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SELECTION IN CONTEXTS OF INTERSPECIFIC
COMPETITION

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The classical theory of community dynamics, as set forth in the work of Volterra (1926) and Lotka (1925), and in most of its modern outgrowths, does not take into account the genetic heterogeneity of the interacting populations. Not unexpectedly, the genetic and evolutionary outlook remains a source of challenges and expectations for the community theory. As an example of a challenge, Pimentel (1965) objected to “the assumption that the competing species themselves and their biotic environment remain genetically constant” and pointed to the need for reappraising the competitive exclusion principle—that intended touchstone of the theory. With regard to expectations, the explanation of the stability of complex ecosystems as the very consequence of complexity is now known to be quite problematic (May 1973*b*), and we are left with few explanatory alternatives, the main one being coevolution. As Maynard Smith put it in his provocative essay on neo-Darwinism (1969), “In evolutionary ecology these constants [which characterize the interactions between populations] become variables, but with a relaxation time large compared to the ecological time scale. Each species would evolve so as to maximize the fitness of its members. . . . What then are the criteria to be satisfied if an ecosystem not only is to be permanent, but is to give rise by evolution to permanent ecosystems of greater species diversity?”

The view given above may be presented the other way around: most of the recent enrichment of population genetics springs from ecology, not the least from community ecology. The adaptive values—phenomenological constants in population genetics—should be analyzed in terms of ecological, behavioral and developmental constraints and variables. As has been aptly summarized by Wimsatt (1970), the fitness coefficients, which population genetics takes as given, may depend on features of the environment, phenotypes, and organic and social interactions of the members of a population with one another and with members of other populations of the same and different species. “Population genetics then uses a parameter, the adaptive value, which must be further analyzed by theories of all other types of interaction. It is incomplete (though not incorrect) as a theory of evolution without them” (Wimsatt 1970). Clearly this “further analysis” underlies

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some recent developments, for instance, two which I use here: fitness set analysis (Levins 1968) and the concept of density-dependent fitness (Wright 1959; MacArthur 1962; Wallace 1968; Turner and Williamson 1968; Roughgarden 1971; Charlesworth 1971; Anderson 1971; Clarke 1972). This paper hinges on the prospects of interplay between community ecology and population genetics. The concept of density-dependent fitness is widened to include the density of competing species. The population genetics of one locus becomes, through this ecologically extended fitness, relevant for considering coevolution of competing species. The operation of selection in situations of interspecific competition was recently considered by Levin (1971) for the special case of asexual species. Here, a model for sexual species is put forward, and this leads to obtaining criteria for the polymorphic coexistence of two species and to examining some other outcomes of the concurrent action of selection and competition. Fitness set analysis is used to frame a discussion of a proposal by Pimental (1965) and Ayala (1966) that "reversals of competitive dominance," brought about by the different direction of selection when one species is abundant and when it is rare, constitute an evolutionary exit for situations of interspecific competition, leading eventually to coexistence.

SELECTION AT ONE LOCUS AFFECTING INTERSPECIFIC COMPETITION

1. *The Adaptive Values*

Consider two diploid sexually reproducing competing species with discrete generations. Suppose that a single autosomal locus with alleles A_1 and A_2 is segregating in the population of species A and another autosomal locus with alleles B_1 and B_2 is segregating in the population of species B . Suppose that both loci somehow affect the ongoing competition. The fitness measure used should portray the fact that there are genotypic differences in sensitivity to density-governing factors and to the inhibitory effect of the competitor species. To this end I will use as a measure of fitness a form of the "absolute selective value" of Wright (1959). Roughgarden (1971) and Anderson (1971) introduced a discrete-generation version of the density-dependent adaptive value of Wright (1959) and MacArthur (1962) in which genotypic fitnesses are given by linear functions of population size (or density) inspired in the familiar logistic equation of population growth. As the classical Gause-Witt (1935) equations of interspecific competition are pertinent extensions of the logistic equation, I will take them as the basis for extending the Roughgarden "adaptive values" to the competition context in the following fashion. The selective value of a genotype is assumed to drop off linearly with the size of its conspecific population and with the population size of the competitor species. Let the population size of species A in the generation t be $N^A(t)$ and that of the species B , $N^B(t)$, both measured as the number of newly formed zygotes in the t th generation. Then the adaptive values of the A_iA_j and B_iB_j genotypes will be

$$W_{ij}(t) = 1 + \frac{R_{ij}^A}{K_{ij}^A} [K_{ij}^A - N^A(t) - \alpha_{ij}N^B(t)], \quad (1)$$

$$V_{ij}(t) = 1 + \frac{R_{ij}^B}{K_{ij}^B} [K_{ij}^B - N^B(t) - \beta_{ij}N^A(t)]. \quad (2)$$

For any genotype, R_{ij} is the excess above 1 of its fitness, in the limit situation of absence of crowding, while K_{ij} is the reciprocal of the fraction by which each additional individual of the same species and of whatever genotype depresses that excess; α_{ij} (or β_{ij}) is also a relative—as compared with $1/K_{ij}$ —curbing of that excess caused by each additional individual of the competitor species. Some other interpretations of these parameters can be easily inferred from those given by Roughgarden (1971) and Anderson (1971).

Some restrictions should be imposed here. It is known (see Maynard Smith 1968, p. 26) that, unlike the continuous logistic model, the discrete one can exhibit oscillations about K provided R is outside the interval $(0, 1)$. To avoid these irregularities, I restrict R to within $(0, 1)$. Furthermore, because the number of offspring which a genotype produces cannot fall below zero, I must add the restriction that every W_{ij} of $V_{ij} \geq 0$.

