

# Fitness patterns and phenotypic plasticity in a spatially heterogeneous environment

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(Received for publication 14 March 1996 and in revised form 15 July 1996)

## Summary

We analyse patterns of the means and variances of genotypic fitnesses across different niches in a randomly mating haploid population. The population inhabits a spatially heterogeneous environment where it is subject to mutation and weak multilocus additive selection, with different selection coefficients in different niches. Approximate analytical expressions are derived for the stationary mean and variance of genotypic fitnesses among the niches in terms of environmental and genetic parameters. As a special case, we analyse an environment described by a variable  $t$ , distributed among the niches with mean  $t_*$  and variance  $D_*$ , and quadratic decrease in correlation between environments as a function of the difference in values of  $t$ . If the niches have the same qualities, the mean and variance of genotypic fitnesses evolve to be quadratic functions of  $t$  that achieve their maximum and minimum, respectively, at  $t_*$ . With unequal niche qualities, these are non-polynomial functions that attain their extrema at different, usually intermediate values of  $t$ , although the coefficient of variation of the genotypic fitnesses still attains its minimum near  $t_*$ . The functions involve the total mutation rate, the contribution of the loci to genotypic fitnesses, and the frequency and quality distributions of the niches. Thus, for this relatively simple model the norms of reaction may be calculated in terms of the detailed properties of the environmental heterogeneity, and the genetic system.

## 1. Introduction

Understanding the relationship between the phenotypic variability of organisms and the variability of the environment in which they live has long been one of the central goals of evolutionary biology (Schmalhausen, 1938, 1946; Gause, 1947; Waddington, 1959; Robertson, 1960; Bradshaw, 1965; Levins, 1968, and many others). The evolution of phenotypic plasticity, the capacity of a given genotype to produce different phenotypes under different environmental and ecological conditions, has usually been couched in terms of selection on quantitative traits, because morphological and physiological traits differ greatly when development occurs at different temperatures or densities, in different media, etc. (see recent discussions by Scheiner, 1993; Schlichting & Pigliucci, 1993; Via, 1993*a, b*, 1994; de Jong, 1995; Via *et al.*, 1995; Zhivotovsky *et al.*, 1996*a*, following Via & Lande's (1985) treatment).

Phenotypic plasticity may be regarded as the result of genotypic selection induced by phenotypic selection on traits in a heterogeneous environment. The corresponding distribution of genotypic fitnesses with respect to the array of environments is, therefore, of central importance to any general evolutionary theory of phenotypic plasticity. In early work on *Drosophila* it was shown that different genotypes may react differently to environmental changes. For example, Timofeeff-Ressovsky (1933) showed that different strains (genotypes) of *Drosophila melanogaster* and *D. funebris* survive differently under different environmental conditions. Dubinin & Tiniakov (1945) working with *D. funebris*, Dobzhansky and his colleagues (see e.g. Dobzhansky, 1970) working with *D. pseudoobscura*, and many others have shown that different chromosomal arrangements have different reactions to temperature changes. Thus, the evolution of populations in heterogeneous environments through differential survival and reproduction by different phenotypes in the different environments (niches) should properly be analysed in terms of the

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frequencies of genotypes and their fitnesses in these niches. In this paper, we consider the dynamics of genotypic fitnesses (*per se*), without reference to a particular model of a phenotypic trait under selection.

In modelling the evolution of phenotypic plasticity in terms of genotypic fitnesses we must consider the analytical description of reaction norms and the distribution of the environments experienced (Hartl and Clark, 1989, pp. 472–476). Concerning the former, two mathematically related descriptions of environmental influence on phenotypic expression, although with different biological interpretations, may be considered: the ‘character state approach’ and the ‘polynomial approach’ (Van Tienderen, 1994; de Jong, 1995; Via *et al.*, 1995, and others). The character state approach does not assume any particular environmental parameters, and, following Falconer (1952), considers the expressions of a trait in different environments as different correlated traits; the evolution of plasticity then entails changes in mean value of the trait toward their optima within niches (Via & Lande, 1985). The polynomial approach expresses environments in terms of some continuous variable, and the reaction norm is a polynomial function of this variable (de Jong, 1990, 1995; Gavrillets & Scheiner, 1993; Gimelfarb, 1994). The evolution of plasticity is then viewed in terms of changing the corresponding coefficients of the polynomial, although it may be difficult to interpret the polynomial coefficients in terms of the environmental and selection parameters.

