

A continuum of selection on life-history traits under differential environmental heterogeneity. A commentary on ‘Chasing the fitness optimum: temporal variation in genetic and environmental expression of life-history traits for a perennial plant’

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Under rapid environmental change, both genetic and plastic changes are critical to reaching the ‘optimum’ phenotype where fitness is maximized (Merilä and Hendry, 2014). Unfortunately, we often have limited knowledge of what constitutes an optimal trait value in a given environment (Gauzere *et al.*, 2020), which requires parameterizing how whole fitness landscapes change with the environment (Chevin *et al.*, 2015). Individuals can move along these fitness landscapes via both phenotypic plasticity and adaptive evolution, but little is understood about how evolutionary and plastic responses might interact as populations respond to climate change (Kelly, 2019).

Fitness is determined by the similarity between an individual’s realized phenotype and the environmentally determined optimum phenotype (Eriksson *et al.*, 2023). Limited variation in either heritable effects or plastic responses can constrain this (mis)match between realized and optimal phenotypes, but the relative amount of phenotypic variation attributable to heritable vs. plastic components differs with traits, time and environment (Price and Schluter, 1991). Life-history theory presents an excellent example of this – some level of heritability is needed to initiate life-history events, but the same degree of heritability may not be necessary as phenological schedules progress (Fig. 1). Moreover, some amount of phenotypic plasticity may be required to achieve maximum fitness in the inherently variable environments an organism will experience over the course of its life cycle.

In this issue of *Annals of Botany*, Kulbaba and colleagues assess how trait heritability and plasticity vary across both environments and time. More specifically, quantitative genetic theory suggests stronger genetic control in environments with predictable cues (Scheiner, 2013; Fig. 1) and earlier in ontogeny, whereas plasticity might be important in unpredictable environments and later in ontogeny. To test this theory, Kulbaba *et al.* utilized the differences in environmental variability experienced over the life cycle by *Geum triflorum* from both alvar (limestone floodplains that exhibit predictable annual flooding) and prairie (native grasslands that exhibit variability in annual water availability) populations. Using a common garden experiment sourced with ecotypic variants from the predictable–heterogeneous alvar populations and the unpredictable–heterogeneous prairie environments, they investigated the relative genetic vs. environmental contributions to various life-history stages in this perennial plant. They then parameterized fitness landscapes using aster models, which allowed them to assess the magnitude of selection (i.e. steepness of the landscape) and how mismatched populations were from the optimum.

As predicted, heritability of earlier phenological events (emergence) was higher than later phenological events (seed mass). This genetic basis could provide a consistent starting point for life-history events. Heritability declined with later life-history events, with the timing of flowering potentially representing an intermediate point with somewhat equal heritable and plastic drivers. The authors suggest a continuum of the relative effects of heritable vs. environmental variance on life-history variation, with flowering time representing a mid-point where plasticity begins to overcome heritable variation. Not only did heritability decrease with successive life-history events, it also decreased over successive years. This is promising for long-lived perennials, as plants far from the fitness optimum can traverse the fitness landscape to be closer to the optimum as they age. This novel result highlights potential avenues of research on inter- vs. intra-annual variation in heritable vs. environmental effects on phenotypes, especially for perennials that live for hundreds of years. Could

increased plasticity as they age allow them to survive the climate change that they experience within a single generation? Could early life-history events decrease in heritability as plants age?

Plants from the more predictable habitat (alvars experiencing annual seasonal variation in water availability) demonstrated higher heritability in life-history traits (especially for emergence) than plants from the unpredictable prairie habitat. While this confirmed the authors’ hypotheses, the greater fitness associated with predictable populations was surprising. Even with less plasticity for shifting realized phenotypes towards the optimum, and despite not being in their ‘home’ habitat, alvar (rather than prairie) populations were closer to the fitness optima predicted for the prairie common garden. This was potentially due to higher water-use efficiency in drought-stressed alvar environments and release from water limitation, such that greater water availability in the prairie common garden increased fitness. This finding suggests that historical levels of environmental predictability could influence local adaptation. However, seedlings were watered regularly throughout this experiment, potentially allowing the alvar populations, which have historically experienced predictable flooding–desiccation cycles, to more easily track a fitness optimum under a consistent watering regime. In contrast, the prairie populations might utilize a bet-hedging strategy to cope with environmental variability (Gremer and Venable, 2014). A future experiment might expose these less- vs. more-heterogeneous populations to consistent vs. stochastic watering regimes. In this case, we might expect alvar populations to experience some fitness penalty for committing to rapid growth as soon as possible, whereas prairie populations might demonstrate reduced fitness in a given year but less variation in fitness over time. Testing the fitness benefits of bet-hedging would also require monitoring life-history traits over multiple seasons to assess whether sacrificing average annual fitness maximizes long-term stochastic population growth rates.

Typically, when genotypes are moved from their home range to a novel environment, a fitness decrease would signal local adaptation (Hereford, 2009).

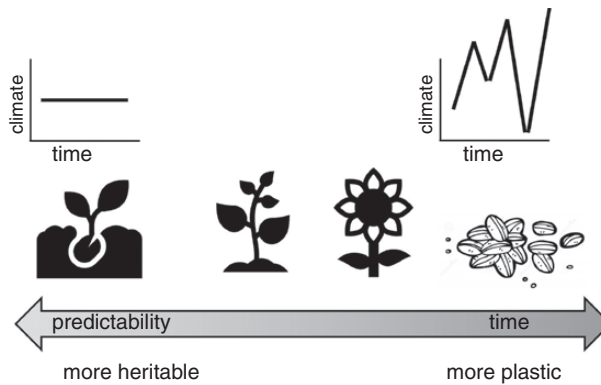


FIG. 1. Quantitative genetic theory predicts that the relative contributions of heritability vs. plasticity will vary spatially and temporally. Specifically, plasticity should be favoured in more unpredictable environments and later in ontogeny (e.g. seed mass) to let individuals adjust phenotypes to environmental variation. In more predictable environments and earlier in ontogeny (e.g. emergence), stronger genetic controls (higher heritability) might dominate. In this issue of *Annals of Botany*, Kulbaba *et al.* present this pattern as a continuum where flowering time might represent an intermediate point at which plasticity is more important than heritability.

Instead, the movement of alvar genotypes to the prairie environment increased fitness. In contrast, maladaptation (here defined as distance from the fitness optimum) was greater for the prairie genotypes. This suggests that reduced heritability under less predictable seasonal cues could limit the ability of a perennial species to traverse the fitness landscape, although, as noted above, more data on the long-term costs of reducing annual fitness in favour of minimizing long-term variation in fitness is needed. This raises interesting questions about the heritability of plasticity itself. If natural selection favours more plastic individuals (i.e. if steeper individual reaction norms correlate with higher fitness; Arnold *et al.*, 2019), where does this phenomenon fall on a continuum of heritable to plastic phenotypic variation? Understanding the nature of heritability vs. plasticity is a challenging and open research area, and the ability of a species to use both strategies to optimize fitness will be crucial to population persistence under global change.

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