



Effects of polymorphism for locally adapted genes on rates of neutral introgression in structured populations

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ABSTRACT

Adaptation to local conditions within demes balanced by migration can maintain polymorphisms for variants that reduce fitness in certain ecological contexts. Here, we address the effects of such polymorphisms on the rate of introgression of neutral marker genes, possibly genetically linked to targets of selection. Barriers to neutral gene flow are expected to increase with linkage to targets of local selection and with differences between demes in the frequencies of locally adapted alleles. This expectation is borne out under purifying and disruptive selection, regimes that promote monomorphism within demes. In contrast, overdominance within demes induces minimal barriers to neutral introgression even in the face of very large differences between demes in the frequencies of locally adapted alleles. Further, segregation distortion, a phenomenon observed in a number of interspecific hybrids, can in fact promote transmission by migrants to future generations at rates exceeding those of residents.

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1. Introduction

Bengtsson (1985) proposed an index of the rate of interspecific gene flow at a neutral locus linked to an incompatibility factor. This framework has been applied to incompatibility selection, under which factors that are selectively neutral in their native species contribute to deleterious effects in interspecific hybrids and their descendants (e.g., Barton and Bengtsson, 1986; Navarro and Barton, 2003; Fusco and Uyenoyama, *in press*).

Seminal theoretical work has addressed neutral gene flow across zones of hybridization between species (e.g., Barton, 1979; Gavrillets, 1997). It has provided a theoretical basis for empirical studies of interspecific introgression (see Barton and Hewitt, 1985; Teeter et al., 2008, and references therein). These models typically postulate fixed differences between pure-species populations at both neutral marker loci and targets of selection, implicitly assuming the extinction of foreign alleles on a shorter time scale than their introduction through hybridization. In contrast, Rieseberg and Blackman (2010) have noted that the majority of the candidate loci for speciation genes in plants appear to show intraspecific polymorphism, a marked departure from the rule in animals.

Intraspecific polymorphism may reflect adaptation to local conditions within demes of a structured population. Under certain

conditions, local adaptation can proceed to the point of speciation (Rundle and Nosil, 2005). Here, we apply the approach of Fusco and Uyenoyama (*in press*) to explore the implications for neutral introgression of various forms of local adaptation within a two-deme system, irrespective of whether the barriers to gene flow may eventually delineate species.

Numerous workers (e.g., Levene, 1953; Moran, 1962; Maynard Smith, 1966; Karlin and McGregor, 1972a) have derived conditions for the maintenance of genetic polymorphism under various forms of geographically structured selection. One class entails migration acting in opposition to purifying or disruptive selection. In addition to mechanisms of this kind, we address selection regimes capable of maintaining polymorphism within demes even in the absence of migration: overdominance and purifying selection balanced by segregation distortion.

Segregation distortion contributes to the syndrome expressed upon hybridization in a number of exemplar systems for the study of speciation (e.g., Dermitzakis et al., 2000; Tao et al., 2001). Frank (1991) and Hurst and Pomiankowski (1991) suggested that the unmasking upon hybridization of selfish factors that induce meiotic drive of sex chromosomes may account for Haldane's (1922) rule. Assessments of the role of meiotic drive in postzygotic isolation between species have concentrated on distortions of the sex ratio (Orr and Presgraves, 2000; Coyne and Orr, 2004, Chap. 8). While perhaps less easily detected than driving sex chromosomes, autosomal segregation distortion also occurs in interspecific hybrids (Fishman and Willis, 2005), and moreover within pure-species populations (Fishman and Saunders, 2008).

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We find that barriers to neutral introgression decline with differences between the local gene pools in the frequencies of alleles subject to purifying or disruptive selection. Less expected is that unless linkage to the target of selection is virtually complete, overdominance favoring different allele frequencies in the two demes imposes minimal barriers to introgression of neutral markers. Segregation distortion balanced by purifying selection also induces weak barriers and can in fact enhance the contribution of migrants to future generations beyond that of residents.

2. General approach

2.1. Local adaptation

Selection in each deme of a two-deme population reflects adaptation to local conditions, with the rate of reproduction determined by genotype at the biallelic A locus:

$$\begin{array}{rcc} & AA & Aa & aa \\ \text{Deme 1} & \alpha_0 & \alpha_1 & \alpha_2 \\ \text{Deme 2} & \beta_0 & \beta_1 & \beta_2. \end{array} \quad (1)$$

Following random union of gametes sampled from the local gene pool, selection on the zygotes, and gametogenesis by reproductives, the frequencies of the A allele among gametes produced in the two demes correspond to

$$p_1 = f_1(x_1) = \frac{x_1[x_1\alpha_0 + 2d_1(1-x_1)\alpha_1]}{x_1^2\alpha_0 + 2x_1(1-x_1)\alpha_1 + (1-x_1)^2\alpha_2} \quad (2a)$$

$$p_2 = f_2(x_2) = \frac{x_2[x_2\beta_0 + 2d_2(1-x_2)\beta_1]}{x_2^2\beta_0 + 2x_2(1-x_2)\beta_1 + (1-x_2)^2\beta_2}, \quad (2b)$$

for x_i the frequency of A in the gamete pool of deme i ($i = 1, 2$), p_i the frequency of A among gametes produced by reproductives, and d_i the expected proportion of A -bearing gametes among gametes produced by Aa individuals ($d_1 = d_2 = 1/2$ under Mendelian segregation).