In describing the distribution of environments, it is necessary to consider how often particular niches are visited and how productive the niches are. This is true for clonal organisms (Houston & McNamara, 1992; Kawecki & Stearns, 1993) and randomly mating populations (Zhivotovsky *et al.*, 1996a). Lynch & Gabriel (1987) analysed factors that influence the distribution of genotypic fitnesses over environments, and found that both the environmental optimum and the environmental variance affect how populations adjust to a changing environment (see also Bradshaw, 1965; Levins, 1968).

The purpose of this study is the theoretical analysis of the role of the distribution of the different environments. We consider a randomly mating haploid population evolving in a multiple-niche environment under hard selection and mutation, and use a simple additive model of within-niche genotypic fitnesses which permits us to obtain some qualitatively important results. We show that the relative contribution of each niche to the dynamics of the population, the *niche weight*, is the product of the frequency of this niche and its relative success in the production of progeny, and that averages across niches of all populational parameters should use these weights. The correlations between environments in the fitness pattern of the loci also turn out to be important. Initially, the model is analysed in terms of the character state approach, but we show how the

final results can be transformed to the functional form if the environment is expressed in terms of a continuous environmental parameter. It is shown that the mean reaction norm of genotypic fitnesses is unlikely to be a linear function of the environmental parameter. A quadratic mean reaction norm, whose coefficients appear as a combination of the model parameters, may arise in a very special case. Otherwise, the reaction norm curves are essentially non-linear with respect to the environmental parameters. The principal features of the mean-fitness reaction norm are that it attains its maximum and the variance of the genotypic fitnesses attains its minimum at some intermediate values of the environmental parameter.

## 2. The model

The population is haploid with non-overlapping generations. Genotypes are composed of  $n$  loci, each with two possible alleles,  $A_i$  and  $a_i$  at locus  $i$ . Label allele  $A_i$  as 1 and allele  $a_i$  as 0. Then each genotype,  $G_i$ , may be represented as a string of  $n$  binary variables,  $l = (l_1, l_2, \dots, l_n)$ , where  $l_i = 1$  or 0 according to whether the genotype  $G_i$  carries allele  $A_i$  or  $a_i$  at locus  $i$ .

### (i) The fitness function

The population is supposed to inhabit a spatially heterogeneous environment with  $T$  niches. To simplify notation, we consider the fitness of the genotype with all alleles  $a_i$  as the reference fitness level, and other genotypic fitnesses are measured relative to this fitness which is taken to be 1 in each niche. We introduce  $v_{it}$ , the *relative selection coefficient* against (if  $v_{it}$  is positive) or for (if  $v_{it}$  is negative) allele  $A_i$  at locus  $i$  in niche  $t$ , with respect to the reference genotype. These selection coefficients are assumed to be sufficiently small that linkage disequilibrium may be ignored. Local viability selection acts so that in niche  $t$  a developing zygote of genotype  $G_i$  has fitness that is additive across the loci. We also introduce the scaling factor  $\varphi_t$  as a baseline fitness level in niche  $t$ , which we call the ‘*quality*’ of niche  $t$ . These values are introduced to emphasize possible differences among niches in the quality of ecological and environmental conditions which may diminish (if  $\varphi_t < 1$ ) or enhance (if  $\varphi_t > 1$ ) the reproduction (survival) of the individuals independently of their genotypes. The total fitness of genotype  $G_i$  at niche  $t$  is therefore

$$w_t(l) = \varphi_t \left( 1 - \sum_{i=1}^n v_{it} l_i \right). \quad (1)$$

The *niche-mean fitness*  $\bar{w}_t$  is the average of the genotypic fitnesses of individuals that develop in niche  $t$ :

$$\bar{w}_t = \varphi_t \left( 1 - \sum_{i=1}^n v_{it} p_i \right), \quad (2)$$

where  $p_i$  is the frequency of allele  $A_i$ . If the frequency of genotype  $G_i$  among zygotes is  $P_i$ ,  $\sum_i P_i = 1$ , then its

frequency among surviving adults in niche  $t$  is  $w_t(l) P_t/\bar{w}_t$ .