2. The Model

Having defined the absolute adaptive values, I now formulate a model which will attend simultaneously to both gene pool evolution and population growth in conditions of interspecific competition. Let frequencies of A_1 and A_2 in the t th generation be, respectively, $p_1^A(t)$ and $p_2^A(t)$ and frequencies of B_1 and B_2 be, in turn, $p_1^B(t)$ and $p_2^B(t)$. These frequencies are measured among new zygotes of the t th generation. Suppose that there is random mating and absence of random variation in gene frequencies. Then the gene frequencies in $t+1$ th generation will be, by the equation of Wright (1955),

$$p_i^A(t+1) = p_i^A(t) \frac{W_i(t)}{\bar{W}(t)}, \quad i = 1, 2, \quad (3a)$$

$$p_i^B(t+1) = p_i^B(t) \frac{V_i(t)}{\bar{V}(t)}, \quad i = 1, 2. \quad (3b)$$

The population sizes (number of zygotes) in $t+1$ th generation will in turn be

$$N^A(t+1) = \bar{W}(t)N^A(t), \quad (4a)$$

$$N^B(t+1) = \bar{V}(t)N^B(t). \quad (4b)$$

Averages in these equations are defined as follows:

$$W_i(t) = \sum_j p_j^A(t) W_{ij}(t), \quad (5a)$$

$$V_i(t) = \sum_j p_j^B(t) V_{ij}(t), \quad (5b)$$

$$\bar{W}(t) = \sum_i \sum_j p_i^A(t) p_j^A(t) W_{ij}(t), \quad (6a)$$

$$\bar{V}(t) = \sum_i \sum_j p_i^B(t) p_j^B(t) V_{ij}(t). \quad (6b)$$

We might also cast these equations in another form, expressing changes in gene frequency and population numbers. Let changes in gene frequencies and population sizes be denoted by $\Delta p_i = p_i(t+1) - p_i(t)$ and $\Delta N = N(t+1) - N(t)$, respectively. Now the changes in gene frequency are

$$\Delta p_i^A = p_i^A(t) \frac{W_i(t) - \bar{W}(t)}{\bar{W}(t)}, \quad (7a)$$

$$\Delta p_i^B = p_i^B(t) \frac{V_i(t) - \bar{V}(t)}{\bar{V}(t)}, \quad (7b)$$

whereas the changes in population size are

$$\Delta N^A = N^A(t) \bar{R}^A(t) \left[1 - \frac{N^A(t)}{\tilde{K}^A(t)} - \frac{N^B(t)}{\tilde{C}^A(t)} \right], \quad (8a)$$

$$\Delta N^B = N^B(t) \bar{R}^B(t) \left[1 - \frac{N^B(t)}{\tilde{K}^B(t)} - \frac{N^A(t)}{\tilde{C}^B(t)} \right]. \quad (8b)$$

The last two equations include arithmetic means over the genotypes, the \bar{R} 's, and weighted harmonic means over the genotypes, the \tilde{K} 's and \tilde{C} 's. They are defined as follows:

$$\bar{R}^A(t) = \sum_i \sum_j p_i^A(t) p_j^A(t) R_{ij}^A, \quad (9a)$$

$$\bar{R}^B(t) = \sum_i \sum_j p_i^B(t) p_j^B(t) R_{ij}^B, \quad (9b)$$

$$\tilde{K}^A(t) = \frac{\bar{R}^A(t)}{\sum_i \sum_j p_i^A(t) p_j^A(t) (R_{ij}^A/K_{ij}^A)}, \quad (10a)$$

$$\tilde{K}^B(t) = \frac{\bar{R}^B(t)}{\sum_i \sum_j p_i^B(t) p_j^B(t) (R_{ij}^B/K_{ij}^B)}, \quad (10b)$$

$$\tilde{C}^A(t) = \frac{\bar{R}^A(t)}{\sum_i \sum_j p_i^A(t) p_j^A(t) [R_{ij}^A/(K_{ij}^A/\alpha_{ij})]}, \quad (11a)$$

$$\tilde{C}^B(t) = \frac{\bar{R}^B(t)}{\sum_i \sum_j p_i^B(t) p_j^B(t) [R_{ij}^B/(K_{ij}^B/\beta_{ij})]}. \quad (11b)$$

Equations (8a) and (8b) are formally analogous to a discrete version of the Gause-Witt continuous equations of interspecific competition. But the constant parameters of the classical model now vary as the gene frequencies change under selection. We are therefore in a situation proper of evolutionary ecology—as pointed in the excerpt by Maynard Smith, quoted

above—because here the constants of ecological dynamics become variables “but with a relaxation time large compared to the ecological time scale.” Hence, on interpreting equations (8), one can say that $1/\tilde{K}^A(t)$ and $1/\tilde{C}^A(t)$ are the inhibitory effects on species A ’s population growth rate of one individual of the species A itself and of the competing species, B , respectively, at generation t only. In general, as a result of selection, the parameters will continue to change until either an equilibrium is obtained or variability is exhausted. Consequently, the nature and range of genetic variability in values of these parameters affect the outcome of competition.

3. *The Outcomes of Selection and Interspecific Competition*

One might, as Levin (1971) did in his paper on competitive coevolution of asexual species, consider the consequences of admitting genetic variability in only one parameter at one time, or in combinations of two parameters. But since these cases are mere restrictions of the general one, namely, simultaneous genetic variability in the three parameters, R , K , and the competition coefficient, I will attack this situation at the outset by finding out what emerges from the use of stability theory as applied to the equilibrium points, both “internal” and “boundary.” Names given to points refer to their location inside or at the boundaries of the available state space (of the variables N^A , N^B , p^A , p^B) in which the process is represented. These points are those toward which the simultaneous operation of selection and competition can drive the process.

3.1. *Coexistence of two polymorphic species.*—To see whether this case is feasible, one must first look for the existence of an “internal” or “non-trivial” equilibrium point and then test the stability of the system at this point.

The “internal” equilibrium point is that at which simultaneous numerical and genetical equilibrium exists without any variable reaching the boundaries (0 for the numbers N^A and N^B , 0 or 1 for the frequencies). The obvious procedure in seeking this point is to obtain a nontrivial solution for the system of equations (7) and (8) all equated in zero. But this is a system of nonlinear equations. Of course, if one disregards in turn the genetical or the numerical variables, one is led to a pair of linear nonhomogeneous equations in N^A and N^B and to four linear homogeneous equations in p_1^A , p_2^A , p_1^B , and p_2^B . Thus, from (8) we have, for $\Delta N^A = 0$ and $\Delta N^B = 0$ (writing \hat{N} for the equilibrium population sizes and omitting the brackets of the \tilde{K} ’s and \tilde{C} ’s to indicate that they are evaluated at the equilibrium gene frequencies),

$$\begin{aligned}\tilde{C}^A \hat{N}^A + \tilde{K}^A \hat{N}^B - \tilde{C}^A \tilde{K}^A &= 0, \\ \tilde{K}^B \hat{N}^A + \tilde{C}^B \hat{N}^B - \tilde{C}^B \tilde{K}^B &= 0.\end{aligned}\tag{12}$$

