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Abundant Multilocus Polymorphisms Caused by Genetic Interaction Between Species on *Trait-for-Trait* Basis

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This paper deals with the problem of polymorphism maintenance in species coevolution mediated by selection for quantitative traits controlled by *Mendelian* genes. We showed here that the conditions for polymorphism maintenance in interacting species can be deduced from the behavior of the isolated partners in stable and changing environments. This allows also to address such difficult questions as evolution of sex and recombination, that can not be considered properly in non-Mendelian models. An abundance of polymorphic regimes was revealed in the proposed genetic model. The obtained results demonstrate a remarkable property of trait-dependent coevolution concerning the conditions for maintenance of genetic polymorphism: what seems to be more realistic, that is, non-equal gene effects and deviation from purely additive within-locus gene action, promotes polymorphism.

1. Introduction

Theoretical ecology is rich in models of the dynamics of multispecies communities. But what about genetic evolution of the species within the communities? This is an extremely challenging and complex problem and hence, from an evolutionary perspective, relatively little effort has been invested in the analysis of complex multispecies interactions influenced by multiple genes. The fact that species evolution is directed by both abiotic and biotic factors makes this poorly studied problem a primary target for evolutionary theory. A genetic perspective is essential for ecological theory: even qualitative features of community dynamics may crucially depend on the population genetic structure of the participating species. Here we analyse a key factor underpinning evolutionary biology, namely, the *maintenance of polymorphism* resulting from genetic interactions of species, which are governed by mutual selection for additively controlled quantitative traits.

Attempts to specify and model interactions between species at the *genotype level* inevitably encounter difficulties associated with a great number of genotypes involved. For example, complex genetic systems control the relationships between plants and their pests and pathogens (Burdon, 1987; Frank, 1994a). Even more elaborate are the polymorphic systems determining resistance and virulence in animals (especially vertebrates) and their parasites (May & Anderson, 1983; Hamilton, 1990). "Gene-for-gene" (G&G) interactions are the best known example of antagonistic relationships (Vanderplank, 1978; Bell & Maynard Smith, 1987; Thompson & Burdon, 1992). However,

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less specific interactions are also known, like those characterizing durable polygenic, or horizontal, resistance of plants to pathogens; these are of great evolutionary and agricultural importance (Thompson & Burdon, 1992). Such interactions can be formalized in terms of "trait-for-trait" (T&T) models and may also be characteristic for other interacting communities such as "predator–prey", "several competitors for a common limited resource", "plant–pollinator systems", etc. Unfortunately, the question of polymorphism maintenance in such systems is quite difficult to analyse (Hamilton, 1990, 1993).

Several ecological–genetic models have been proposed to analyse the coevolution of species assuming heritable variation and evolution of quantitative traits determining the species relationships (Kiester *et al.*, 1984; Abrams, 1986; Saloniemi, 1993; Frank, 1994b; Dieckmann *et al.*, 1995; Gavrilets, 1997; Law *et al.*, 1997). However, when addressing such questions as polymorphism maintenance, and especially, sex and recombination evolution, direct genetic (*Mendelian*) formulation becomes crucial. We are familiar with only a few attempts of multilocus genetic modelling of T&T interspecific interaction (Hamilton, 1993; Preygel & Korol, 1990; Korol *et al.*, 1994; Doebeli, 1996a, b, 1997). Multilocus trait-based models have also been used to analyse intraspecific competition (Loeschcke & Christiansen, 1984; Korol *et al.*, 1994; Doebeli, 1996a, b). Here we consider the conditions of polymorphism maintenance in a simple and natural class of T&T multilocus models of species genetic interaction allowing the modelling of multispecies communities.

2. The Model

Consider a community of q panmictic populations (of diverse species) with non-overlapping generations. We assume that each population can be characterized by a set of quantitative traits that determine its interactions with the remainder members of the community. Let Z_s be the vector of mean values of these traits concerning selection pressure experienced by the s-th population ($s = 1, \ldots, q$) from all others. Then, the selection regime of the s-th population can be defined by fitness function $w_s(U_j,Z_s)$, where U_j is the set of trait values of a genotype j. We assume that each of the traits of the set U is controlled by multiple loci with additive (across loci) effects. This general scheme can be easily implemented in the form of a computer model for a system with a large enough number of species and traits loci.

