Interaction in Metapopulations:
Effects on Adaptation and Diversity

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Introduction

The "genetic architecture" of a phenotype includes the direct effects of genes and environments, as well as the interactions (G x E) between genes and environment. In genetics, genes can be identified by observing patterns of Mendelian segregation associated with function or phenotypic value and often they can be mapped relative to other genes. Environmental factors generally cannot be so easily defined, distinguished from one another, or mapped co-linearly with respect to other environmental factors and this complicates the study of genotype-by-environment interactions (G x E). I will discuss the relationship between gene interactions (g x g or "epistasis") and the more familiar genotype-by-environment interactions (G x E) in genetically subdivided populations, or "meta-populations." Using G x E as a model concept, I will illustrate how epistasis acts both as a genetic constraint to adaptation within populations and as a source of genetic diversity among them.

Individual organisms are complex even without considering genetic or environmental interactions because of the sheer multiplicity of factors acting to produce the phenotype. Interactions among factors (g x g and G x E) lead to a combinatorial explosion of possible effects, difficult to identify and to understand. It is the interactions that make an individual's phenotype quantitatively and qualitatively different from the sum of its parts. Most evolutionary genetic models assume strictly or purely additive gene action with no interactions of any kind. Under this assumption, the effects of genes on the phenotype or on fitness appear in the models as fixed properties of the genes themselves, independent of context.

The Dual Nature of Interactions

Epistasis and G x E share two important features critical to adaptive evolution:

1. Each functions as a **constraint on local adaptation** whenever populations are genetically subdivided and there is gene flow among them. The degree of constraint depends upon the nature of the interactions and the degree of population genetic subdivision and the amount of gene flow.

2. In the absence of gene flow, interactions result in genetic **differentiation among populations** within a metapopulation and, eventually, to speciation. This second feature of interactions is fundamental to the origins of biodiversity.

Although the process of local adaptation can be understood without reference to interactions of any sort (Coyne et al. 1997), it is more difficult (perhaps impossible) to understand the origins of biodiversity without them. Standard micro-evolutionary genetic theory assumes no interactions. If genetic and ecological interactions are the essence of species differences, then omitting interactions from the theory places an enormous conceptual barrier between micro- and macro-evolution. When interactions act as constraints on local adaptation, their omission from micro-evolutionary theory supports the illusion that adaptation has no limits and that every aspect of the phenotype has adaptive function.

Genetic Correlations, Genetic Constraints, and G x E

Adaptation by natural selection to differing local environments is believed to be important in the speciation process because it leads to descendant populations well adapted to one environment but not as well adapted to others. Fitness trade-offs or constraints are implicit in all speciation scenarios and they arise by divergent natural selection to differing local environments. In micro-evolutionary genetic theory, genetic correlations among traits constrain adaptive evolution whenever the direct response to selection for one trait is reduced by the indirect effects of selection on other traits with which the first trait is genetically correlated. An adaptive constraint exists when the rate and direction of evolution of one trait is different from and slower than it would be if selection

operated solely on it and not at all on the other genetically correlated trait(s).

Whenever there is gene flow among populations in different environments, G x E may act as a genetic constraint on local, adaptive evolution. Falconer (1952) showed that G x E can be understood by treating one trait measured in two different environments as two different but genetically correlated traits. In this view, there are two ways that G x E ca act as a genetic constraint to local evolution. First, if the genetic correlation is positive, then G x E is a constraint when selection is disruptive, i.e., selection differs in direction in different environments. Here, the adaptive response within one deme to local natural selection is limited by the influx of genes with opposite effects from other demes. Second, if the genetic correlation is negative (Fig. 1 Upper), then G x E is a constraint when selection is uniform, i.e., the direction of selection is the same in all environments. With G x E and gene flow, selection favors adaptive plasticity, i.e., aspects of development that weaken the genetic constraint of G x E by making development conditional on the environment. In the first case, adaptive plasticity means that one genotype produces different phenotypes in different environments. In the second case, adaptive plasticity means that different genotypes produce the same phenotype in different environments. Adaptive plasticity is favored because it weakens the genetic constraint but it opposes the genetic diversification or specialization of sub-populations in response to the different environments.

When G x E acts as a genetic constraint, natural selection favors modifiers that restrict migration for the same reason that it favors plasticity: diminishing gene flow weakens the genetic constraint on adaptation. Unlike adaptive plasticity, diminishing gene flow enhances the propensity toward specialization. The direction taken by selection in the face of G x E, toward flexibility (adaptive plasticity) or diversification (speciation), depends heavily on initial conditions. Owing to G x E for fitness, evolution in a metapopulation with local variation in selection pressures is different from that in a single large, randomly mating population experiencing the same average environment (i.e., the same average selection pressure). G x E has a dual nature: (a) it is a genetic constraint on genetic divergence with gene flow; and, (b) it is an accelerant of adaptive divergence in the absence of gene flow.

