Behavior of Dobzhansky-type epistatic hybridization models under varying dominance and selection: preliminary numerical simulations

Research report to the Worldwide Universities Network (W.U.N.)

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Research supported by a W.U.N. Global Exchange Award
to Andrew L. Hipp for the period 1 June – 30 June 2004

Introduction

Dobzhanksy (1937) formulated a two-locus model of genetic divergence under which derivative populations are reproductively isolated from one another but not from the ancestral population. Models of this type, referred to as Dobzhansky-type epistatic models, have the potential to explain hybridization and speciation scenarios in which fertile genetic and morphological intermediates exist despite the fact that F1 hybrids between the source populations are sterile. Such models can also explain asymmetrical clines in characters that vary between the source populations, as well as offsets in those clines from the hybrid zone center.

Sergey Gavrilets (1997) studied the properties of hybrid zones under Dobzhansky-type epistatic selection using mathematical perturbation methods that allowed him to analytically approximate equilibrium gamete and allele frequencies under varying selection and migration parameters. He also simulated equilibrium allele frequencies across a hybrid zone for parameter values beyond the range for which perturbation methods are expected to be robust. The conclusions of his study included the findings that Dobzhansky-type epistatic selection does indeed permit limited hybridization while posing less of a barrier to neutral gene flow.

In this study, we further investigate the properties of Dobzhansky-type hybrid zones using deterministic numerical simulations based on the two-locus model formulated in Gavrilets (1997). We investigate multivariate cline properties across a wide range of selection parameters, including scenarios in which derived alleles are completely dominant, scenarios in which they are completely recessive, and scenarios in which they are codominant. We build on Gavrilets' model by incorporating a separate parameter for selection on derived alleles, allowing us to evaluate cases in which derived alleles became fixed by genetic drift versus those in which derived alleles became fixed by natural selection or became adaptive subsequent to fixation. We also demonstrate how varying degrees of asymmetry in selection parameters affect the frequency of recombinant gametes at the center of the hybrid zone and evaluate the effects of individual parameters on the degree of hybridization.

Methods

Gavrilets' (1997) numerical method of simulating equilibrium allele and gamete frequencies across hybrid zones was implemented in R version 2.0.0 (R Development Core Team, 2004) by iterating his equations (2) and (4a-c); neutral alleles were not analysed for this paper. To address the effects of selection on derived alleles in the case in which alleles are codominant, fitness matrix (3) an additional factor *nw* was added to each cell of the fitness matrix, where n = number of derived alleles in the genotype (e.g., $n = 4$ for genotype AAbb, $n = 2$ for genotypes AaBb, AABB, and aabb) and w = the increase in relative fitness for each derived allele. The matrix was normalized such that maximum fitness = 1. The effects of treating derived alleles as dominant were simulated by setting $\beta = \beta_1 = s > 0$, $\alpha = \alpha_1 = 0$; derived alleles were treated as recessive in alternative simulations by setting $\alpha = \alpha_1 = \beta = s = 0$, $\beta_1 > 0$. Simulations for direct comparison with Gavrilets were run for 1000 generations with 12 islands, with migration rates $m = m_0 = 0.005$, the value used by Gavrilets in his numerical simulations (the reported $m = m_0 = 0.05$ in Gavrilets 1997 is an error).

To simultaneously compare the effects of several parameters on hybrid zone dynamics, mean fitness across all genotypes in the central islands and frequency of recombinant (hybrid) gametes in the central islands was graphed against the parameters of interest. Initial trials demonstrated that the same trends in these two dependent variables were found across a range of eight to twenty islands. Simulations were consequently run for 1000 generations with eight islands. Initial trials indicated that 1000 generations was adequate to investigate trends, though some of the clines change subtly when run for 2000 generations. Code for performing simulations is available upon request.

Results and Discussion

Effects of disentangling selection for derived alleles from selection against hybrids

The fitness matrices used for numerical simulations in Gavrilets (1997, pp. 1032 ff.) appear to approximate the selection expected when positive selection on derived alleles = 0.01 (Table 1). This models the situation in which derived alleles have become fixed under natural selection or become adaptive subsequent to fixation. Simulations run under the assumption that $\alpha = \alpha_1 = 0$ and $w = 0.01$ recover allele frequency clines that are virtually indistinguishable from simulations run at $\alpha = 0.01$ and $\alpha_1 = 0.02$ with $w = 0$ (Figure 1), suggesting that the numerical simulations in Gavrilets 1997 may not generalize well to cases in which derived alleles arose by drift alone.