In this article we confine our analysis mainly to the class of two-species communities (hence in the T&T model the vectors U_j and Z_s are reduced to a single coordinate each). The species interaction will be described by fitness functions with arguments dependent on *differences* between the genotype's trait value and mean value of the corresponding trait of the partner population. In our further numerical examples, we will use fitness functions of Gaussian type. Then, our system can be represented as

$$w_1(u_{1j},z_1) = \exp\{\gamma_1(u_{1j} - z_1)^2/\sigma_1^2\}$$

and

$$w_2(u_{2j},z_2) = \exp\{\gamma_2(u_{2j} - z_2)^2/\sigma_2^2\}. \qquad (1)$$

Here z_1 is the selected for (the best) or selected against (the worst) value of the trait u_1 for genotypes of the first population that depends on (i.e. is equal to) the mean value of the corresponding trait in the partner, and σ_1^2 determines the strength of selection. Consequently, z_2 is the selected (for or against) trait value in the second population that depends on (i.e. is equal to) the mean value of the partner. The coefficients γ_1 and γ_2 could be equal to $+1$ or -1. If $\gamma_1\gamma_2 < 0$ then the resulting system can be referred to as the "host–parasite" type; the case when both γ_1 and γ_2 are positive—as competitive interaction, and when both γ negative—as mutualistic interaction.

We will consider mainly the situations when the traits u_1 and u_2 in the model (1) are each under two-locus control. This is in fact quite close to some gene-for-gene situations already treated (Hamilton *et al.*, 1990; Hamilton, 1993) and similar to one of two cases in Bell & Maynard Smith (1987) (see also Doebeli, 1996a, b; Haraguchi & Sasaki, 1996). It is noteworthy that the two-locus case includes the main parameters of the multilocus system and is easier for analysis. But the two-locus assumption is not a real constraint in our model: any number of loci can be considered, at least in the form of a computer model. To illustrate how natural is the proposed formalization as applied to more complex ecological–genetic situations, an example of a three-species system will also be provided which amounts to eight loci (Fig. 4).

The current state X_s of the population s ($s = 1, \ldots, q$) can be characterized by its two-locus haplotype frequencies $X_s = (x_{ab}, x_{aB}, x_{Ab}, x_{AB})_s = (x_{s1}, x_{s2}, x_{s3}, x_{s4})$. A sequence of states $\{X_s(n)\} = \{X_s(1), X_s(2), \ldots\}$ will be referred to as a population trajectory. We employ standard equations of population genetics to describe the population dynamics (Nagylaki, 1992):

$$x_{si}(n+1) = [W_{si}x_{si}(n) + \varepsilon_i r_s D_s(n)]/W_s(n), \qquad i = 1, \ldots, 4 \tag{2}$$

where $D_s(n) = x_{s1}(n)x_{s4}(n) - x_{s2}(n)x_{s3}(n)$ is the linkage disequilibrium coefficient, r_s—the recombination rate; $\varepsilon_1, \varepsilon_4 = -1$ and $\varepsilon_2, \varepsilon_3 = 1$; $W_s(n)$ is the mean fitness in generation n, whereas W_{si} is the marginal fitness of i-th haplotype:

$$W_{si} = \Sigma_j w_s[u_{sij}, m_s(n)]x_{sj}.$$

The genotypic values of the selected trait u are defined as:

$$\begin{array}{cccc} & aa & Aa & AA \\ bb & m - \frac{1}{2}dA - \frac{1}{2}dB & m + hA - \frac{1}{2}dB & m + \frac{1}{2}dA - \frac{1}{2}dB \\ Bb & m - \frac{1}{2}dA + hB & m + hA + hB & m + \frac{1}{2}dA + hB \\ BB & m - \frac{1}{2}dA + \frac{1}{2}dB & m + hA + \frac{1}{2}dB & m + \frac{1}{2}dA + \frac{1}{2}dB \end{array} \tag{3}$$

where m is the mean value of the trait, d are the additive effects of the involved loci and h are the dominance effects.