(ii) *Population structure*

Random mating occurs among all adults pooled across all niches, and the progeny are then randomly distributed among the niches according to the *niche frequencies*  $f_t, \sum_t f_t = 1$ ; this is the Levene (1953) model of a heterogeneous environment. We assume hard selection (Dempster, 1955; Christiansen, 1975), under which the contribution of niche  $t$  to the adult pool is proportional to its niche-mean fitness,  $\bar{w}_t$ . Thus, the frequency of  $G_i$  prior to mating, and the grand mean fitness of the whole population are, respectively,

$$\tilde{P}_i = \bar{w}^{-1} \sum_{t=1}^T f_t w_t(l) P_t, \quad \bar{w} = \sum_{t=1}^T f_t \bar{w}_t. \tag{3}$$

From (3) and (2), the niche frequency,  $f_t$ , and niche quality,  $\varphi_t$ , both contribute to all genotypic frequencies and to the grand mean fitness of the whole population. It therefore seems natural to define *niche weights*,  $\xi_t$ , in terms of the normalized products,

$$\xi_t = \frac{\varphi_t f_t}{\varphi}, \quad \text{where } \varphi = \sum_{t=1}^T f_t \varphi_t, \tag{4}$$

so that  $\sum_t \xi_t = 1$ . The ratio  $\varphi_t/\varphi$  can be interpreted as the relative success of niche  $t$  in production of progeny.

It follows from (3) that the form of selection imposed by (1) induces the following total genotypic fitnesses averaged over niches:

$$w(l) = \varphi \left( 1 - \sum_{i=1}^n v_i l_i \right), \tag{5}$$

where

$$v_i = \sum_{t=1}^T \xi_t v_{it}; \quad i = 1, 2, \dots, n, \tag{6}$$

are the mean values (over niches) of the selection coefficients for locus  $i$ . From (5), the grand mean fitness (3) then becomes

$$\bar{w} = \varphi \left( 1 - \sum_{i=1}^n v_i p_i \right). \tag{7}$$

It is well known (Feldman, 1971) that a haploid population under multilocus selection becomes monomorphic at each locus. Given fitness functions,  $w_t(l)$ , and frequencies of the niches,  $f_t$ , (i.e. given the average selection coefficients  $v_i$ ), we may label alleles so that the fixed alleles would be  $a$  at all loci if selection were the only force acting. This state is locally stable if each  $v_i$  is positive, which we assume in what follows.

(iii) *Allele frequencies under mutation and selection*

Suppose that mutation occurs at each locus. Since we have renumbered the alleles so that  $a_i$  are fixed under the action of selection of the form (5), we may assume that their frequencies do not deviate far from 1 under

mutation, and for locus  $i$  consider only mutation of  $a_i$  to  $A_i$  at the rate  $\mu_i$  neglecting reverse mutations to  $a_i$ . In this treatment, we assume that the selection coefficients are small enough that they can be represented in the form  $v_{it} = \epsilon \tilde{v}_{it}$ , where  $\tilde{v}_{it}$  are  $\mathcal{O}(1)$  and  $\epsilon$  is a small parameter, and that the recombination rates are  $\mathcal{O}(1)$  with respect to  $\epsilon$ . Also, we assume that mutation rates are  $\mathcal{O}(\epsilon^2)$ , i.e.  $\mu_i = \epsilon^2 \tilde{\mu}_i$ , where  $\tilde{\mu}_i$  are  $\mathcal{O}(1)$ . We do not exclude the case of a large number of loci, so that the *total mutation rate per gamete*,  $U = \sum_i \mu_i$ , may be large.

For a particular niche,  $t$ , we consider the distribution of selection coefficients  $v_{it}$  over loci and calculate its mean and variance. To this end, we set the weight of a locus proportional to its mutation rate, i.e. locus  $i$  has an associated weight  $\mu_i/U$ . As a special case, we will assume later in Propositions 1–4 that the mean and variance of the selection coefficients taken over loci have the same values, denoted by  $\bar{v}$  and  $\sigma^2$ , for all niches, i.e. the quantities

$$\bar{v} = \sum_{i=1}^n \frac{\mu_i}{U} v_{it}, \quad \sigma^2 = \sum_{i=1}^n \frac{\mu_i}{U} (v_{it} - \bar{v})^2 \tag{8}$$

are independent of  $t$ .

