

## Long-term adaptive diversity in Levene-type models

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### ABSTRACT

Assuming a linear trade-off function between the habitat-specific fitness values in Levene's model, De Meeûs and Goudet found that an evolutionarily stable strategy always exists and that polymorphism cannot be maintained on an evolutionary time-scale. On the other hand, Kisdi and Geritz showed that, in a broad parameter region, evolution necessarily leads to polymorphism in a Levene-type model with stabilizing selection within each habitat. Here I reconcile these results by demonstrating that the convexity of the trade-off function plays an essential role in the evolution of polymorphism.

*Keywords:* adaptive dynamics, co-existence, evolutionarily stable strategy, evolutionary branching, heterogeneous environment, polymorphism, soft selection, trade-off.

### INTRODUCTION

In a recent paper published in this journal, De Meeûs and Goudet (2000) investigated adaptive diversity in heterogeneous environments for populations regulated by soft selection, hard selection or a mixture of the two. They found that an evolutionarily stable strategy (ESS) haplotype will always take over the population and, therefore, genetic polymorphism cannot be maintained on an evolutionary time-scale. This conclusion is in direct contradiction with the results of Kisdi and Geritz (1999; see also Geritz and Kisdi, 2000), who showed that, under soft selection, there is a large parameter region where no monomorphic ESS exists and the population evolves a polymorphism. Here, I seek to resolve the apparent contradiction between these results and highlight the conditions for adaptive diversity in Levene-type models.

### THE LEVENE MODEL

Consider a population that occupies two habitats. In each habitat, the population first undergoes viability selection. Next, within-habitat density dependence operates such that the numbers of individuals are cut off to  $cN$  and to  $(1 - c)N$  in the first and in the second habitat, respectively. Finally, offspring are produced and dispersed randomly over the two

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habitats. With two haploid genotypes  $A$  and  $a$ , the frequency of  $a$  after one generation is

$$q_{t+1} = \left[ c \frac{w_1(a)}{pw_1(A) + qw_1(a)} + (1 - c) \frac{w_2(a)}{pw_2(A) + qw_2(a)} \right] q \quad (1)$$

where  $p$  and  $q$  are the frequencies of  $A$  and  $a$  in generation  $t$  respectively,  $c$  and  $(1 - c)$  are the relative sizes of the habitats, and  $w_i(a)$  denotes the within-habitat fitness of allele  $a$  in habitat  $i$  (Levene, 1953; see also Strobeck, 1979).

Assume that there is a continuum of possible alleles (haploid genotypes) that determine the continuous trait under selection. Alleles that are superior in both habitats will exclude those that are inferior in both habitats; thus non-trivial evolutionary dynamics involve alleles with a trade-off between the habitat-specific fitness values. I restrict the analysis for a range of alleles in which  $w_1(a)$  is a strictly monotonic function, such that the value of  $w_1$  unequivocally determines  $a$  (and the derivative  $w'_1$  is different from zero). In this case,  $w_2$  can be given as a function of  $w_1$ , such that, for any allele  $a$ ,  $w_2(a) = u(w_1(a))$ . The function  $u$  then specifies the trade-off.

To find the ESS allele (if any), consider a rare allele  $a$  in a population otherwise monomorphic for  $A$ . Taking the limit  $q \rightarrow 0$  in equation (1), the frequency of the rare allele increases if its fitness across the entire population,

$$F_A(a) = c \frac{w_1(a)}{w_1(A)} + (1 - c) \frac{w_2(a)}{w_2(A)} = c \frac{w_1(a)}{w_1(A)} + (1 - c) \frac{u(w_1(a))}{u(w_1(A))} \quad (2)$$

is greater than 1. Consequently, a necessary condition for  $\hat{A}$  to be an ESS is that the inequality

$$F_A(a) \leq 1 \quad (3)$$

holds for any  $a$ .

The model outlined above corresponds to the pure soft selection model of De Meeûs and Goudet (2000), the results of which are directly comparable to those of Kisdi and Geritz (1999). De Meeûs and Goudet (2000) used a haploid model as above, whereas Kisdi and Geritz (1999) assumed diploid genetics with additive allelic effects. This, however, makes no difference for the existence of a monomorphic ESS (see Van Dooren, in press). For simplicity, I present all results in the haploid model and follow the notations of De Meeûs and Goudet (2000).

### LINEAR TRADE-OFF

De Meeûs and Goudet (2000) assumed a linear trade-off between the habitat-specific fitness values such that  $w_2(a) = u(w_1(a)) = 1 - w_1(a)$ . Substituting this linear trade-off function into inequality (3), it follows that allele  $a$  at zero frequency is unable to invade the monomorphic population of  $A$  if

$$(w_1(A) - w_1(a))(c - w_1(A)) \geq 0 \quad (4)$$

(cf. De Meeûs and Goudet, 2000, p. 990). The allele  $\hat{A}$  for which  $w_1(\hat{A}) = c$  (and  $w_2(\hat{A}) = 1 - c$ ) satisfies condition (4) for every alternative allele  $a$  and, therefore,  $\hat{A}$  is the ESS.