From (7), $\Delta p = 0$ implies $W_i = \bar{W}$ or $V_i = \bar{V}$, respectively, for any i and either species A or species B . Hence, as $\bar{W} = 1$ and $\bar{V} = 1$ at numeri-

cal equilibrium (see eqq. [4]) and $p_1^A + p_2^A = 1$, $p_1^B + p_2^B = 1$, we have for species *A*

$$\begin{aligned} \hat{p}_1^A \frac{R_{11}^A}{K_{11}^A} (K_{11}^A - \hat{N}^A - \alpha_{11} \hat{N}^B) + \hat{p}_2^A \frac{R_{12}^A}{K_{12}^A} (K_{12}^A - \hat{N}^A - \alpha_{12} \hat{N}^B) &= 0, \\ \hat{p}_1^A \frac{R_{12}^A}{K_{12}^A} (K_{12}^A - \hat{N}^A - \alpha_{12} \hat{N}^B) + \hat{p}_2^A \frac{R_{22}^A}{K_{22}^A} (K_{22}^A - \hat{N}^A - \alpha_{22} \hat{N}^B) &= 0, \end{aligned} \quad (13)$$

and for species *B*

$$\begin{aligned} \hat{p}_1^B \frac{R_{11}^B}{K_{11}^B} (K_{11}^B - \hat{N}^B - \beta_{11} \hat{N}^A) + \hat{p}_2^B \frac{R_{12}^B}{K_{12}^B} (K_{12}^B - \hat{N}^B - \beta_{12} \hat{N}^A) &= 0, \\ \hat{p}_1^B \frac{R_{12}^B}{K_{12}^B} (K_{12}^B - \hat{N}^B - \beta_{12} \hat{N}^A) + \hat{p}_2^B \frac{R_{22}^B}{K_{22}^B} (K_{22}^B - \hat{N}^B - \beta_{22} \hat{N}^A) &= 0. \end{aligned} \quad (14)$$

One can solve (12) for numerical equilibrium using Cramer's rule:

$$\begin{aligned} \hat{N}^A &= \frac{\tilde{K}^A \tilde{C}^B (\tilde{C}^A - \tilde{K}^B)}{\tilde{C}^A \tilde{C}^B - \tilde{K}^A \tilde{K}^B}, \\ \hat{N}^B &= \frac{\tilde{K}^B \tilde{C}^A (\tilde{C}^B - \tilde{K}^A)}{\tilde{C}^A \tilde{C}^B - \tilde{K}^A \tilde{K}^B}. \end{aligned} \quad (15)$$

Subtracting in each pair, (13) or (14), the second equation from the first, remembering that $p_1 + p_2 = 1$, and putting

$$\begin{aligned} f_{ij}(\hat{N}^A, \hat{N}^B) &= \frac{R_{ij}^A}{K_{ij}^A} (K_{ij}^A - \hat{N}^A - \alpha_{ij} \hat{N}^B), \\ g_{ij}(\hat{N}^A, \hat{N}^B) &= \frac{R_{ij}^B}{K_{ij}^B} (K_{ij}^B - \hat{N}^B - \beta_{ij} \hat{N}^A), \end{aligned}$$

respectively, one can also solve for genetic equilibrium, which turns out to be

$$\begin{aligned} \hat{p}_1^A &= \frac{f_{22}(\hat{N}^A, \hat{N}^B) - f_{12}(\hat{N}^A, \hat{N}^B)}{f_{11}(\hat{N}^A, \hat{N}^B) + f_{22}(\hat{N}^A, \hat{N}^B) - 2f_{12}(\hat{N}^A, \hat{N}^B)}, \\ \hat{p}_1^B &= \frac{g_{22}(\hat{N}^A, \hat{N}^B) - g_{12}(\hat{N}^A, \hat{N}^B)}{g_{11}(\hat{N}^A, \hat{N}^B) + g_{22}(\hat{N}^A, \hat{N}^B) - 2g_{12}(\hat{N}^A, \hat{N}^B)}. \end{aligned} \quad (16)$$

Results (15) and (16) are deceiving in that they are circular. In (15), the numerical equilibrium can only be calculated if one already knows the equilibrium gene frequencies, and vice versa in (16). Nevertheless, there is a way out of this dilemma. Note that equations (13) and (14) may be regarded as two pairs of homogeneous linear equations in p_1^A , p_2^A , and p_1^B , p_2^B , respectively. Determinants of matrices of their coefficients must be zero for having nontrivial solutions. This leads to the following pair of quadratic equations:

$$\begin{aligned}
\frac{R_{11}^A}{K_{11}^A} (K_{11}^A - \hat{N}^A - \alpha_{11}\hat{N}^B) \frac{R_{22}^A}{K_{22}^A} (K_{22}^A - \hat{N}^A - \alpha_{22}\hat{N}^B) \\
= \left[\frac{R_{12}^A}{K_{12}^A} (K_{12}^A - \hat{N}^A - \alpha_{12}\hat{N}^B) \right]^2, \\
\frac{R_{11}^B}{K_{11}^B} (K_{11}^B - \hat{N}^B - \beta_{11}\hat{N}^A) \frac{R_{22}^B}{K_{22}^B} (K_{22}^B - \hat{N}^B - \beta_{22}\hat{N}^A) \\
= \left[\frac{R_{12}^B}{K_{12}^B} (K_{12}^B - \hat{N}^B - \beta_{12}\hat{N}^A) \right]^2.
\end{aligned}
\tag{17}$$

This system can be solved for N^A and N^B , though the procedure is tedious (Littlewood 1958): to find out the Bezout eliminant obtaining thus a quartic equation in, say, \hat{N}^A ; to solve this by the classical method of Descartes; and then to obtain the corresponding values of \hat{N}^B . It will be shown below that only one point (\hat{N}^A , \hat{N}^B) is satisfactory for a globally stable equilibrium. This can be substituted into (16) for calculating the equilibrium gene frequencies \hat{p}_i^A and \hat{p}_i^B .