It is also useful to introduce the correlation in selection coefficients between arbitrary environments  $s$  and  $t$ ,

$$r_{st} = \sum_{i=1}^n \frac{\mu_i}{U} (v_{is} - \bar{v})(v_{it} - \bar{v})/\sigma^2. \tag{9}$$

Via & Lande (1985; see also Falconer, 1952) treated the evolution of a plastic trait in terms of genetically correlated traits evolving in different environments. Our correlation coefficients  $r_{st}$  may also be interpreted in such terms.

Under the assumptions discussed above, linkage disequilibrium may be ignored (Zhivotovsky & Pylkov, 1996), and thus the change in the frequency of allele  $A_i$  due to selection is approximately  $-\varphi v_i p_i (1 - p_i)/\bar{w}$ . Since the change in the frequency of allele  $A_i$  due to mutation is  $(1 - p_i)\mu_i$ , if we neglect terms of order  $\epsilon^3$ , then at equilibrium under mutation and selection the following equation holds:  $\varphi v_i \hat{p}_i/\hat{w} = \mu_i$ . (Hereafter, we assume that the population has already attained this equilibrium, and use the ‘hat’ to denote the value of a variable at equilibrium.) Since mutation rates are  $\mathcal{O}(\epsilon^2)$  and selection coefficients are  $\mathcal{O}(\epsilon)$ , we conclude that at equilibrium the frequencies of alleles  $A$  will be  $\mathcal{O}(\epsilon)$ , that is  $\hat{p}_i = \epsilon \hat{w} \tilde{\mu}_i/\tilde{v}_i \varphi + \mathcal{O}(\epsilon^2) = \hat{w} \mu_i/v_i \varphi + \mathcal{O}(\epsilon^2)$ . From (7) we obtain the following expression for the grand mean fitness at equilibrium:

$$\hat{w} = \frac{\varphi}{1 + U} + \mathcal{O}(\epsilon). \tag{10}$$

Hence, the equilibrium allele frequencies are

$$\hat{p}_i = \frac{1}{1 + U} \frac{\mu_i}{v_i} + \mathcal{O}(\epsilon^2). \tag{11}$$

The mean fitness at mutation–selection balance in (10) corresponds to the result of Kimura & Maruyama (1966, p. 1340) for the case of no linkage (recall that we assume selection to be weak relative to recombination); see also Bürger & Hofbauer (1994).

(iv) *Niche-mean fitnesses*

From (2) and (11), the niche-mean fitnesses are

$$\hat{w}_t = \varphi_t \left( 1 - \frac{1}{1+U} \sum_{i=1}^n \mu_i \frac{v_{it}}{v_i} \right) + \mathcal{O}(\epsilon). \tag{12}$$

It is seen from (12) and (6) that the average of the niche-mean fitnesses with respect to the niche frequencies,  $\sum_t f_t \hat{w}_t$ , coincides with the grand mean fitness (10). Therefore, from the definition of  $\varphi$  – see (4) – in some niches the mean fitness may exceed and in others be less than  $\varphi/(1+U)$ .

In order to interpret the expression in (12), consider the special case of homogeneous means and variances of the relative selection coefficients given by formulae (8) and (9). In this case, both the mean and variance are calculated with respect to the distribution  $\{\mu_1/U, \mu_2/U, \mu_3/U, \dots\}$ . We say that this distribution is *concentrated around  $\bar{v}$*  if (8) and (9) hold and, additionally, if each higher cross-moment of order  $k$  for niches  $t_1, t_2, \dots, t_k$ ,

$$\sum_{i=1}^n \frac{\mu_i}{U} (v_{it_1} - \bar{v})(v_{it_2} - \bar{v}) \dots (v_{it_k} - \bar{v}), \quad k > 2, \tag{13}$$

is negligible compared with  $\bar{v}^k$ . This condition also entails that  $\sigma^2/\bar{v}^2$  is small. Under this assumption, we may write  $1/v_i$  as  $1/[\bar{v} + (v_i - \bar{v})] = (1/\bar{v}) \{1/[1 + (v_i - \bar{v})/\bar{v}]\} \approx (1/\bar{v}) [1 - (v_i - \bar{v})/\bar{v} + (v_i - \bar{v})^2/\bar{v}^2]$  and neglect terms with  $(v_{it} - \bar{v})^3$  and higher powers. Then the sum in (12) is approximately  $U[1 - (\sigma^2/\bar{v}^2)(R_t - R)]$ , where  $R_t$  and  $R$  are, respectively, the marginal average and the total average of the between-niche correlation coefficients (9):

$$R_t = \sum_{s=1}^T \xi_s r_{st}, \quad R = \sum_{s=1}^T \sum_{t=1}^T \xi_s \xi_t r_{st}. \tag{14}$$

