Developmental Biology 419 (2016) 175–183

Contents lists available at ScienceDirect

Developmental Biology

journal homepage: www.elsevier.com/locate/developmentalbiology

Review article

Accessibility, constraint, and repetition in adaptive floral evolution

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ARTICLE INFO

Article history:
Received 29 January 2016
Received in revised form
29 April 2016
Accepted 2 May 2016
Available online 3 May 2016

Keywords:
Developmental constraint
Bias
Pleiotropy
Floral morphology
Repeated evolution
Gene duplication

ABSTRACT

Adaptive phenotypic evolution is shaped by natural selection on multiple organismal traits as well as by genetic correlations among traits. Genetic correlations can arise through pleiotropy and can bias the production of phenotypic variation to certain combinations of traits. This phenomenon is referred to as developmental bias or constraint. Developmental bias may accelerate or constrain phenotypic evolution, depending on whether selection acts parallel or in opposition to genetic correlations among traits. We discuss examples from floral evolution where genetic correlations among floral traits contribute to rapid, coordinated evolution in multiple floral organ phenotypes and suggest future research directions that will explore the relationship between the genetic basis of adaptation and the pre-existing structure of genetic correlations. On the other hand, natural selection may act perpendicular to a strong genetic correlation, for example when two traits are encoded by a subset of the same genes and natural selection favors change in one trait and stability in the second trait. In such cases, adaptation is constrained by the availability of genetic variation that can influence the focal trait with minimal pleiotropic effects. Examples from plant diversification suggest that the origin of certain adaptations depends on the prior evolution of a gene copy with reduced pleiotropic effects, generated through the process of gene duplication followed by subfunctionalization or neofunctionalization. A history of gene duplication in some developmental pathways appears to have allowed particular flowering plant linages to have repeatedly evolved adaptations that might otherwise have been developmentally constrained.

1. Introduction

Organisms are complex systems of developmentally and functionally related traits (characters), and natural selection acts on more than one trait at a time. For example, selection may favor evolutionary change in one or more traits, while at the same time favor stability in others. The response to selection on multiple traits will depend on the structure of underlying genetic and developmental pathways, which can limit the production of variation in certain phenotypic directions compared to others. This phenomenon is generally known as developmental bias, developmental constraint, or developmental drive (Maynard Smith et al., 1985; Arnold, 1992; Arthur, 2001) and is predicted to shape evolutionary trajectories of complex phenotypes (Wagner and Altenberg, 1996).

Flowers, in particular, are complexes of multiple morphological and physiological traits. While floral evolution has produced a spectacularly diverse array of phenotypes, individual floral traits are functionally and developmentally interrelated. Therefore, flowers are an attractive system in which to investigate evolutionary change in complex phenotypes, the interaction between natural selection and developmental bias, and the emergence of repeated patterns in evolution.

2. Developmental bias and pleiotropy in phenotypic evolution

The concept of developmental bias represents an important link between the fields of developmental biology, quantitative genetics, and the evolution of development (Maynard Smith et al., 1985; Futuyma, 2010; Losos, 2011). This is because a population's response to selection will be influenced by the structure of genetic correlations among the phenotypic traits under selection (Lande and Arnold, 1983). Genetic correlations are correlated patterns of variation among phenotypic traits across individuals in a population. If two or more traits are uncorrelated, traits can independently respond to selective pressures. However, if traits are correlated, selection acting on one trait can produce a corresponding effect on a second trait. An important source of genetic correlation is pleiotropy, where mutational variation in individual genes affects multiple traits, thereby generating the observed phenotypic correlation.

As an example, consider a developmental pathway that influences two traits. Mutations to this pathway that increase the

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http://dx.doi.org/10.1016/j.ydbio.2016.05.003

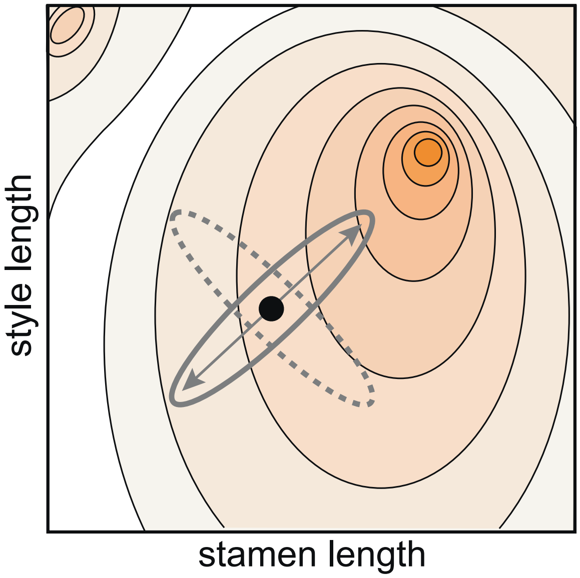

Fig. 1. The effect of trait correlation on accessibility of adaptive phenotypes. The background depicts the contours of a fitness landscape that displays fitness (Z axis, represented using contour lines) associated with different combinations of stamen filament length (X axis) and style length (Y axis). The adaptive peak is denoted by the darkest orange point. The black dot represents the current population mean for stamen filament and style lengths. If the two traits are correlated in a direction parallel to the direction of natural selection (solid ellipse) then evolution towards the fitness peak is more easily accessible than a situation in which the two traits are correlated perpendicular to the direction of natural selection (dotted ellipse).