Additionally,  $\hat{A}$  can also invade any other monomorphic population. Once  $\hat{A}$  is established, no polymorphism can be maintained. As De Meeûs and Goudet (2000, p. 993) conclude, ‘adaptive diversity will be very difficult to maintain at an evolutionary time-scale in Levene-type models, because an ESS will always eventually invade the environment’.

Note, however, that  $w_1(\hat{A}) = c$  yields equality in condition (4):  $\hat{A}$  represents a ‘borderline case’ ESS such that all alternative alleles are exactly neutral if their frequency is zero. Two questions must be considered when such a borderline ESS is found. First, is invasion impossible if an alternative allele is present at a low but positive frequency? In the present model, the ESS passes this check (see Appendix). Second, is the model structurally stable – that is, is the ESS robust with respect to changes in the functional forms assumed? The borderline ESS found in the case of a linear trade-off may suggest that the existence of an ESS depends on the convexity or concavity of the trade-off function. Below I argue that this is indeed the case.

### NON-LINEAR TRADE-OFF FUNCTIONS

Assume now an arbitrary trade-off between the habitat-specific fitness values such that function  $u$  may have any shape, including concave, linear or convex. Since  $F_A(A) = 1$ , inequality (3) implies that the ESS allele  $\hat{A}$  must satisfy the local condition

$$\left. \frac{\partial F_A(a)}{\partial a} \right|_{a=A=\hat{A}} = \left[ \frac{c}{w_1(\hat{A})} + \frac{(1-c)u'(w_1(\hat{A}))}{u(w_1(\hat{A}))} \right] w_1'(\hat{A}) = 0 \quad (5)$$

Otherwise, a rare allele either with a slightly smaller or with a slightly larger allelic value would be able to invade. [With linear trade-off  $u' \equiv -1$ , and equation (5), yields  $w_1(\hat{A}) = c$  as before.] The solution of equation (5) is, however, not necessarily an ESS. Since the first-order condition (5) vanishes, invasion against  $\hat{A}$  depends generically on the second derivative of  $F_A(a)$ .  $\hat{A}$  is thus resistant to invasion by alleles similar to itself ( $a = \hat{A} \pm \varepsilon$ ) if

$$\left. \frac{\partial^2 F_A(a)}{\partial a^2} \right|_{a=A=\hat{A}} = (1-c) \frac{[w_1'(\hat{A})]^2}{u(w_1(\hat{A}))} u''(w_1(\hat{A})) < 0 \quad (6)$$

[for conditions (5) and (6), see Maynard Smith, 1982, Appendix H; Geritz *et al.*, 1998; Kisdi and Geritz, 1999, Appendix C].

The sign of expression (6) is determined by  $u''$  – that is, by the convexity of the trade-off function. With a concave trade-off function  $u''$  is negative and  $\hat{A}$  is at least a local ESS. [Inequality (6) guarantees only local evolutionary stability; global stability also depends on the higher derivatives of  $F_A(a)$ .] In the case of a linear trade-off,  $u''$  is zero and all higher derivatives of  $F_A(a)$  with respect to  $a$  are also zero:  $\hat{A}$  is a ‘borderline case’ ESS such that all alternative alleles are neutral at zero frequency. If the trade-off function is convex at  $\hat{A}$  (i.e.  $u''(w_1(\hat{A})) > 0$ ), then condition (6) is violated and  $\hat{A}$  can be invaded. The model then has no monomorphic ESS, and polymorphism may be maintained on an evolutionary time-scale.

More predictions can be made if mutations of only small phenotypic effect occur (see Geritz *et al.*, 1998).  $\hat{A}$  is convergence-stable (i.e. evolution by successive allele invasions and substitutions will lead towards  $\hat{A}$ ) if

$$\left[ \frac{\partial^2 F_A(a)}{\partial A \partial a} + \frac{\partial^2 F_A(a)}{\partial a^2} \right]_{a=A=\hat{A}} = (1-c) \frac{[w'_1]^2}{u} \left[ u'' - u' \left( \frac{u'}{u} - \frac{1}{w_1} \right) \right] < 0 \quad (7)$$

(Eshel, 1983; Christiansen, 1991). Since  $u'$  must be negative at  $\hat{A}$  [cf. equation (5)], this condition is always satisfied if the trade-off is concave ( $u'' < 0$ ), linear ( $u'' = 0$ ) or moderately convex ( $u'' > 0$ ). For large positive values of  $u''$ , condition (7) does not hold, and gradual evolution leads away from  $\hat{A}$ . However, if extreme alleles are not fit in either habitat, such that  $w'_i(-\infty) > 0$  and  $w'_i(\infty) < 0$  for  $i = 1, 2$ , then divergent evolution cannot proceed indefinitely and evolution must converge to another solution of equation (5).

