

Back to the future: genetic correlations, adaptation and speciation

Sara Via^{1,2} & David J. Hawthorne²

¹*Department of Biology, University of Maryland, College Park, MD 20742, USA (Phone: 301-405-8941; Fax: 301-314-9358; E-mail: svia@umd.edu);* ²*Department of entomology, University of Maryland, College Park, MD 20742, USA*

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Abstract

Genetic correlations can affect the course of phenotypic evolution. Although genetic correlations among traits are a common feature of quantitative genetic analyses, they have played a very minor role in recent linkage-map based analyses of the genetic architecture of quantitative traits. Here, we use our work on host-associated races in pea aphids to illustrate how quantitative trait locus (QTL) mapping can be used to test specific hypotheses about how genetic correlations may facilitate ecological specialization and speciation.

Introduction

Phenotypic traits are genetically correlated if they are affected by the same genes or sets of genes through pleiotropy or linkage disequilibrium (Lande, 1979; Lynch & Walsh, 1998). Genetic correlations can have important evolutionary consequences on phenotypic evolution, because changes in allele frequencies due to selection on one trait produce correlated responses to selection in other traits influenced by the same genes or sets of genes. Correlated responses can lead to evolutionary change in neutral traits that are correlated with traits under selection, or they may constrain evolution by slowing the joint evolution of multiple characters (Lande, 1979; Via & Lande, 1985). However, if the signs of the correlations produce correlated responses in the direction of multivariate selection, genetic correlations can also facilitate adaptive evolution (Lande, 1979). In heterogeneous environments, appropriate patterns of genetic correlations among key traits expressed in different environments may speed population divergence and make speciation more likely (review in Via, 2001). This paper concerns an

example in which genetic correlations among key traits may have facilitated simultaneous divergence and reproductive isolation between populations of the same species of an herbivorous insect (pea aphid) that use different host plants as a food resource (background in Via, 1991).

Early quantitative geneticists understood the effects that genetic correlations could have on the evolution of the phenotype. From the 1930s through the 1970s, quantitative genetics was largely the province of animal and plant breeders, who elaborated the theory and statistical analysis of individual quantitative traits (e.g., Falconer, 1952; Jinks, 1954; Kempthorne, 1957; Robertson, 1959a, b; Van Vleck & Henderson, 1961; Hill & Robertson, 1966; Eberhart & Russell, 1966; Hill, 1970). They also devised selection indices that exploit genetic correlations among traits in order to speed the response to artificial selection on trait groups (e.g., Kempthorne, 1957).

In the mid-1970s, the theory of quantitative genetics came back to the attention of evolutionary biologists when Lande (1975, 1976) illustrated how the ‘breeder’s equation’ can be used to describe phenotypic evolution ($R = h^2S$, where R is

the response to selection in one generation, h^2 is the proportion of phenotypic variance that is genetically based, and S is the difference between the phenotypic mean of the parents of the next generation and the population as a whole before selection). Soon, the application of quantitative genetics theory to phenotypic evolution was expanded to the multivariate case (Lande, 1979, 1980a), and the crucial roles of genetic correlations in life history evolution (Lande, 1982), sexual dimorphism (1980c), sexual selection (1980c, 1981), speciation (Lande, 1980b), and evolution in heterogeneous environments (Via & Lande, 1985) were studied.

Quantitative genetics describes phenotypic evolution in terms of parameters that can be estimated in natural populations (trait means, genetic variances and covariances, selection gradient), in contrast to the largely unmeasurable gene frequencies and selection coefficients of classical population genetics (p , q , s). This provided empiricists with new tools for the study of the genetic basis of phenotypic evolution in continuously varying traits in natural populations. By the mid-1980s a cottage industry of evolutionary biologists was estimating genetic variances and covariances in natural populations (review in Roff, 1997).

Within the past decade, the increased accessibility of DNA markers and improved analytical tools have made it possible to use linkage maps to localize loci that influence characters of importance in adaptation and speciation [so-called quantitative trait loci (QTL), see Bradshaw et al., 1995; Via & Hawthorne, 1998, Hawthorne & Via, 2001]. To date, most QTL analyses have focused on basic issues of genetic architecture: how many QTL influence particular traits, where they are located, and what is the magnitude and type of their effects on the traits of interest (Tanksley, 1993; Liu, 1997; Paterson, 1997). When different environments have been considered, interest has largely centered on the extent of variation in expression of QTL among environments, measured as QTL \times environment interactions (e.g., Fry et al., 1996; Juenger et al., this volume). In contrast, the role of QTL in genetic correlations among traits has received relatively little attention.

We assert that QTL analyses may be useful in understanding the profound impact of genetic correlations on adaptation and speciation. Using

an analysis of adaptation in heterogeneous environments as an example, we consider ways in which unique insights on the nature and evolutionary impact of genetic correlations among traits can be obtained from QTL mapping analyses. By focusing attention on how individual chromosomal blocks may influence multiple traits, map-based analyses may allow us to take another step toward understanding the roles of genetic correlations in phenotypic evolution.

Genetic correlations, adaptation and speciation

Evolutionary biologists considering genetic correlations usually stress their constraining influence on phenotypic evolution (e.g., Lande, 1982; Via & Lande, 1985). However, phenotypic evolution can be greatly facilitated when selection favors trait combinations that happen to be most likely, given the pattern of genetic correlations among traits. For example, if selection on two traits is in the same direction (i.e., favoring large or small values of both traits, Figure 1(A)), then a positive genetic correlation will facilitate response to selection, while a negative one will constrain it. The opposite is true if selection on the two traits is in opposite directions (Figure 1(B)). In this paper, we discuss how genetic correlations among demographic and behavioral traits in a heterogeneous environment may act to speed population divergence and facilitate speciation.

Genetic correlations in heterogeneous environments

The genetics of traits expressed in different environments can be quantified in two ways. First, if alleles affecting a particular character vary in their phenotypic effects in different environments, or if different alleles are expressed in different environments, a genotype \times environment interaction will result for that trait (Falconer & Mackay, 1996, p. 132). Alternatively, a character expressed in two environments may be considered to be two genetically correlated character states (Falconer, 1952; Via & Lande, 1985; Falconer & Mackay, 1996, p. 321). A lack of perfect correlation (i.e., $r < +1$) between character states in different environments indicates that alleles affecting the trait differ in their effects in different environments.

The relationship between $g \times e$ and the genetic correlation across environments is relatively straightforward (Falconer, 1952; Via, 1987). If most