magnitude of one trait also increase the magnitude of the second trait. The two traits will display a positive genetic correlation across individuals in a population due to pleiotropy. The evolutionary consequences of this genetic correlation will depend on how natural selection acts on these two traits. If natural selection happens to favor phenotypic change in both traits that is parallel to the genetic correlation (i.e., selection favors increased magnitude in both traits or a decrease in both traits), adaptive evolution towards the fitness optimum will be relatively rapid compared to when selection favors a phenotypic change in these traits that is perpendicular to the pattern of genetic correlation (Fig. 1; Lande and Arnold, 1983; Maynard Smith, et al., 1985; Schluter, 1996; Conner, 2012). In other words, depending on the alignment between natural selection and genetic correlations among traits, certain novel phenotypes may be more accessible (selected phenotype is more quickly attained by a population) than others.

Some genes participate in the development of multiple essential organismal phenotypes. When selection favors adaptive change in one trait but exerts strong stabilizing selection on other traits, selection acts perpendicular to a genetic correlation. Adaptation in these cases can be constrained by the availability of trait-specific mutations – those that can generate the favored change in one aspect of phenotype with minimal pleiotropic effects (Futuyma, 2010). The opportunity for such trait-specific mutations can arise through processes of genome evolution. One example is gene duplication followed by the evolution of a narrowed expression domain in one or more gene copies. This process can generate a gene paralog with reduced developmental scope and subsequent mutations to this paralog may enable adaptive evolution of the focal trait with minimal pleiotropic effects (Carroll, 2005).

Other mechanisms besides pleiotropy can generate and maintain genetic correlations between traits within a population. For example, genetic correlation can result from tight genetic linkage between loci that affect different traits. In this case, genetic variation at each of the trait-specific loci produces corresponding phenotypic variation. A genetic correlation between the traits is generated because recombination events between the tightly linked loci are rare. Alternatively, strong selection for certain combinations of traits (correlational selection) can generate linkage disequilibrium between unlinked loci affecting different traits, yielding genetic correlations among traits (Lynch and Walsh, 1998). Genetic correlations between unlinked loci are unlikely to contribute to developmental bias since they are the result of selection and can be altered by a change in the direction of natural selection (Sinervo and Svensson, 2002). Yet consistent correlational selection over long periods of time may alter the genetic and developmental architecture underlying traits – favoring developmental integration of functionally related traits that experience correlational selection, and parcellation of functionally unrelated traits into separate developmental modules (Wagner and Altenberg, 1996).

Here we discuss how the evolution of certain novel phenotypes may be accessible or may be constrained due to developmental bias, using examples from floral evolution.

3. Genetic correlations among floral traits that may facilitate adaptation

A flower is a complex set of organs that facilitate reproduction through pollen movement by abiotic and biotic factors. Animal-pollinated flowers additionally have adaptations that attract and reward pollinators. Floral traits are functionally integrated in order to ensure successful pollination and reproduction; therefore floral adaptation requires coordinated change in multiple morphological and physiological traits. Despite this required complexity for adaptive floral evolution, closely related species often exhibit strikingly divergent floral phenotypes (Stebbins, 1970, 1974). This observation generates a paradox – how does coordinated phenotypic change in multiple traits happen on a short evolutionary timescale? This paradox may be resolved in part by the occurrence of developmental biases that facilitate correlated change in floral morphological traits.

Genetic correlations among floral traits are pervasive (Ashman and Majetic, 2006) and a material source of genetic correlations among floral traits is pleiotropy (Conner, 2002; Smith, 2016). Pleiotropy among floral traits derives in part from the developmental homology of different floral organs. The flower is comprised of serially homologous organs: sepals, petals, stamens, and carpels, which share developmental control (Bowman et al., 1991). Genetic correlations also may be generated between floral organs by tight linkage or by consistent correlational selection, for example by pollinators (Conner et al., 2009).

Two examples of evolutionary change in floral phenotype that have occurred frequently during angiosperm evolution are shifts from flowers adapted for outcrossing to flowers adapted to self fertilization (a selfing syndrome), and adaptation to a novel pollinator. Both types of evolutionary change occur on a short evolutionary timescale, with closely related species (e.g., outcrossing versus selfing, or bee-pollinated versus hummingbird-pollinated) differing in multiple floral traits (Stebbins, 1970, 1974).

3.1. Evolution of selfing syndromes

Transition in mating system from predominantly outcrossing to highly selfing is considered to be one of the most common evolutionary transitions in flowering plants (Stebbins, 1974). Shifts to selfing can be selectively favored for reproductive assurance when potential mates or pollinators are scarce, for example in marginal habitats. If a self-incompatibility mechanism exists in the outcrossing species, the evolution of selfing requires the disintegration of this system. Shifts to selfing also frequently involve the