If a convergence-stable allele  $\hat{A}$  lacks local evolutionary stability [i.e. the trade-off function is convex at  $\hat{A}$  and therefore condition (6) is violated], then  $\hat{A}$  is a so-called evolutionary branching point (Geritz *et al.*, 1998; see also Metz *et al.*, 1996; Geritz *et al.*, 1997). In the vicinity of  $\hat{A}$ , the population necessarily becomes polymorphic. Since mutations have small phenotypic effect, the initial polymorphism contains two very similar alleles. By a series of allele invasions and substitutions, however, the two alleles undergo divergent co-evolution such that a polymorphism of two distinctly different alleles develops. In the Levene model, this happens if  $u''$  is positive but not too large, such that the condition for convergence stability (7) holds, whereas the condition for evolutionary stability (6) does not.

Kisdi and Geritz (1999) assumed Gaussian fitness functions with different optima and equal width in the two habitats – that is,  $w_1(a) = \exp(-(a - m_1)^2/2\sigma^2)$  and  $w_2(a) = \exp(-(a - m_2)^2/2\sigma^2)$ , respectively. They found that, in this model,  $\hat{A}$  is always convergence-stable and it is an evolutionary branching point if

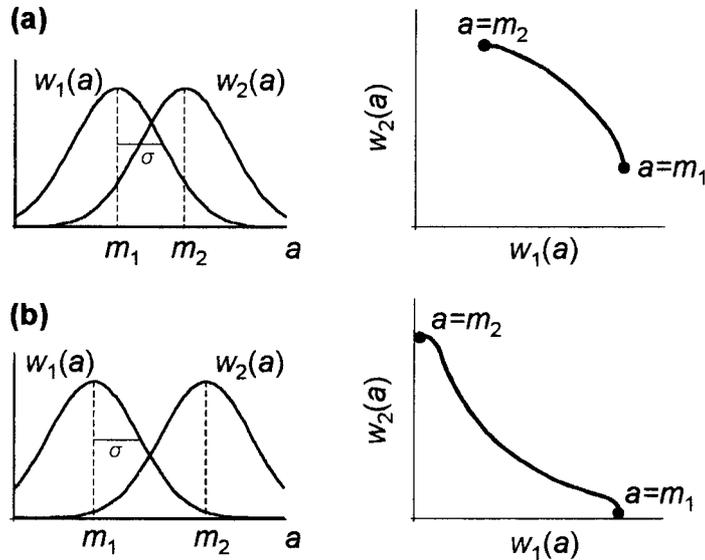
$$[(m_2 - m_1)/\sigma]^2 > 1/c(1 - c) \quad (8)$$

When condition (8) is satisfied, there is no monomorphic ESS and the population necessarily becomes polymorphic by evolutionary branching.

Let us now see how this result conforms to the condition of the fitness trade-off being convex. The allele that satisfies condition (5) is  $\hat{A} = cm_1 + (1 - c)m_2$ ; that is, it is always in between the two habitat-specific optima. Within the range  $[m_1, m_2]$ , the fitness trade-off is concave if  $(m_2 - m_1)/\sigma < 2$ , but its middle part is convex if  $(m_2 - m_1)/\sigma > 2$  (Fig. 1; cf. Levins, 1962). Accordingly,  $\hat{A}$  is always an ESS if  $(m_2 - m_1)/\sigma < 2$ ; note that the minimum value of the right-hand side in condition (8) is indeed 2. With  $(m_2 - m_1)/\sigma > 2$ , the evolutionary stability of  $\hat{A}$  depends on whether it falls in the concave or in the convex part of the trade-off. For intermediate values of  $c$ ,  $\hat{A} = cm_1 + (1 - c)m_2$  is in the middle convex part of the trade-off function and, accordingly,  $\hat{A}$  lacks evolutionary stability. With  $c$  sufficiently near to zero or to one,  $\hat{A} = cm_1 + (1 - c)m_2$  is near  $m_2$  or  $m_1$  respectively, where the fitness trade-off is concave and  $\hat{A}$  is evolutionarily stable. As  $(m_2 - m_1)/\sigma$  increases, the convex part of the trade-off widens and  $\hat{A}$  becomes an evolutionary branching point for a wider range of  $c$  [cf. condition (8); see also Fig. 3 in Kisdi and Geritz, 1999].