Formation of the gamete pool from which zygotes of the subsequent generation will be derived entails mixing of gametes generated by reproductives in the two demes:

$$x_1^* = (1-m)p_1 + mp_2 \quad (3a)$$

$$x_2^* = mp_1 + (1-m)p_2, \quad (3b)$$

in which m represents the proportion of the local gene pool derived from gametes of individuals born in the other deme (backward migration rate). These expressions reflect symmetric gene flow between the demes, but of course asymmetric gene flow can easily be accommodated. At equilibrium, $x_i^* = x_i$.

It is well known that $f_1(\cdot)$ and $f_2(\cdot)$ in Eq. (2) represent monotone transformations, which in the absence of gene flow ($m = 0$) implies convergence of allele frequency to the nearest locally stable fixed point (see Karlin and Feldman, 1972).

2.2. Genealogical migration rate

In classical neutral models of structured populations (Wright, 1969), the backward migration rate (m) represents the fraction of the gene pool of a deme that derives from a different deme in the immediately preceding generation. Apart from genes that influence the propensity of individuals to reproduce in a deme other than their birth deme, all genomic regions are subject to the same backward migration rate (m). The sampling of a gene from the present population entails its descent through ancestors that succeeded in contributing to the present generation, a locus-specific process that may reflect selection targeted either to the gene itself or to associated sites (Karlin, 1982).

Central to the distribution of F_{ST} and other summary statistics of genetic variation in structured populations is the rate of

coalescence between lineages sampled from different demes. This rate in turn depends on the waiting time between interdeme transfers in the line of descent of a gene sampled at random from the present population. Modeling the distribution of waiting time as exponential, Fusco and Uyenoyama (in press) termed the parameter of that distribution the “genealogical migration rate”:

$$g = \omega m \quad (4)$$

for ω the relative reproductive rate. Relative reproductive rate ω (defined in (5)) represents the expected contribution to future generations of a neutral marker gene introduced into the local gene pool on a gamete transmitted by a migrant relative to a gene on a gamete transmitted by a resident. It is conceptually similar to Bengtsson’s (1985) “gene flow factor”, which he defined in terms of “the probability of ultimate inclusion” of a foreign allele into the local gene pool, although he did not address the modification of this allele-based (rather than lineage-based) index for cases involving polymorphism in the foreign and local gene pools. Results from numerical simulations indicated that the distribution of waiting times between migration events along a lineage conforms well to an exponential distribution with parameter g , determined by the method of Fusco and Uyenoyama (in press).

Genealogical migration rate (4) is related to the “neutral effective migration rate” of Kobayashi et al. (2008). While their definition is formulated in terms of the frequency of an allele introduced by migrants, they noted its equivalence under certain conditions to the probability that a lineage sampled at random from the local deme traces back to a different deme in the preceding generation. The allele-based index of Gavrillets (1997) corresponds to the inverse of the frequency of a marker allele in a deme in which it would be absent but for gene flow.

Relative reproductive rate represents the expected number of descendants far in the future of a marker gene on a migrant gamete relative to gene on a resident gamete:

$$\omega = \lim_{t \rightarrow \infty} \frac{\mathbf{v}_m \mathbf{C}^t \mathbf{e}}{\mathbf{v}_r \mathbf{C}^t \mathbf{e}}, \quad (5)$$

for \mathbf{C} a matrix specifying transmission of the marker on various backgrounds; t the number of generations since the focal transmission events; \mathbf{v}_m the distribution of haploid gametic backgrounds of a marker allele introduced on a migrant gamete; \mathbf{v}_r the background distribution for a gamete derived from a resident; and \mathbf{e} the vector with all elements equal to 1 (Fusco and Uyenoyama, in press). The dimension of \mathbf{v}_m and \mathbf{v}_r corresponds to the number of gametic backgrounds on which the focal marker allele can occur: $b = 2^n$, for n the number of biallelic local adaptation loci. Let z denote the number of possible zygotic genotypes; if all local adaptation loci are autosomal, for example, $z = \binom{b+1}{2}$. Transmission matrix \mathbf{C} depicts the gamete-to-gamete cycle:

$$\mathbf{C} = \mathbf{ZSG},$$

for \mathbf{Z} ($b \times z$) describing the generation of zygotes from gametes, diagonal matrix \mathbf{S} ($z \times z$) the change in zygote numbers due to selection, and \mathbf{G} ($z \times b$) the production of gametes by reproducing zygotes.

In the case of a single biallelic locus subject to local adaptation selection, for example, $b = 2$, with the gametic background of a focal marker gene corresponding to either the A or the a allele. Among gametes of individuals originating in deme i , these backgrounds occur in frequencies p_i and $(1 - p_i)$. In deme 1, for example, the background distributions of marker alleles on gametes generated by a migrant and a resident correspond to

$$\mathbf{v}_m = (p_2, 1 - p_2) \quad \mathbf{v}_r = (p_1, 1 - p_1), \quad (6)$$

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