3. Polymorphism Maintenance in Interacting Populations

Our aim is to demonstrate that T&T interaction is capable of producing abundant polymorphisms. Clearly, two forms of polymorphism maintenance should be considered: (a) stable polymorphic fixed points, and (b) "dynamic" polymorphism existing in a form of complex limiting behavior (like limit cycles, chaos, etc.). Consequently, we will analyse the conditions that can result in either of these dynamic modes.

3.1. STABLE POLYMORPHIC FIXED POINTS

Clear criteria for existence of an interior (polymorphic) fixed point for a pair of interacting species can be formulated. Let us denote such a fixed point (if it exists) as $X = (X_1, X_2)$, where X_1 and X_2 stand for the corresponding fixed points in the two species. Let $z_1 = z(X_1)$ and $z_2 = z(X_2)$ be the mean values of the selected traits at X_1 and X_2. According to the foregoing description of species interaction, this actually implies that the dynamic equation (2) for the first population has a fixed point X_1 in a *constant* environment with the selected "optimum" z_2. Likewise, this also implies that the dynamic equation (2) for the second population has a fixed point X_2 in a constant environment with the selected "optimum" z_1. On the other hand, if: (i) for the first population with the selected "optimum" z_2 a fixed point X_1 exists and $z_1 = z(X_1)$, and (ii) for the second population with the selected "optimum" z_1 a fixed point X_2 exists and $z_2 = z(X_2)$, then the fixed point of the interacting populations should also exist. Therefore, for existence of an interior fixed point in a system of two interacting populations it is necessary and sufficient that each of the populations have an interior fixed point that obeys the conditions (i) and (ii).

It is worthwhile to complement this analysis by the following comment. Let X_1 be an interior fixed point of the first population for some value z_2 of the selected "optimum" and let $z(X_1) = z_1$. By changing consequently z_2 we can obtain a sequence of z_1 values as a function of z_2, i.e. $z_1 = f(z_2)$. Clearly, $f(z)$ can be considered as a continuous function if X_1 varies continuously with the selected "optimum". Noteworthy, for a current value of z_2 several fixed points could exist, hence the function $f(z)$ can be multiple-valued. By analogy, we can obtain $z_2 = \phi(z_1)$ for the second population. Clearly, the conditions

(i) and (ii) are equivalent to interception of the curves $f(z_2)$ and $\phi(z_1)$. Noteworthy, from the fact that the traits under consideration characterize qualitatively different species, follows immediately the existence of a scale transformation, e.g. like $z \rightarrow \alpha z + \beta$ (any other transformation can also be relevant either formally or biologically; clearly, these transformations will affect the stability of the fixed point). Therefore, if each of the populations has interior fixed polymorphic points under a constant selection regime, then the last comment means a possibility of interception of the foregoing curves upon corresponding scale transformation. However, this would not be possible if at least one of the populations has no interior fixed points in constant environment. It would be especially convenient to represent the foregoing trait-for-trait relationships between the species by a special "trait diagram" [see Fig. 1, sections (a) for the three types I–III of genetic control of the selected traits]. In the considered example for additive loci (type I in Fig. 1) the curves $z_2 = \phi(z_1)$ and $z_1 = f(z_2)$ correspond to unstable interior fixed points in each of the isolated systems. Interception results in mean trait values (point ω) corresponding to a stable polymorphic point $X = (X_1, X_2)$ [see Fig. 1(b)]. The distinctive feature of the second example (type II, semi-dominant loci) is that the functions $f(z)$ and $\phi(z)$ are multiple-valued. It is also noteworthy, that in the third example (type III, haploid selection) we used transformation $z \rightarrow \alpha z + \beta$ to achieve interception (hence interior fixed point). Under haploid selection in a stable environment all interior fixed points in an isolated population can be calculated as suggested in Kirzhner *et al.* (1995a, b; Proposition 1) and all these points are unstable (Rutschman, 1994).