Some restrictions imposed by the former equations will prove to be useful in establishing the existence of the equilibrium point(s) and in elucidating the stability conditions. Thus, the conditions for equilibrium $\bar{W} = 1$ and $\bar{V} = 1$ can be written

$$\begin{aligned}
\sum_i \sum_j p_i^A p_j^A \frac{R_{ij}^A}{K_{ij}^A} (K_{ij}^A - \hat{N}^A - \alpha_{ij}\hat{N}^B) &= 0, \\
\sum_i \sum_j p_i^B p_j^B \frac{R_{ij}^B}{K_{ij}^B} (K_{ij}^B - \hat{N}^B - \beta_{ij}\hat{N}^A) &= 0.
\end{aligned}
\tag{18}$$

These are, of course, the same as equations (12), expanded in a slightly different form. As two of the four terms in each summation are equal, we have only three terms on the left-hand side of each equation. This implies that at least one of the terms is bound to be negative and at least one positive. Hence, the equilibrium point in the (N^A , N^B) plane will be above at least one of the straight lines $K_{ij}^A - N^A - \alpha_{ij}N^B = 0$ and below at least one other. Also, two of the lines $K_{ij}^B - N^B - \beta_{ij}N^A = 0$ are boundaries within which the equilibrium point should lie. So we have one admissible region for the equilibrium point to be in, imposed, so to speak, by species *A*, and another region imposed by species *B*. Obviously, the actual equilibrium point must lie inside the overlapping of these regions, the overlapping being a necessary condition for the existence of equilibrium. It is possible to show that in each of these regions the line of the heterozygote has to be the "superior" (or external) boundary or the "inferior" (or internal) one. If this were not the case, both boundaries of each admissible region would be lines of homozygous genotypes. Therefore, the respective left-hand sides of equations (17) would consist of a negative factor (that whose line

$K_{ij}^A - N^A - \alpha_{ij}N^B = 0$ or $K_{ij}^B - N^B - \beta_{ij}N^A = 0$ is below the equilibrium point) and a positive factor (that whose line lies above \hat{N}^A, \hat{N}^B). But the right-hand sides of (17) are squares, that is, necessarily positive, and (17) could not be satisfied. So, over- or underdominance in the boundaries of the admissible regions is another necessary condition for the existence of a nontrivial equilibrium. This will mean over- or underdominance in the K 's and/or in the (K^A/α) 's or (K^B/β) 's, depending on the location of the admissible region. Note that the equilibrium point will be above both homozygous lines; this constraint helps fix the edges of the admissible region for each species. Some cases are shown in figure 1.

Curves in the plane (N^A, N^B) defined by equations (17) are second-degree curves, segments of which are contained within admissible regions. Every intersection of these two curves would be an equilibrium point. Now, if both admissible regions completely intersect each other, curves within them intersect at one and only one point. In other words, there will be a unique equilibrium point if each boundary line of the admissible region for one species passes across both boundaries of the other species' region. This is sufficient but not necessary for the existence of equilibrium points.

I now discuss the stability of the "internal" equilibrium point(s). The pertinent Jacobian matrix to be evaluated at equilibrium is

$$J = \begin{vmatrix} \frac{\partial N^A(t+1)}{\partial N^A(t)} & \frac{\partial N^A(t+1)}{\partial N^B(t)} & \frac{\partial N^A(t+1)}{\partial p_1^A(t)} & \frac{\partial N^A(t+1)}{\partial p_1^B(t)} \\ \frac{\partial N^B(t+1)}{\partial N^A(t)} & \frac{\partial N^B(t+1)}{\partial N^B(t)} & \frac{\partial N^B(t+1)}{\partial p_1^A(t)} & \frac{\partial N^B(t+1)}{\partial p_1^B(t)} \\ \frac{\partial p_1^A(t+1)}{\partial N^A(t)} & \frac{\partial p_1^A(t+1)}{\partial N^B(t)} & \frac{\partial p_1^A(t+1)}{\partial p_1^A(t)} & \frac{\partial p_1^A(t+1)}{\partial p_1^B(t)} \\ \frac{\partial p_1^B(t+1)}{\partial N^A(t)} & \frac{\partial p_1^B(t+1)}{\partial N^B(t)} & \frac{\partial p_1^B(t+1)}{\partial p_1^A(t)} & \frac{\partial p_1^B(t+1)}{\partial p_1^B(t)} \end{vmatrix}.$$

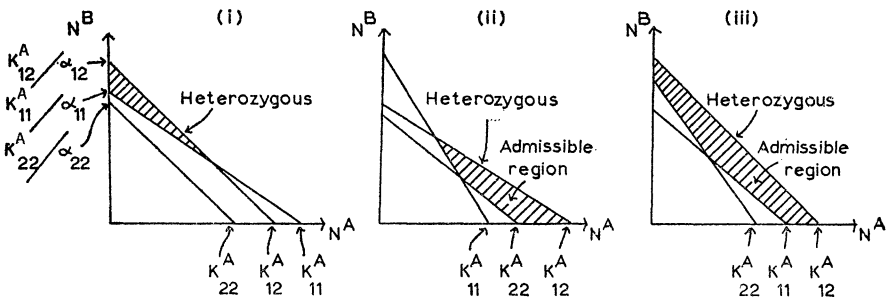


FIG. 1.—Admissible region for the equilibrium points to be in as determined by species A . (i) Heterozygote superior in K^A/α . One homozygous line is consistently below the other two lines. (ii) Heterozygote superior in K^A . One homozygous line crosses the other two lines. (iii) Heterozygote superior in both K^A and K^A/α . The homozygous lines intersect each other.

Two of these derivatives are zero at equilibrium,

$$\left. \frac{\partial N^A(t+1)}{\partial p_1^A(t)} \right|_{eq} = \hat{N}^A \left. \frac{\partial \bar{W}(t)}{\partial p_1^A(t)} \right|_{eq} = 0,$$

$$\left. \frac{\partial N^B(t+1)}{\partial p_1^B(t)} \right|_{eq} = \hat{N}^B \left. \frac{\partial \bar{V}(t)}{\partial p_1^B(t)} \right|_{eq} = 0,$$

because the partial derivatives on the right-hand sides are equivalent to the left-hand sides of equations (13) and (14). Furthermore, four derivatives are identically zero:

$$\frac{\partial N^A(t+1)}{\partial p_1^B(t)} \equiv 0, \quad \frac{\partial N^B(t+1)}{\partial p_1^A(t)} \equiv 0,$$

$$\frac{\partial p_1^A(t+1)}{\partial p_1^B(t)} \equiv 0, \quad \frac{\partial p_1^B(t+1)}{\partial p_1^A(t)} \equiv 0.$$

