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Evolution in heterogeneous environments and the potential of maintenance of genetic variation in traits of adaptive significance

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Abstract

The maintenance of genetic variation in traits of adaptive significance has been a major dilemma of evolutionary biology. Considering the pattern of increased genetic variation associated with environmental clines and heterogeneous environments, selection in heterogeneous environments has been proposed to facilitate the maintenance of genetic variation. Some models examining whether genetic variation can be maintained, in heterogeneous environments are reviewed. Genetic mechanisms that constrain evolution in quantitative genetic traits indicate that genetic variation can be maintained but when is not clear. Furthermore, no comprehensive models have been developed, likely due to the genetic and environmental complexity of this issue. Therefore, I have suggested two empirical approaches to provide insight for future theoretical and empirical research. Traditional path analysis has been a very powerful approach for understanding phenotypic selection. However, it requires substantial information on the biology of the study system to construct a causal model and alternatives. Exploratory path analysis is a data driven approach that uses the statistical relationships in the data to construct a set of models. For example, it can be used for understanding phenotypic selection in different environments, where there is no prior information to develop path models in the different environments. Data from *Brassica rapa* grown in different nutrients indicated that selection changed in the different environments. Experimental evolutionary studies will provide direct tests as to when genetic variation is maintained.

Introduction

Ultimately, the extent of genetic variation in traits influencing fitness of an organism will determine the rate of evolution in these traits and the rate of fitness increase for the species (Falconer & Mackay, 1996). This is commonly referred to as Fisher's fundamental theorem, where 'the rate of increase in fitness of any organism at any time is equal to its genetic variance in fitness at that time' (Fisher, 1999). This statement underscores the importance of genetic variation in traits of adaptive significance since a lack of variation will limit their response to selection. The loss of genetic variation due to selection would be balanced by new genetic variation via mutations. Traits closely associated with fitness due to the greater intensity of selection are expected to exhibit a lower level of genetic variation than traits less associated with fitness (Mousseau & Roff, 1987).

However, genetic variation in traits associated with adaptations and fitness in wild populations has usually been found to be greater than expected considering the estimates of spontaneous mutation rates (Mousseau & Roff, 1987; Bulmer, 1989). Given the observed levels of genetic diversity of species

that occur across ecological clines, for example, selection in heterogeneous environments has been one of the mechanisms proposed to maintain genetic variation. Both population and quantitative genetic models have examined the potential of selection in heterogeneous and variable environments to maintain genetic variation, with mixed conclusions (i.e., Levene, 1953, Maynard Smith & Hoekstra, 1980; Gillespie & Turelli, 1989; Prout & Savolainen, 1996; Sasaki & de Jong, 1999). Furthermore, studies have examined the expression of genetic variation given contrasting selection histories in natural environments such as clines to determine if there is support for the models (i.e., Harris & Jones, 1995; Li et al., 1998). More recently, a few studies have taken an experimental evolution approach, where environmental variation is the source of selection (i.e., Mackay, 1981, Rose et al., 1996, Bell, 1997a, Elena & Lenski, 1997). Some of the studies experimentally address the genetic mechanisms and selection dynamics underlying maintenance or loss of genetic variation.

Here I will review some of the theory as to the potential that environmental heterogeneity maintains genetic variation, as well as mechanisms. I will discuss some of the empirical evidence and illustrate an approach for examining phenotypic selection in different environmental conditions. I will conclude by reviewing the particular insights from an experimental evolutionary approach and future directions for addressing the potential role of heterogeneous environments for maintenance of genetic variation.

The dilemma of the maintenance of genetic variation in adaptive traits

Under directional selection, as may be expected of many adaptive traits, selection is expected to eliminate genetic variation (Bulmer, 1985, 1989; Falconer & Mackay, 1996). Assuming no migration (of contrasting genotypes) and no differential selection due to a variable environment, new mutations will be the main source and the ultimate source of new genetic variation. Selection acts to decrease genetic variation (permanent effect) and also to increase linkage disequilibrium (transient effect-as long as selection is occurring). Linkage disequilibrium among alleles that are not favorable can also increase the loss of genetic variation through selection. Considering the transitory nature of linkage, its dynamics can be ignored in examination of the balance between selection and mutation for genetic variation (Bulmer, 1989).

Balance between selection and mutation to produce heritability of 0.5 for a trait would require very weak selection, a very high rate of mutation per locus, or a very large number of loci affecting the trait, which are unlikely given current estimates of mutation rates (Bulmer, 1989). In addition, the models require that the existing variance be attributed to rare alleles, which does not follow empirical data from selection experiments and allozyme variation. Therefore, it has generally been concluded that the dynamics between mutation and selection cannot explain the observed genetic variation in natural populations (Bulmer, 1989). In general, models disagree if the dynamics between mutation and selection can account for the extent of genetic variation (Roff, 1997). Hence, the maintenance of quantitative genetic variation in traits under selection is still considered to be a major dilemma and an important question in evolutionary biology (Hedrick, 1986; Bulmer, 1989; Curtsinger et al., 1994; Prout & Savolainen, 1996; Roff, 1997).

Adaptive traits, in addition to having substantial genetic variation, are highly variable in their level of genetic variation (Mousseau & Roff, 1987; Houle, 1992). Spontaneous mutations in reproductive traits in *Arabidopsis thaliana* were found to have bidirectional effects (i.e., increases and decreases in seed and fruit production) which would be supportive of a diversity of mutational effects (Shaw et al., 2000). Under laboratory conditions, *Daphnia pulex* was found to accumulate mildly deleterious mutations, which if reoccurring could explain much of the standing variation in life-history traits (Lynch et al., 1998). It was further suggested that these mutations contributing to variation are likely conditionally deleterious, such that their effect on fitness traits depends on the rest of the genes and/or environment of the individual (Lynch et al., 1998). These results and conclusions suggest a role for heterogeneous environments. Traits that are consequences of complex genetic correlations and those expressed later in the life cycle are predicted to have higher mutational variances as found in these studies (Houle, 1998). While the relative importance of environmental heterogeneity is not addressed in these studies (although it is discussed in Lynch et al., 1998), the finding of mutations whose effects are conditionally dependent is consistent with