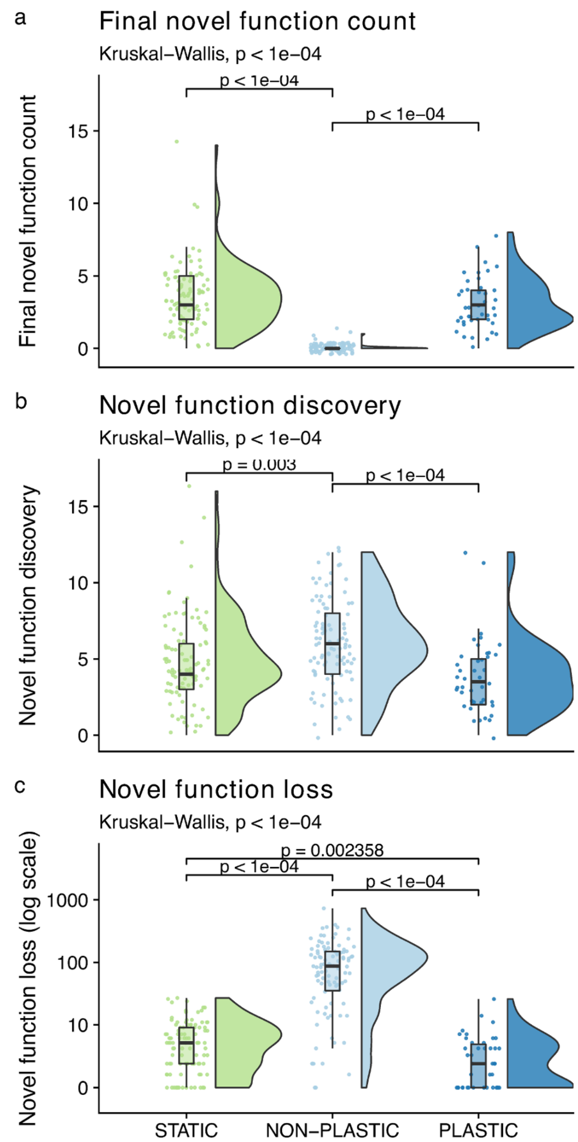

Figure 1: **Novel function evolution.** Raincloud plots of (a) final novel function count, (b) novel function discovery, and (c) novel function loss. See (Lalejini et al., 2021, Table 1) for further descriptions of each metric. Each plot is annotated with statistically significant comparisons (Bonferroni-corrected pairwise Wilcoxon rank-sum tests). Figure adapted from (Lalejini et al., 2021).

for how digital evolution experiments can be used to study the evolutionary consequences of phenotypic plasticity in a range of contexts. Future work will build on these experiments, investigating the evolutionary consequences of maladaptive and non-adaptive plasticity as well as expanding the types of environmental change studied.

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