Genetic Constraints and Intra-genomic Epistasis (g x g)

Similar to GxE, in a metapopulation with gene flow among demes, epistatic variance represents a genetic constraint on adaptive evolution. The response to local selection is faster in the absence of gene flow than it is in the presence of gene flow. Gene flow mixes genetic backgrounds on which a gene has positive effects on fitness with backgrounds on which it has negative effects. With limited or no gene flow,

as in allopatry, this constraining effect of epistasis is removed. Each deme can respond to local selection as permitted by the local genetic background. When the ancestral pattern of epistasis is such that a gene's effect on relative fitness on one background changes in a different genetic background (Fig. 1 Lower), then selection within each local deme results in a genetically heterogeneous response among demes. When the pattern of epistasis admits this kind of possibility, then epistasis for fitness has dual effects similar to G x E for fitness. Epistasis acts as a genetic constraint on the divergence of demes with gene flow, because it reduces the statistical "additive" effect of genes. At the same time, it is an accelerant for adaptive divergence in the absence of gene flow.
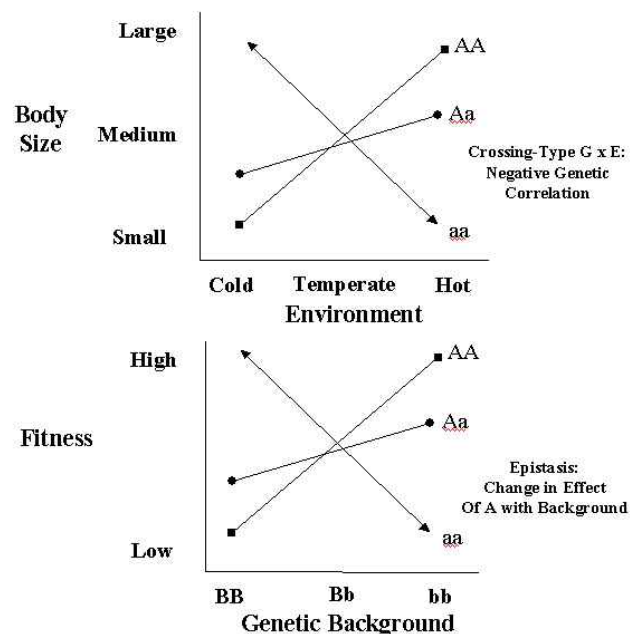

Figure 1. (Upper) Crossing-type G x E resulting in a negative genetic correlation in body size between hot and cold environments. (Lower) Epistatic interaction between loci A and B with resulting change in effect of A on fitness on BB background versus a bb background.

Genetic Constraints and Inter-genomic Epistasis (G x G)

Social interactions with conspecifics, G x G, are an important component of an individual's environment, whether they have positive fitness effects, like altruism and mutualism, or negative ones, like interference competition or cannibalism. They will vary among-demes even in the absence of climatic or abiotic variations in the local environment, owing to random genetic drift affecting the underlying genetic variation for these indirect social effects. Thus, random genetic drift even under uniform selective conditions can result in G x G. On average, 'crossing-type' G x G (cf. Fig. 1)

per se also contributes to population genetic subdivision because it reduces the effective rate of gene flow among demes by increasing the variance in gene flow. Because some migrating individuals are less successful entering the social structure in some demes and more successful entering that in other demes, G x G increases the variance in migration. This decreases the mean effective rate of gene flow below what it would be under the random or island model. Like G x E, in the absence of gene flow, G x G and the variance among demes in indirect social effects can lead to adaptive local divergence. This kind of G x G has been found in experimental meta-populations of flour beetles (McCauley and Wade 1980; Wade 1985; see also below) and it shares some similarity to G x E for inter-specific competitive ability (Wade 1990).

Conclusions

Epistasis, like G x E, can have important effects on adaptation and speciation in metapopulations. Both constrain local adaptation in the face of gene flow, and both can contribute to speciation in its absence. Although natural selection within isolated demes will tend to enrich interactions that are positive for fitness, the genetic architecture of the response to selection can be different in different demes, possibly even incompatible. As among-deme genetic differences increase through time in isolation (i.e., with no migration), owing to drift and local selection, the average epistatic interaction manifest by inter-demic hybrids must deteriorate at least in relative terms regarding the common ancestor as a reference. As among-deme genetic differences increase through time in allopatry owing to selection with G x E, then the average inter-population hybrid fitness will also deteriorate. This occurs because each descendant population evolves to different adaptive gene combinations but the inter-population hybrids recreate the unselected, ancestral pattern of epistatic interactions. When g x g, G x G, and G x E are coincident in their effects speciation may be most rapid. As suggested by Wade and Goodnight (1998) speciation may "…be the inevitable result of divergence with complex genetic architectures." The hope for connecting macro with micro-evolutionary genetic theory may lie in developing more models incorporating interactions of all sorts.

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