In further analysis we employed an important class of fitness functions $w = w(|u - z|)$, logarithmically-concave or log-convex [i.e. the function $\log(w)$ is concave or convex, correspondingly]. This class is of common use in theoretical population genetics, and the functions in our foregoing example [eqns (1)] also belong to this class. In particular, the logarithmically-concave function [$\gamma < 0$ in eqns (1)] describes in our model a "pursuing strategy" type, when the fitness of a genotype is maximal if its trait value is equal to the mean value of the corresponding trait in the partner species population. This strategy is formally characteristic to parasitic and mutualistic species. Likewise, the logarithmically-convex function [$\gamma > 0$ in eqns (1)] describes a "running-away strategy" type, when the fitness of a genotype is minimal if its trait value is equal to the mean value of the corresponding trait in the partner population. This strategy is formally characteristic to hosts and species competing for a common resource. Gavrilets & Hastings (1994) proved, for logarithmically-concave fitness functions, that in a constant environment no interior fixed points are possible (either stable or unstable) if the selected trait is defined by purely additive genes of equal effects (see also Kirzhner *et al.*, 1995a, b; Korol *et al.*, 1996). Analogous consideration for logarithmically-convex functions leads to the conclusion that an interior fixed point may exist only with equal allele frequencies at the selected loci (Gavrilets & Hastings, 1994; Kirzhner *et al.*, 1995a, b; Korol *et al.*, 1996). This means that the foregoing conditions (i) and (ii) are violated. Therefore, if the selected trait of the pursuing strategist is controlled by purely additive genes of equal effects, no interior fixed point is possible in a community consisting of such a species and any other partner. We should stress here, that this statement holds, given the foregoing conditions, for any possible dependence of the fitness function on population density (e.g. in the ecological–genetic version of T&T model proposed by Doebeli, 1996a). Nevertheless, this does not exclude the possibility of polymorphism in the partner. With the same condition of equal additive gene effects, a species that is a running-away strategist may have a polymorphic point, albeit with a constraint of equal allele frequencies at the two loci.

It is known that stabilizing selection in a constant environment for a trait controlled by two loci with unequal effects or semi-dominant effects may result in (multiple) interior fixed points (Kojima, 1959; Lewontin, 1964; Nagylaki, 1989; Gavrilets & Hastings, 1993). Together with the foregoing analysis, this implies that the same conditions will result in an interior fixed point for any type of interacting populations. This