Now, from (12) and (14), we obtain

**Proposition 1.** *Consider a Levene-type population subject to weak within-niche selection with additive contributions to the fitness across loci that are concentrated around  $\bar{v}$  with variance  $\sigma^2$ . Then, at a mutation–selection equilibrium, the mean fitnesses within the niches are*

$$\hat{w}_t \approx \frac{\varphi_t}{1+U} \left[ 1 + U \frac{\sigma^2}{\bar{v}^2} (R_t - R) \right], \quad t = 1, 2, \dots, T. \tag{15}$$

Note that in (14),  $R$  is the average of the  $R_t$  values so that some  $R_t$  values exceed and some are less than  $R$ .

In particular, if niche  $t$  is major (i.e. its weight  $\xi_t$  is sufficiently large), and if it correlates sufficiently closely with the other major niches, then  $R_t > R$ . At the opposite extreme,  $R_t < R$ . Now, it follows from (15) that if the selection coefficients did not vary among niches, then the mean fitness in niche  $t$  would be approximately  $\varphi_t/(1+U)$ . Therefore, under the assumption (8) heterogeneous local selection increases mean fitness in some niches and decreases it in others, although the grand mean fitness remains the same.

(v) *Within-niche variances of genotypic fitnesses*

As is well known, the variance of genotypic values is the sum over loci of the products of the squared relative contributions from each locus and the frequencies of both alternative alleles (Falconer, 1989). Since  $p_i$  values are assumed to be small – see (11) – the frequencies of alleles  $a_i$  are approximately equal to 1. Therefore, from (1) and (11), the variance of the genotypic fitnesses in niche  $t$  is:

$$\hat{V}_t = \frac{\varphi_t^2}{1+U} \sum_{i=1}^n \mu_i \frac{v_{it}^2}{v_i} + \mathcal{O}(\epsilon^2). \tag{16}$$

Using the expansion for  $1/v_i$  given in the previous section, again neglecting terms of  $(v_i - \bar{v})^3$  and higher powers, and representing  $v_{it}^2$  as  $[\bar{v} + (v_{it} - \bar{v})]^2$  and expanding, we may rewrite (16) in a form corresponding to (15) and obtain

**Proposition 2.** *Consider a Levene-type population subject to weak within-niche selection with additive contributions to the fitness across loci that are concentrated around  $\bar{v}$  with variance  $\sigma^2$ . Then, at mutation–selection equilibrium, the within-niche variances of the genotypic fitnesses are*

$$\hat{V}_t \approx \frac{\varphi_t^2 U \bar{v}}{1+U} \left[ 1 + \frac{\sigma^2}{\bar{v}^2} (1 + R - 2R_t) \right], \quad t = 1, 2, \dots, T. \tag{17}$$

It follows from (17) that if selection coefficients did not vary among niches, then the variance in niche  $t$  would be  $\varphi_t^2 U \bar{v}/(1+U)$ . The values  $1 + R - 2R_t$  seem to be positive (at least if all  $r_{st}$  are non-negative) and, therefore, heterogeneous local selection causes the variance to increase within niches. Note that this increase in variance is greater in the minor niches that do not correlate with the major niches and thus have small values of  $R_t$ , whereas major correlating niches, whose  $R_t$  values are close to 1 and  $R$ , show less increase in variance. In the following section we discuss this point in more detail.

(vi) *A parameter for the environment*

Suppose that the environment can be expressed in terms of a quantitative parameter,  $t$ , that may be one- or multidimensional and either discrete or continuous.