Now, partitioning the Jacobian matrix in four 2×2 matrices,

$$J = \begin{bmatrix} J_{11} & J_{12} \\ J_{21} & J_{22} \end{bmatrix},$$

one can see that $J_{12} = 0$ and that only the principal diagonal of J_{22} consists of nonzero elements. Hence, the characteristic equation of J can be written as

$$\det(J_{22} - I\lambda) [\lambda^2 - (Tr J_{11})\lambda + \det(J_{11})] = 0, \quad (19)$$

where \det and Tr denote, respectively, determinant of and trace of a certain matrix. The eigenvalues will be

$$\lambda_1 = \left. \frac{\partial p_1^A(t+1)}{\partial p_1^A(t)} \right|_{eq}, \quad \lambda_2 = \left. \frac{\partial p_1^B(t+1)}{\partial p_1^B(t)} \right|_{eq},$$

as well as the two roots of the quadratic equation obtained by equating to zero the expression between brackets in (19). Now, for local stability at the equilibrium point(s), each eigenvalue must be less than 1 in modulus. The first two eigenvalues are

$$\lambda_1 = 1 - \left[\frac{R_{12}^A}{K_{12}^B} (K_{12}^A - \hat{N}^A - \alpha_{12}\hat{N}^B) - \frac{R_{11}^A}{K_{11}^A} (K_{11}^A - \hat{N}^A - \alpha_{11}\hat{N}^B) \right], \quad (20)$$

$$\lambda_2 = 1 - \left[\frac{R_{12}^B}{K_{12}^B} (K_{12}^B - \hat{N}^B - \beta_{12}\hat{N}^A) - \frac{R_{11}^B}{K_{11}^B} (K_{11}^B - \hat{N}^B - \beta_{11}\hat{N}^A) \right],$$

both of which are less than 1 if there is overdominance in the boundaries of the admissible regions of species A and B , respectively.

The necessary and sufficient conditions for both roots of the quadratic equation $\lambda^2 - (Tr J_{11}) \lambda + \det(J_{11}) = 0$ to be less than 1 in modulus are (see Goldberg 1958)

$$-[1 + \det(J_{11})] < \text{Tr } J_{11} < [1 + \det(J_{11})], \quad \det(J_{11}) < 1. \quad (21)$$

To look for the fulfillment of the conditions, we need the following derivatives, which are the elements of J_{11} :

$$\begin{aligned} \left. \frac{\partial N^A(t+1)}{\partial N^A(t)} \right|_{eq} &= 1 - \hat{N}^A \sum_i \sum_j \hat{p}_i^A \hat{p}_j^A \frac{R_{ij}^A}{K_{ij}^A} \equiv 1 - \hat{N}^A \bar{Z}^A, \\ \left. \frac{\partial N^B(t+1)}{\partial N^B(t)} \right|_{eq} &= 1 - \hat{N}^B \sum_i \sum_j \hat{p}_i^B \hat{p}_j^B \frac{R_{ij}^B}{K_{ij}^B} \equiv 1 - \hat{N}^B \bar{Z}^B, \\ \left. \frac{\partial N^A(t+1)}{\partial N^B(t)} \right|_{eq} &= -\hat{N}^A \sum_i \sum_j \hat{p}_i^A \hat{p}_j^A \frac{R_{ij}^A}{K_{ij}^A / \alpha_{ij}} \equiv -\hat{N}^A \bar{Q}^A, \\ \left. \frac{\partial N^B(t+1)}{\partial N^A(t)} \right|_{eq} &= -\hat{N}^B \sum_i \sum_j \hat{p}_i^B \hat{p}_j^B \frac{R_{ij}^B}{K_{ij}^B / \beta_{ij}} \equiv -\hat{N}^B \bar{Q}^B. \end{aligned}$$

Therefore,

$$\begin{aligned} \text{Tr } J_{11} &= 2 - \hat{N}^A \bar{Z}^A - \hat{N}^B \bar{Z}^B \\ \det(J_{11}) &= 1 - \hat{N}^A \bar{Z}^A - \hat{N}^B \bar{Z}^B + \hat{N}^A \hat{N}^B (\bar{Z}^A \bar{Z}^B - \bar{Q}^A \bar{Q}^B). \end{aligned}$$

Since $\hat{N}^A \bar{Z}^A$ and $\hat{N}^B \bar{Z}^B$ are both less than 1, the condition $\det(J_{11}) < 1$ is always satisfied. As to the other conditions, we have

$$\begin{aligned} -(2 - \hat{N}^A \bar{Z}^A - \hat{N}^B \bar{Z}^B) - \hat{N}^A \hat{N}^B (\bar{Z}^A \bar{Z}^B - \bar{Q}^A \bar{Q}^B) &< 2 - \hat{N}^A \bar{Z}^A - \hat{N}^B \bar{Z}^B \\ &< (2 - \hat{N}^A \bar{Z}^A - \hat{N}^B \bar{Z}^B) + \hat{N}^A \hat{N}^B (\bar{Z}^A \bar{Z}^B - \bar{Q}^A \bar{Q}^B). \end{aligned}$$

Obviously, this can be true only if $\bar{Z}^A \bar{Z}^B > \bar{Q}^A \bar{Q}^B$. This condition can be easily converted to $\tilde{C}^A \tilde{C}^B > \tilde{K}^A \tilde{K}^B$, and, since we can only admit \hat{N}^A and \hat{N}^B positive, we are left, by virtue of equation (15), with the pair of conditions $\tilde{C}^A > \tilde{K}^B$ and $\tilde{C}^B > \tilde{K}^A$.

In summary, the following four conditions must be satisfied for local stability at the equilibrium point: (1) and (2), overdominance in the boundaries of the (necessarily overlapped for the existence of equilibrium) admissible regions of both species; (3) and (4), $\tilde{C}^A > \tilde{K}^B$ and $\tilde{C}^B > \tilde{K}^A$ at equilibrium. Note the analogy of (3) and (4) with the usual ecological conditions for the stable coexistence of two competing species.

Of course, fulfillment of these conditions does not exclude the possibility of having $f_{12} - f_{11} \geq 2$ or $g_{12} - g_{11} \geq 2$. However, Charlesworth (1971) considered an analogous exception for density-dependent selection in one species, pointing out that even the most extreme case of this kind, which is rather farfetched, would only lead to sustained oscillations. So the conditions given are necessary and sufficient for stability if not for asymptotic stability.