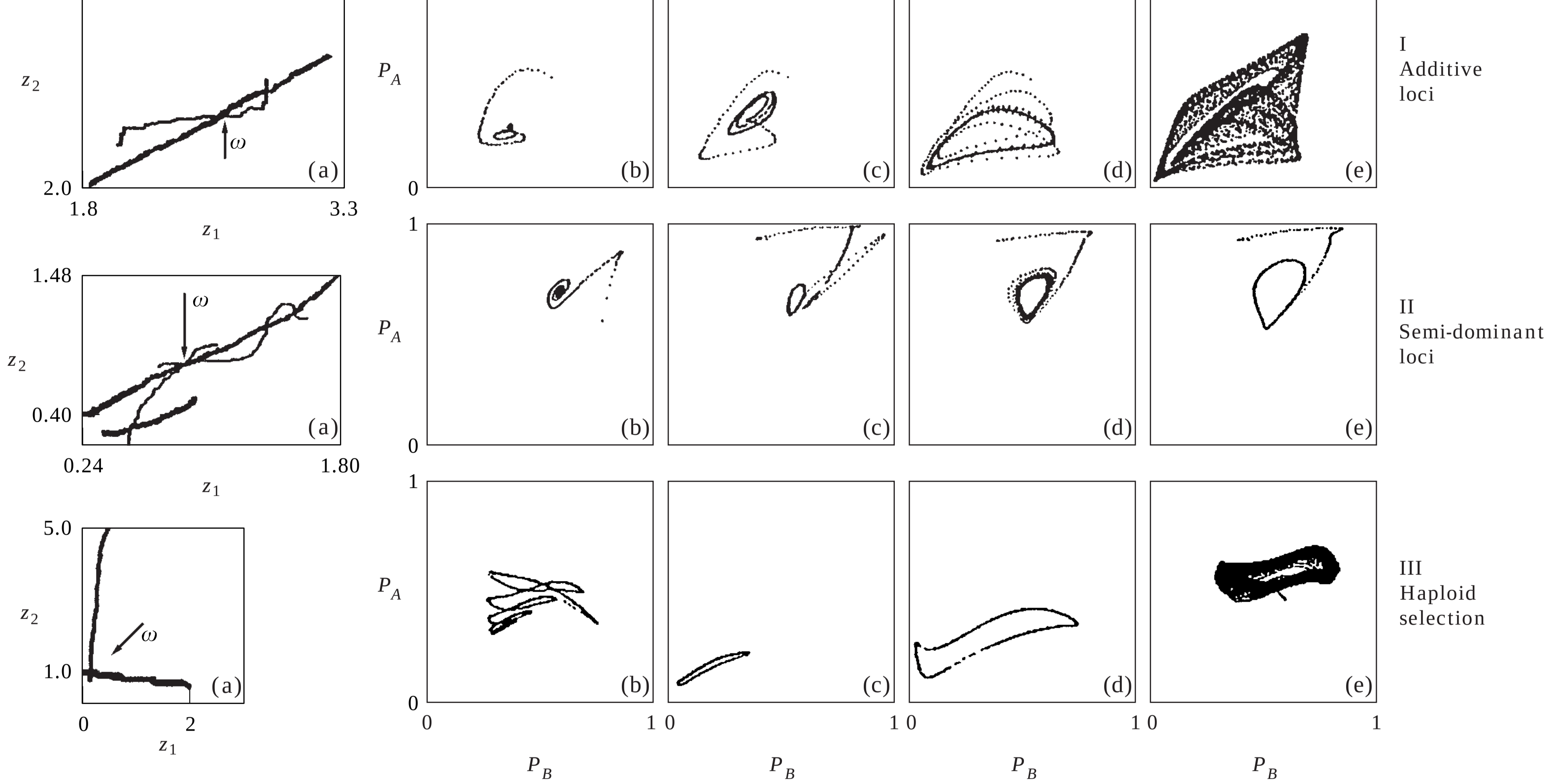

FIG. 1. Trait diagrams and limiting behaviour for different types of genetic control of the selected traits in host–parasite systems. The dynamic system (2) was considered with fitness functions as defined in (1) ($\gamma_1 = 1$ for host and $\gamma_2 = -1$ for parasite). (a) Trait diagrams: bold curve represents $z_2 = \phi(z_1)$, where z_2 is the mean trait value at the polymorphic fixed point of the host (if it exists at all) in constant environment with the selected "optimum" z_1; thin curve—$z_1 = f(z_2)$, where z_1 is the mean trait value at the polymorphic fixed point of the parasite (if it exists at all) in constant environment with the selected "optimum" z_2; the interception of the curves corresponding to the fixed point of the entire system is denoted by ω; (b)–(e) dynamics of allele frequencies P_A and P_B of the trait loci in the host population. (I) *Purely additive loci*: (a) trait diagram for a system with the following parameter values: for the host $r = 0.1$, $d_A = 1.5$, $d_B = 1.0$, $h_A = h_B = 0$, $\sigma = 2.4$; for the parasite $r = 0.1$, $d_A = 1.3$, $d_B = 1.0$, $h_A = h_B = 0$, $\sigma = 0.4$; (b) stable fixed point for the same parameters, corresponding to point ω, maximum eigenvalue of linear approximation of evolutionary operator (2) at this point is $0.81 \pm 0.48i$; (c) trajectory converging to a limiting cycle [the same parameters as in (a), but with $\sigma = 2.0$ for the host]. Note, that for an intermediate σ between $\sigma = 2.0$ and $\sigma = 2.4$ ($\sigma = 2.2$) the fixed point was also stable, but with an increased eigenvalue $0.99 \pm 0.10i$; (d) trajectory converging to a limiting cycle [the same parameters as in (a), but $r = 0.05$ for the host]; with an intermediate r between $r = 0.1$ and $r = 0.05$ ($r = 0.09$) the fixed point was also stable, but with an increased eigenvalue $0.98 \pm 0.10i$; (e) trajectory converging to a complex attractor [the same parameters as in (a), but $\sigma = 2.0$ and $r = 0.05$ for the host]. (II) *Semi-dominant loci*: (a) trait diagram for a system with the following parameter values: for the host $r = 0.03$, $d_A = d_B = 1$, $h_A = 0.2$, $h_B = -0.44$, $\sigma = 0.5$; for the parasite $r = 0.25$, $d_A = d_B = 1$, $h_A = -0.5$, $h_B = 0.2$, $\sigma = 2.0$; (b) stable fixed point for the same parameters, corresponding to point ω; maximum eigenvalue in linear approximation at this point is $0.98 \pm 0.08i$; (c) trajectory converging to a limiting cycle [the same parameters as in (a), but with $\sigma = 0.4$ for the host]. For an intermediate σ between $\sigma = 0.4$ and $\sigma = 0.5$ ($\sigma = 0.49$) the fixed point was also stable, but with an increased eigenvalue $0.99 \pm 0.09i$; (d) trajectory converging to a limiting cycle [the same parameters as in (a), but $r = 0.01$ for the host]; with an intermediate r between $r = 0.01$ and $r = 0.03$ ($r = 0.02$) the fixed point was also stable, but