We will call a Levene-type population that inhabits such an environment a *parametrized Levene-type population*. Then, in general, the expressions for the mean fitnesses (15) and the variances (17) remain valid, with sums replaced by integrals. As a special case, consider a one-dimensional environment (say, temperature) ranging between  $t_{\min}$  and  $t_{\max}$ , with  $\xi_t$  a continuous distribution of niche weights,  $\xi_t = \varphi_t f_t / \varphi$ . Here, the distribution of the niche frequencies,  $f_t$ , is continuous and  $\int_{t_{\min}}^{t_{\max}} f_t dt = 1$  with  $\varphi = \int_{t_{\min}}^{t_{\max}} f_t \varphi_t dt$ : see (4). Of course,  $\int_{t_{\min}}^{t_{\max}} \xi_t dt = 1$ . With respect to the environmental weight distribution, define the average environmental value,  $t_{\star}$ , and the environmental variance,  $D_{\star}$ :

$$t_{\star} = \int_{t_{\min}}^{t_{\max}} t \xi_t dt, \quad D_{\star} = \int_{t_{\min}}^{t_{\max}} (t - t_{\star})^2 \xi_t dt. \quad (18)$$

Suppose that correlations between environments, defined by (9), decrease as the squared difference in the values of the environmental parameters, with rate parameter  $A$  so that

$$r_{st} = 1 - A(s - t)^2. \quad (19)$$

The correlation between very close environments, i.e. those with  $t \approx s$ , is close to 1, while it decreases quadratically with increasing absolute difference  $|t - s|$  between the parameter values. Distant environments may have positive correlations, although the possibility that they are negative is not excluded. Therefore, it is required that  $t_{\min}$  and  $t_{\max}$  be such that  $|r_{st}| \leq 1$ ; that is,  $A(t_{\max} - t_{\min})^2 \leq 2$ . If we assume that these correlations must be non-negative, then  $A(t_{\max} - t_{\min})^2 \leq 1$ .

Represent  $(s - t)^2$  as  $[(s - t_{\star}) + (t_{\star} - t)]^2$ , expand and integrate in (14) to obtain

$$R_t = 1 - A[D_{\star} + (t - t_{\star})^2], \quad R = 1 - 2AD_{\star}. \quad (20)$$

Finally, from (15) and (17), we have

**Proposition 3.** *Consider a parametrized Levene-type population subject to weak within-niche selection with additive contributions to fitness across loci that are concentrated around  $\bar{v}$  with variance  $\sigma^2$ . Then, at a mutation–selection equilibrium, the mean fitnesses within niches and the within-niche variances of genotypic fitnesses, respectively, are*

$$\hat{w}_t \approx \frac{\varphi_t}{1 + U} \left\{ 1 + U \frac{\sigma^2}{\bar{v}^2} A[D_{\star} - (t - t_{\star})^2] \right\} \quad (21)$$

and

$$\hat{V}_t \approx \frac{\varphi_t^2 U \bar{v}}{1 + U} \left\{ 1 + 2 \frac{\sigma^2}{\bar{v}^2} A(t - t_{\star})^2 \right\}, \quad t = 1, 2, \dots, T. \quad (22)$$

It is easy to see in (21) that the relative increase in the mean fitness (i.e. compared with the values of  $\varphi$ ) caused by environmental heterogeneity attains its

maximum at the average environment,  $t_{\star}$ . If the environmental parameter  $t$  deviates far from the average environment, the mean fitness decreases. This decrease may be significant at the boundaries of the environmental range,  $(t_{\min}, t_{\max})$ , if the environmental variance is small with respect to the width of the range.

The within-niche variances, given by (22), increase in each environment as compared with the squared values of  $\varphi$ , and the more the environmental parameter  $t$  deviates from the average value  $t_{\star}$ , the greater is the relative increase in the variance.

Although the relative increase in mean fitness and relative decrease in within-niche variances of genotypic fitnesses attain their maxima at the mean environmental value  $t_{\star}$ , their absolute values may attain their extrema at values of  $t$  different from  $t_{\star}$  because the niche qualities may also depend on  $t$ . Only in the special case of equal niche qualities (i.e. all  $\varphi$  values are, say, 1), do both the mean fitnesses,  $\hat{w}_t$ , and the variances of genotypic fitnesses,  $\hat{V}_t$ , approach their maximum and minimum, respectively, at  $t = t_{\star}$ . Nevertheless, the mean fitnesses and the variances have the remarkable property that their dependence on  $\varphi_t$  can be eliminated by considering the coefficient of variation,  $\hat{C}_{tw} = \sqrt{\hat{V}_t} / \hat{w}_t$ :