Local stability is not enough if one is interested in the possibility of two species coexisting at large, both being polymorphic. Global stability is what

is relevant here, and I now turn to this. As Lewontin (1969) remarked, global stability is a negative condition because a point is globally stable only if no other point in the available state space is a stable or a cyclic point. Therefore, I shall now look for the instability of the "boundary" equilibrium points to prove the following: *the necessary and sufficient conditions for an equilibrium point to be globally stable are* (1) *overdominance in both K^A and K^A/α in species A*; (2) *overdominance in both K^B and K^B/β in species B*; (3) $K_{11}^A/\alpha_{11}, K_{22}^A/\alpha_{22} > \tilde{K}^{*B}$; and (4) $K_{11}^B/\beta_{11}, K_{22}^B/\beta_{22} > \tilde{K}^{*A}$.

They are necessary. To see this, assume that one internal point is stable and the boundary points unstable. Look at the boundary equilibrium point ($N^A = 0, N^B = \tilde{K}^{*B}, p_1^A = 1, p_1^B = p_{1^B}^*$) where the asterisk denotes the equilibrium attained by species *B* when it is alone and there is overdominance in K^B . The \tilde{K}^{*B} can easily be calculated independent of gene frequencies, as shown by Charlesworth (1971) and Anderson (1971). Suppose, further, that one of the conditions does not hold, for example, condition (3), $K_{11}^A/\alpha_{11} < \tilde{K}^{*B}$. Now, the equation for change in numbers of species *A* is at the point $\Delta N^A = (R_{11}^A/K_{11}^A) (K_{11}^A - \alpha_{11}\tilde{K}^{*B})$; since the bracket will be negative, species *A* would not increase and the point would be stable, in contradiction with the assumption. The same contradiction would occur at the point ($N^A = 0, N^B = \tilde{K}^{*B}, p_1^A = 0, p_1^B = p_{1^B}^*$) if $K_{22}^A/\alpha_{22} < \tilde{K}^{*B}$. Suppose now that, instead of (3), the condition not fulfilled is (1), because $K_{11}^A/\alpha_{11} < K_{12}^A/\alpha_{12} < K_{22}^A/\alpha_{22}$. Look again at the last boundary point considered. The adaptive values W_{22} and W_{12} at that point are $W_{22} = 1 + (R_{22}^A/K_{22}^A) (K_{22}^A - \alpha_{22}\tilde{K}^{*B})$ and $W_{12} = 1 + (R_{12}^A/K_{12}^A) (K_{12}^A - \alpha_{12}\tilde{K}^{*B})$. Here $W_{22} > 1, W_{12} > 1$, and $W_{22} > W_{12}$, because of condition (3) and the assumed intermediacy of the heterozygote in K^A/α . Since $p_1^A = 0$ and $p_2^A = 1$ at the point, $W_1 = W_{12}$ and $W_2 = W_{22}$ (see eqq. [5]). Moreover $\bar{W} = W_{22}$. Hence, equations (7) show that change in frequency of p_2^A is zero and the change in frequency of p_1^A is negative, the boundary point being stable, in contradiction with our initial assumption. Similar reasoning can be applied to the other conditions—by looking for exceptions at different boundary points—to show that they altogether are necessary.

The proof of sufficiency is straightforward, because if the conditions hold, all the boundary points are unstable and there is one and only one stable internal equilibrium point (see the sufficient conditions for the existence of equilibrium and the necessary and sufficient conditions for local stability). Figure 2 illustrates a case of global equilibrium.

The proof just sketched concludes this examination of polymorphic coexistence. Of course, selection operating in the frame of competitive interactions between species can produce a variety of other outcomes besides this one. But these other cases can be envisaged as particular instances of the one discussed, and criteria for them to be globally stable can be easily assessed by comparison with the given set of conditions. Therefore, I will not discuss this gamut of outcomes.

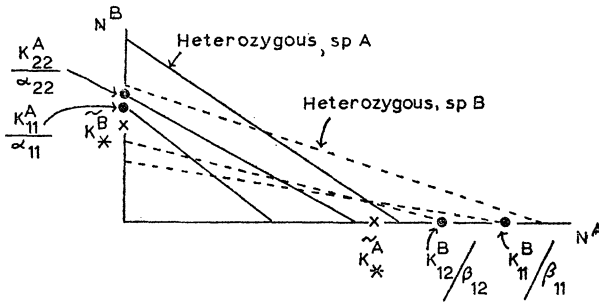


FIG. 2.—Example of a globally stable situation. The lines corresponding to genotypes of species *A* are depicted as full lines, those corresponding to species *B* as broken lines. The lines are so located that the necessary and sufficient conditions for a globally stable equilibrium hold (see text).

FITNESS SET ANALYSIS AND REVERSALS OF DOMINANCE

An interesting hypothesis, concerning the outcome of competition when selection acts concomitantly, is that, if one species, *A*, is excluding another, *B*, as *B* becomes sparse the individuals of *A* will contend principally between themselves whereas the individuals of *B* must face mainly competitive interactions with the other species. Thus, the selective pressure will be toward better intraspecific performance in species *A* and for interspecific competitive ability in the sparse species. If there is enough time left and sufficient genetic variability, species *B* would evolve into a better competitor. As it does so, its numbers increase and *B* becomes the more abundant species. The direction of evolution is then reversed, and the process continues until coexistence is achieved. These reversals of dominance are more likely to occur the more similar the competing species are in their competitive abilities. A first version of this hypothesis was suggested by Park and Lloyd (1955), but experiments on competition between *Tribolium castaneum* and *T. confusum* led them to reject it. Pimentel et al. (1965) and Ayala (1966, 1969) came back to the idea, elaborated it further, and afforded it support by investigating competition between the blowfly and the housefly and between some species of *Drosophila*.

As the argument is cogent and the evidence good, it is worth attempting a mathematical formulation which could render it more precise. A fitness set analysis seems suitable.

Fitness set analysis (Levins 1962, 1968) is a translation to biology of some microeconomics and operation research thinking. The gist is as follows: two different components of fitness, for example, those due to the effect of a phenotypic variable in two kinds of environment, are taken as the axis of a plane coordinate system. As there is usually a constraint between these components, only a subset of the plane defines the collection of realizable genotypes in a certain species. This is called the fitness set. From these genotypes, one is selected as optimal, that is, favored by natural selection, by plotting projections onto the plane of a function, called the adaptive

function, which combines in a proper form both components of fitness, and looking for that genotype of the fitness set which maximizes the adaptive function.

I will use the carrying capacity K , which is the reciprocal of the sensitivity to intraspecific competition, and $1/\alpha$, the reciprocal of the relative sensitivity to interspecific competition, as variables for the fitness set analysis.