## DISCUSSION

In the Levene model, there may be no ESS and, therefore, polymorphism may be maintained on an evolutionary time-scale. This happens if the trade-off between the habitat-specific fitness values is convex; with concave trade-off functions, a monomorphic



**Fig. 1.** (Left panels) Gaussian fitness functions within the two habitats. (Right panels) The qualitative shape of the resulting fitness trade-off [curvature is exaggerated for clarity in (b)]. (a)  $(m_2 - m_1)/\sigma = 1.5$ , the fitness trade-off is concave; (b)  $(m_2 - m_1)/\sigma = 2.5$ , the middle part of the fitness trade-off is convex.

population is evolutionarily stable, whereas a linear trade-off results in a marginally stable allele.

Classic studies have demonstrated the importance of the shape of the trade-off function in the evolution of polymorphism. For example, Levins (1962) found that, in temporally variable environments, a mixture of different phenotypes is optimal if the fitness trade-off is convex, whereas a single phenotype is optimal if the trade-off is concave [as seen from below; Levins (1962) used an alternative definition resulting in the opposite usage of 'convex' and 'concave']. Note that Levins (1962) assumed hard selection and, therefore, always found a single phenotype to be optimal in spatially heterogeneous environments. In a resource competition model, MacArthur and Levins (1964) showed that a single generalist or two specialists will evolve depending on whether a trade-off function is more or less convex than an equilateral hyperbola.

Meszéna *et al.* (1997) investigated evolution in two habitats where density is regulated within each habitat according to the standard logistic growth model. This model resembles 'soft selection' in so far as density dependence operates within the habitats and, consequently, polymorphism can be maintained, but it resembles 'hard selection' in so far as selection affects population density. Like Kisdi and Geritz (1999), Meszéna *et al.* (1997) found that evolutionary branching leads to polymorphism if the difference between the habitats is sufficiently large. For very large differences, however, a monomorphic population specialist for one or the other habitat is evolutionarily stable. Day (2000) modelled resource competition within discrete habitats and found that an adaptive diversity of resource exploitation strategies may result. Although these models deviate from the classic model of

Levene (1953), they too highlight that multiple niche polymorphisms are often stable also in a long-term evolutionary sense.

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### APPENDIX

If the fitness of an allele is less than 1 when its frequency is zero, then the allele goes extinct if sufficiently rare, because a continuous fitness function takes values below 1 at very low frequencies provided that it is below 1 at zero frequency. If, however, the fitness of a rare allele is exactly 1 when the

frequency of the rare allele equals zero (as is the case for the ESS found by De Meeûs and Goudet, 2000), then it may be either greater or smaller than 1 if the allele is present at an arbitrarily low frequency; accordingly, a rare allele may or may not be able to invade the population. It is thus necessary to check whether all alternative alleles have fitness below 1 when they are present at a low positive frequency. (In matrix games, this amounts to the second part of the ESS condition being satisfied; see Maynard Smith, 1982, p. 14.)

Denote the fitness across the entire population of a rare allele  $a$  at a low frequency  $q$  in a population otherwise monomorphic for allele  $\hat{A}$  by  $V(q, a, \hat{A})$ . From equation (1):

$$V(q, a, \hat{A}) = c \frac{w_1(a)}{(1-q)w_1(\hat{A}) + qw_1(a)} + (1-c) \frac{w_2(a)}{(1-q)w_2(\hat{A}) + qw_2(a)} \quad (\text{A1})$$

For low values of  $q$ ,  $V(q, a, \hat{A})$  is approximately  $V(0, a, \hat{A}) + [\partial V/\partial q]_{q=0} q$ . In the model of Meeûs and Goudet (2000),  $V(0, a, \hat{A}) = F_{\hat{A}}(a) = 1$  for all  $a$ , and thus the fitness of a rare allele  $a$  is less than 1 if:

$$\left. \frac{\partial V}{\partial q} \right|_{q=0} = -c \frac{w_1(a)}{w_1(\hat{A})} \left[ \frac{w_1(a)}{w_1(\hat{A})} - 1 \right] - (1-c) \frac{w_2(a)}{w_2(\hat{A})} \left[ \frac{w_2(a)}{w_2(\hat{A})} - 1 \right] < 0 \quad (\text{A2})$$

Using  $V(0, a, \hat{A}) = c(w_1(a))/w_1(\hat{A}) + (1-c)(w_2(a))/w_2(\hat{A}) = 1$ , condition (A2) can be rewritten as

$$\left. \frac{\partial V}{\partial q} \right|_{q=0} = -\frac{c}{1-c} \left( \frac{w_1(a)}{w_1(\hat{A})} - 1 \right)^2 < 0 \quad (\text{A3})$$

which is fulfilled for any rare allele  $a$ .  $\hat{A}$  is thus indeed an ESS.