**Proposition 4.** *Consider a parametrized Levene-type population subject to weak within-niche selection with additive contributions to the fitness across loci that are concentrated around  $\bar{v}$  with variance  $\sigma^2$ . Then, at mutation–selection equilibrium, the coefficients of variation of genotypic fitnesses within niches are*

$$\hat{C}_{tw} \approx \sqrt{\bar{v}U(1 + U)} \frac{\sqrt{1 + 2 \frac{\sigma^2}{\bar{v}^2} A(t - t_{\star})^2}}{1 + U \frac{\sigma^2}{\bar{v}^2} A[D_{\star} - (t - t_{\star})^2]}, \quad t = 1, 2, \dots, T. \quad (23)$$

These attain their minimum at  $t = t_{\star}$ .

### 3. Discussion

In our model, we have found that the principal parameter of the environment (niche) is its weight, obtained by multiplying the frequency of the environment and its productivity, as in (4). Thus, it seems useful to distinguish more important (*major*) environments (with large weights) from less important (*minor*) environments (with small weights). A common and productive environment is important and a rare and poor environment would seem to be unimportant for evolution of the Levene-type population and its plasticity. Also, moderately productive and common environments may contribute importantly to the evolution of the total population, in which case they would be classified as major, etc. Earlier we obtained

a similar result in a model for the evolution of genes that modify the structure of randomly mating populations of diploids (Zhivotovsky *et al.*, 1996a). Houston & McNamara (1992) and Kawecki & Stearns (1993) had also concluded that frequent and favourable conditions have a major influence on the dynamics of reaction norms for life-history-related traits in clonal organisms.

In our analysis, all parameters that are important for the evolution of the whole population (see Propositions 1–4) are averaged across environments using the weights,  $\xi_i$  (equations (4), (6), (14), (18), etc.), which control the direction of evolution in changing environments. Change in the frequencies of niches or in their ability to maintain their level of reproduction or survival, or changes in the behaviour of the individuals that influence their choice of environments, may change the environmental weights, thereby changing the eventual genotypic structure of the population. Thus, regulatory genes, if they control such behavioural and physiological reactions to the environment, may play an important role in the evolution of phenotypic plasticity and the adaptation of populations to heterogeneous external conditions (Schlichting & Pigliucci, 1995; Zhivotovsky *et al.*, 1996a).

The selection mode analysed here is the simplest possible: genotypic fitnesses are the result of small additive contributions across loci. Nevertheless, since these contributions may vary among environments, the dynamics of the population are not simple and depend on the mean,  $\bar{v}$ , variance  $\sigma^2$ , and correlations between all pairs of environments in the relative selection coefficients at the loci contributing to the fitness: see (8) and (9). The variance and correlations come about because of differences in the ranks of the contributions by the separate genes to the genotypic fitnesses in different environments. This is equivalent to the presence of genotype–environment interaction in these contributions and may be regarded as parallel to the conclusion of Via & Lande (1985) concerning the importance of genotype–environment interaction for the evolution of phenotypic plasticity.

In the special case of a quadratic decrease in correlation between environments, as in (19), two environmental parameters turn out to be important: the average environmental value  $t_\star$  and the environmental variance  $D_\star$ , calculated as standard statistics of the distribution of the environmental weights, (18). The parameter  $t_\star$  describes the expected environmental value averaged over all available environmental conditions. In particular, if the environmental weight distribution is unimodal and symmetrical, the average environmental value  $t_\star$  coincides with the mode of the distribution, reflecting an intermediate major environment. If the distribution is U-shaped,  $t_\star$  also reflects an intermediate although minor environment. These two quite different situations are distinguished by the variance of the

distribution,  $D_\star$ . (Note that this variance may be related to the environmental tolerance discussed by Lynch & Gabriel (1987).)

In this special case, the mean fitness within niches and the variance of genotypic fitnesses reduce to the relatively simple and easily interpreted approximations in Proposition 3, which depend crucially on the environmental parameters  $t_\star$  and  $D_\star$ . Indeed, assuming that all niches (all values of  $t$ , in this case) have the same quality, we obtain a theoretically novel and important property of fitness profiles of a population evolving in a spatially heterogeneous environment: *the mean fitness achieves its maximum near the average environment,  $t_\star$ , where the variance of genotypic fitnesses attains its minimum.* If niche qualities depend on  $t$ , it follows from (21) and (22) that the mean and variance attain their extrema at different values of the environmental variable. However, the coefficients of variation still have their minimum near the average environmental value  $t_\star$  (Proposition 4). Generally, we conclude from the analysis of this model that the mean and the variance of genotypic fitnesses achieve their maximum and minimum respectively at some average values of environmental variables. It remains to be determined whether this conclusion is robust with respect to epistatic interactions in fitness, genetic linkage and other features of a more realistic model.