Consider the formulae for K and α in terms of renewable resources given by MacArthur (1972):

$$K^A = \frac{\sum_j K_j w_j a_j - T^A}{\sum_j (K_j/r_j) w_j a_j^2}, \quad \alpha = \frac{\sum_j (K_j/r_j) w_j a_j b_j}{\sum_j (K_j/r_j) w_j a_j^2}.$$

These formulae were arrived at by assuming a "logistic" pattern of resource renewal. The K_j and r_j are carrying capacity and intrinsic rate of growth of resource j , whereas w_j is weight per unit quantity of this same resource. The parameters typical of the consumers (and indirect competitors) A and B are a_j and b_j ; they are exploitative abilities defined as the probability that during a unit time a given individual of species A (or B) encounters and eats a given individual of resource j . Also characteristic of consumer A is T^A , the weight of food needed by each individual of this species for maintenance without population growth. Of course, these formulae give K 's and α 's less general than the original phenomenological constants contained in the Gause-Witt equations. They depend on some debatable specific assumptions made in the derivation, hold only for indirect or exploitative competition, and are valid only at the equilibrium point. But they provide a good starting point. We can see that K and $1/\alpha$ are genotypic variables—each couple of values $(K, 1/\alpha)$ specifies one genotype in the fitness set—because the a 's and T^A are genotypic variables. That is, each feasible genotype of species A is characterized by one value of T^A and a probability distribution (a_1, a_2, \dots, a_n) on the n resources supplied by the environment. Some of the a 's are positive, but some others are zero, since the genotype in question is, in general, unable to catch, or to metabolize, some of the available resources.

Suppose that only two resources are available, that both can be used by any genotype of both competitors, that T^A is the same for any genotype of species A , and that the probability u of failing to obtain any resource per unit time is also the same for every genotype. Then, there is a constraint between the a 's: $a_1 + a_2 = 1 - u$. Therefore, K_A and $1/\alpha$ are parametric functions of one parameter, a_1 , say. By plotting them, or eliminating the parameter, or calculating $dK^A/d(1/\alpha)$, one finds that K^A is a decreasing function of $1/\alpha$, which gives the frontier of the fitness set. But even without the restrictions imposed in this example, we can guess the form of the frontier merely by examining the formulae. Thus, K^A will be increased (1) by enhancing the a 's for the most rapidly growing (high r_j) resources; (2) by adding a new resource, shared or not by species B ; and/or (3) by diminishing T^A . Of these procedures, only recruiting resources not shared

by the competitor will clearly be achieved without simultaneously inflating α . Even depressing T^A may also heighten α , because a direct relationship between T^A and the α 's is likely; to increase the chance of gathering food exacts a cost in maintenance of the phenotypic weapons which enable one to do so. Thus, if the evolutionary moves allowable to the species are phenotypic changes that permit procurement of new, unshared resources, then the enhancement of K and the avoidance of interspecific composition coincide, and the fitness set boundary will rise toward a certain maximum K imposed by the environment. A similar situation would occur if the available variability is such that it is possible to increase the ability to exploit fast-growing resources that are poorly used by other species at the expense of resources better handled by the competitor. Otherwise, the fitness set boundary will fall, starting from a point with high K^A and low $1/\alpha$. Of course, a horizontal boundary, meaning noncorrelated K and $1/\alpha$, is unlikely but not inconceivable. What is most plausible is to recognize that the realizable genotypes can be the kind that conflate all the effects separately portrayed above. Thence, the slope of the fitness set boundary will depend on which factors predominate. The most sensible fitness sets are depicted in figure 3.

In order to provide a germane adaptive function, one need only recall the determinant role played in the previously presented one-locus model by the function $K^A - N^A - \alpha N^B$. If this is used, the adaptive function for conditions of dominance by species A will be $A_1 = K^A$ and for conditions of dominance by species B will be $A_2 = K^A - \alpha K^B$. Plotting the level curves of the first function on the plane $(K^A, 1/\alpha)$ will give a family of horizontal straight lines of equation $K^A = A_1$, one for each constant value of A_1 . The second-function level curves are hyperbolas with the K^A axis and the horizontal line $K^A = A_2$ as asymptotes. The equation of these hyperbolas is $K^A(1/\alpha) - A_2(1/\alpha) - K^B = 0$, one hyperbola for each constant value of A_2 . Both kinds of adaptive function, and one fitness set, are represented in figure 4.

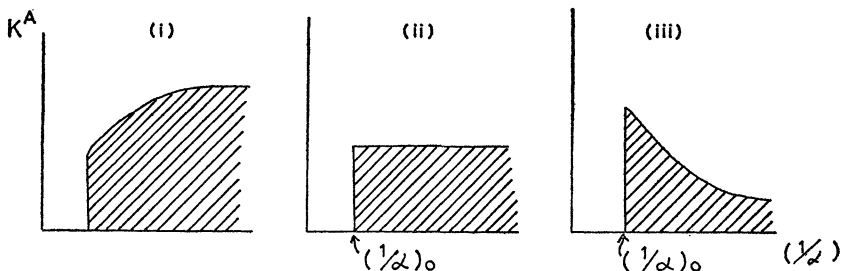


FIG. 3.—Plausible fitness sets. Sets of feasible genotypes of species A . There is a limit in K^A above which no conceivable genotype could exist. Also, it is impossible to diminish $1/\alpha$ below a certain boundary $(1/\alpha)_0$. (i) The insensitivities to intraspecific competition (K^A) and interspecific competition ($1/\alpha$) increase simultaneously. (ii) Uncorrelated insensitivities. (iii) In order to increase one insensitivity, the other must be decreased.

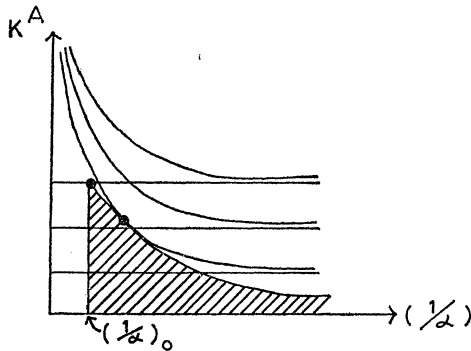


FIG. 4.—Two families of adaptive level lines. Projections on the $(K^A, 1/\alpha)$ plane of the two adaptive functions corresponding to conditions of scarcity (hyperbolas) or abundance (straight lines) of a species engaged in interspecific competition. A fitness set of the kind portrayed in fig. 3(iii) is also included, and the location of the optimal genotypes under one or the other condition is shown.