with an increased eigenvalue $0.99 \pm 0.09i$; (e) trajectory converging to a limiting cycle [the same parameters as in (a), but $\sigma = 0.4$ and $r = 0.01$ for the host]. (III) *Haploid selection*: (a) trait diagram for a system with the following parameter values: for the host $r = 0.0005$, $d_A = 1.3$, $d_B = 1.0$, $h_A = h_B = 0$, $\sigma = 15.0$; for the parasite $r = 0.1$, $d_A = 1.3$, $d_B = 1.0$, $h_A = h_B = 0$, $\sigma = 10.0$. Mean value of the host trait was transformed into the "selected optimum" of the parasite as $z \to \alpha z + \beta = 7.0z - 7.0$, whereas the parasite mean value was replaced by $z \to \alpha z + \beta = 5.0z$. Note that without transformation the corresponding curves do not intercept; (b) stable fixed point for same parameters; (c) trajectory converging to a limiting cycle [the same parameters as in (a), but with $d_A = 1.6$ in the host]; (d) trajectory converging to a limiting cycle [the same parameters as in (a), but with $d_A = 1.6$ for both host and parasite]; (e) trajectory converging to limiting cycle, all parameters as in (a), but without transformation of the parasite trait value, i.e. $z \to 1.0z$.

does not mean that this point will be even locally stable. Nevertheless, even if the corresponding fixed points are unstable in each of the populations subjected to a constant selection regime, the interaction between the populations can convert this pair of points into a stable polymorphic point in the entire system [see Fig. 1(b), types I–III].

The foregoing examples are merely illustrations of how the interaction between species can convert unstable fixed points characteristic of the separate population into stable polymorphisms. Certainly, if an interior fixed point was found for the overall system, its stability should be tested using, for example, the Jacobian matrix technique. This can be done either analytically or numerically, although analytical consideration may encounter serious technical difficulties. We are not aware about general results relating the spectrum of the Jacobian of a combined dynamic system with the spectra of the isolated component systems. Moreover, simple upper estimations of matrix spectra (Gantmacher, 1959) show that the spectral radius of an overall system is expected to be larger than that of each component rather than smaller. However, our examples, and corresponding analytical estimates for single-locus systems (Kirzhner, unpublished results) show that an opposite situation may be no less frequent.

3.2. "DYNAMIC" POLYMORPHISM

A clear possible scenario of appearance of more complex forms of limiting polymorphic dynamics is destabilization of stable polymorphic fixed points. This may be achieved by changing the recombination rates, the ratio of the additive effects or heterozygous deviation of the trait loci, or the intensity of selection, in either of the interacting populations. Figure 1(c–e) demonstrates these possibilities.