Returning to the discussion of the ‘polynomial approach’ (Gavrilets & Scheiner, 1993; Van Tien-deren, 1994; de Jong, 1995; Via *et al.*, 1995), note that linear and even quadratic functions may not correspond to observed data on reaction norms. In our model, only the assumption of equal niche qualities and quadratic decrease in the environmental correlations produced the conclusion that the mean fitness and the within-niche variance of genotypic fitnesses are quadratic functions of the environmental parameter  $t$ : see (21) and (22). Otherwise, the mean fitnesses  $\hat{w}_i$  and the within-niche variances  $\hat{V}_i$  appear to be non-polynomial functions of  $t$ . The coefficients in these functions include interpretable parameters: the genomic mutation rate,  $U$ , the mean,  $\bar{v}$ , and the variance,  $\sigma^2$ , of the contributions of the loci to genotypic fitnesses, the rate of decrease in environmental correlations,  $A$ , as well as the mean and variance of the environmental weight distribution,  $t_\star$  and  $D_\star$  (see Proposition 3). These findings are compatible with Kirkpatrick & Heckman’s (1989) analysis of an infinite-dimensional trait (e.g. reaction norm) evolving to a definite shape under selection on the whole curve, and may serve to connect the ‘character state approach’ (Via & Lande, 1985) and the ‘polynomial approach’.

Our results concern genotypic fitnesses, so that we may apply them to adaptive traits such as viability and other related traits, although we have analysed here only additive fitnesses. For example, Bennet & Lenski (1993) studied the response of *Escherichia coli*

populations to long-term thermal selection (32 °C, 37 °C and 42 °C, with their common ancestor grown at 37 °C) and found that in each population, the maximal mean fitness occurred at the temperature at which this population was selected (their fig. 6). They also found that each of the populations contained a genotype (line) that deviated significantly from the other five lines and that this deviation (the variance of genotypic fitnesses,  $\hat{V}_g$ , in our terms) was smaller at the temperature at which this population was selected. Note that our theoretical predictions concern total genotypic fitness and are not specific about separate fitness components, which may behave quite differently. For example, Gebhardt & Stearns (1988) found that low temperatures negatively influence the developmental rate of *Drosophila melanogaster* while high temperatures have the same effect on viability; considered together, these traits perform better at an intermediate temperature.

Quantitative traits under selection, in particular stabilizing selection, are not described by our findings, although we earlier hypothesized similar conclusions for the evolution of reaction norms (Zhivotovsky *et al.*, 1996a). Therefore, our discussion may be relevant to some traits directly related to fitness components, such as body size in *Drosophila*. Experimental observations are in qualitative agreement with our theoretical predictions, among which we emphasize the increase in the variance of the genotypic fitnesses in the minor environments. For example, Robertson (1960) found increased variance of body size of *Drosophila melanogaster* on deficient diets compared with those on a standard live yeast medium. Tantawy & Mallah (1961) and Zhivotovsky *et al.* (1996b) found that the variance of wing size of *Drosophila melanogaster* and *D. simulans* attained its minimum at intermediate temperatures.

In conclusion, we emphasize that in spite of the simplicity of this model, our findings show that the detailed analysis of phenotypic plasticity may predict definite patterns of phenotypic variability across spatially distributed environments. We also stress that environmental distributions should be included in the evolutionary analysis of phenotypic plasticity. From this point of view, one genotype is more plastic than another, and thus its reaction norm is better adapted to these environments, if the fitness of the former, averaged across environments, is higher than that of the latter *under the given distribution of environmental weights and environmental correlations in selection coefficients*. Changes in the environmental weights and in environmental correlations, which may not be detected in experiments, will eventually result in evolution towards changed reaction norms.

We thank an anonymous reviewer for helpful comments. This research was supported in part by NIH grants GM28016 and 1 R03 TW00491-01 and a grant to the Morrison Institute for Population and Resource Studies from the John D. and Catherine T. MacArthur Foundation.

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