Figure 4 shows that the direction of selection, that is, the genotype selected as optimal, in conditions of competitive dominance either by species A or by species B can differ or coincide, depending on the form of the fitness set. For fitness sets such as those depicted in figure 3(i) and (ii), the preferred genotype in conditions of A dominance is the same as the one favored when species B predominates. On the other hand, a declining slope of the fitness set outer boundary will imply a difference in the choice of selection under one or the other condition. In such a case, selection will work toward the improvement of insensitivity to intraspecific competition of a species when this is competitively dominant and abundant and for the improvement of interspecific competitive ability, or insensitivity to interspecific competition, at the expense of some intraspecific competitive ability when it is sparse. This change in the direction of selection happens as claimed by Pimentel and Ayala. Nevertheless, note that even when the slope of the fitness set border falls, selection may fail in discriminating favored competitive abilities corresponding to one situation or the other (abundance or sparseness). This will occur when the slope is too negative. More precisely, let $f(1/\alpha)$ be the function which describes the external boundary of the fitness set, and note that the slope of the hyperbolas which are the level lines of adaptive function A_2 is $-K^B/(1/\alpha)^2$. Then, if $f'(1/\alpha) < -K^B/(1/\alpha)^2$ at any point beyond $(1/\alpha)_0$ (see fig. 4), the fitness set boundary will intersect somewhere to the hyperbolas and the only possible point of tangency will be that corner of the fitness set at which K^A is maximal and $(1/\alpha)$ minimal. The biological meaning of this is almost obvious: if the "opportunity cost," to borrow a concept from economics, of decreasing α is too high, that is, if, to decrease α a bit, it is necessary to decrease K^A a lot, then selection cannot indulge in the luxury of sometimes preferring a decreased α . Therefore, selection will always work to enhance K^A , irrespective of the abundance or sparseness of the species A population.

DISCUSSION

This paper has a twofold theme: the introduction of competition ecology into the population genetics of selection in sexual species and the connected, though admittedly much less successful, attempt to determine, in selection theory, what begets the stability of communities, currently a main inquiry in ecology.

The extension of classical one-locus selection theory is accomplished without much trouble, occupies most of the paper, and is, alas, less interesting than the ecological theme. As always happens in selection studies, the possibility of nontrivial equilibria was examined and criteria were obtained for the polymorphic coexistence of two species. Here again a familiar condition for selective polymorphism, overdominance, turned out to be required: heterosis in K_{ij} or K_{ij}/α_{ij} for local stability and heterosis in both K_{ij} and K_{ij}/α_{ij} for global stability. The other conditions which must hold are, not unexpectedly, related to the ecological requirement of coexistence.

Note that in some cases interspecific competition can cause polymorphism. For example, if $K_{12}^A \leq K_{11}^A$, K_{22}^A , but $K_{12}^A/\alpha_{12} > K_{11}^A/\alpha_{11}$, K_{22}^A/α_{22} , and K_{11}^A/α_{11} , $K_{22}^A/\alpha_{22} > K^B$, B being monomorphic, then species A on its own would be monomorphic but will coexist and be polymorphic when competing with species B .

The ecological theme is as follows. It has long been argued that increasing the number of links and alternative pathways in a trophic web warrants permanence of the community, so long as this increased connectance helps in absorbing environmental shocks without much perturbation. This conventional view has been recently challenged, mainly by May (1971, 1973*a*, 1973*b*). In fact, the mathematical argument seems to run the other way around: "The moral emerging first from generalized multispecies Lotka-Volterra models, then from models of randomly assembled food webs, and finally from qualitative stability theory, is that as a mathematical generality increased multispecies trophic complexity makes for lowered stability" (May 1973*b*). However, the biological realities happen to be that enhanced complexity is commonly correlated with greater stability. The facts call for an explanation outside the previous complexity-leads-to-stability argument. A promising conjecture is that coevolution gives a key to the riddle of complex and permanent communities. That is, the operation of intraspecific natural selection in interacting species could beget mutual adjustments between the coevolving populations, thus fostering a delicately balanced complex web of such a very special kind that complexity would be stable and, moreover, more complex systems could evolve without getting rid of permanence. But this evolution of balanced complexity is not by any means an obvious consequence of individual selection. Hence, the stage is set to begin questioning the evolutionary consequences of recognizing that genetic variability affects, and natural selection acts on, the parameters of the classical pairwise interactions of ecology. For example, on the basis of the model presented above, we may ask whether abandoning the

usual view of competing species as if monomorphic and admitting genetic variability into the picture render coexistence more likely. If we persist in demanding global stability, we can see from figure 2 that coexistence with variability exacts more restrictive conditions than plain monomorphic coexistence, for each homozygote of one species must be able to coexist with both homozygotes of the other species if polymorphic coexistence is to last. Yet, to have a bet on each side, I insist that my model is clearly limited in some respects. First, it is assumed that each genotype ignores the differentiation into genotypes of the competitor species, experiencing competition as a sort of mass action. Second, only genotype-specific sensitivity to competition is included in the model and not the ability to inhibit the competitor. In fact, Levin (1969), by considering both components of competitive performance, was able to produce reversals of dominance in his computer simulations of competition between sexual species.

Still, more significant, two points are missing in my model: plurality of loci and mutation. A simple method of taking all this into account is fitness set analysis, and a version of it was applied in this paper to investigate a part of the Pimentel argument, namely, that the direction of selection changes according to whether a species involved in competition is numerically dominant or rare. The conclusion is that this should happen except when the same genotypes are the best in both intra- and interspecific competitive ability. Another exception is when improving competitive ability demands a too onerous curtailing of the carrying capacity.

SUMMARY

By extending the concept of density-dependent fitness to include the density of a competitor species, one can study the operation of selection in situations of competition between two sexual species. A model is put forward considering one biallelic locus in each species and assuming these loci to affect competition somehow. The fitnesses are linearly decreasing functions of the population densities. The necessary and sufficient conditions for globally stable polymorphic coexistence of the species are stated. On these grounds, and those provided by a fitness set analysis of the directions of selective pressure when a competing species is abundant or sparse, the relevance of coevolution of ecologically interacting species for the enigma of stability in complex ecosystems is discussed.

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