It is noteworthy, that for each of the interacting species, the sequence of the mean values of the trait of its partner can be considered formally as a *changing environment with some order of environmental states*. Therefore, the existence of dynamic polymorphism in a system of interacting populations means that for each of the partners considered as isolated populations a corresponding regime of (abiotic) environmental changes can be found resulting in the same dynamic pattern. For a single species with equal effects of the selected loci on the trait and any order of environmental states (with either finite or infinite set of states), it was shown that: (a) if the fitness function is log-concave, then two-locus polymorphism cannot be maintained in any form; (b) if the fitness function is log-convex, then two-locus polymorphism can be maintained only with equal allele frequencies at the two loci (Kirzhner *et al.*, 1995a, b; Korol *et al.*, 1996). Therefore, for equal additive effects of the trait loci, two-locus polymorphism is impossible in the "pursuing strategist" in any form, while the "running away strategist" can maintain dynamic polymorphism only with equal allele frequencies at the two loci.

Clearly, according to the definition of the curves $z_2 = \phi(z_1)$ and $z_1 = f(z_2)$ on the two-species trait diagram, any number of loci affecting the selected traits can be considered. Generalization of the trait diagrams for communities with more than two species means an analysis of interception of surfaces of higher dimensionality that is less evident geometrically.

The foregoing analysis can be generalized in a form of simple heuristic rules which help to reveal polymorphic systems as dependent on the peculiarities of the genetic control of selected traits (see Box 1). Actually, these statements can be considered as the necessary condition for two-locus polymorphism maintenance: at least one of the rules (a)–(c) should hold to provide two-locus polymorphism. Otherwise, polymorphism either is impossible (for the "pursuing strategist") or exists in a very special form (for the "running away" strategist).

Box 1: TRAIT-FOR-TRAIT INTERACTION CAN PROMOTE POLYMORPHISM

in a species experiencing selection pressures from other species of the community, if at least one of the following conditions holds:

a. There are non-equal effects of the additive genes controlling the selected trait
b. There is a dominance deviation from the purely intra-locus additivity scheme, preserving additivity across loci
c. Disturbance of the log-concavity/log-convexity of the fitness function of the considered species

Comment on rule b

Overdominance is known to be a routine factor helping in maintaining polymorphism. However, this fact is irrelevant to a situation where the dominance deviations from the "purely additive within-locus" scheme concern the effect *on the selected trait and not on fitness*. Nevertheless, many polymorphisms may result even when dominance deviations for the selected trait are small (see later).

Comment on rule c

No examples are provided in the paper demonstrating that genetic systems with equal additive effects of the trait loci obeying this rule can indeed manifest polymorphism. Nevertheless, such examples can easily be constructed (for more details see Korol *et al*., 1996).

Clearly, the foregoing rules do not provide sufficient conditions, in a strict sense, for two-locus polymorphism. These rules stress only the importance of the deviations, but do not define the precise intervals of the corresponding parameters that ensure polymorphism maintenance. However, they enable to reveal domains in parameter space with abundant polymorphic regimes, both polymorphic stable points and complex limiting behaviour. Figures 2 and 3 illustrate how in a host–parasite system [see eqns (1), for the corresponding fitness functions] the manifestation of polymorphism depends on selection intensity and deviations from equal gene effects or from a purely additive scheme at the intralocus level. For both rules our intention was to cover as broad as possible range of the most important parameters of the system, i.e. characterizing the foregoing deviations and selection intensities in both participating species. For that, the presented computer experiments included the results of 400 000 trajectories for the first group (Fig. 2) and 100 000 for the second one (Fig.3), for different combinations of parameters. The only limitation was in the range of recombination parameters—only two sets were taken for each example that appeared to represent the entire range of recombination values (in fact, our experiments included also detailed scans along the recombination axes). Another limitation was that we presented only "pure" systems with respect to deviations from additivity and equal gene effects. Namely, no "crosses" were made between the deviation types within a species or between species. With the exception of the foregoing limitations, the results can be considered as an attempt for a rather detailed exploration of the system behavior in the parametric space.

In accordance with the foregoing consideration and predictions presented in Box 1, one can see that both deviation from equal gene effects (Fig. 2) and dominance deviation at the loci controlling the selected traits (Fig. 3) result in polymorphism maintenance. It is noteworthy, that the presented sets of parameters encompass three regions: loss of polymorphism, polymorphic fixed points, and dynamic polymorphism (cycles and more complex limiting behavior).

The shape of regions in Figs 2 and 3 indicates the complexity of the corresponding dynamic system for the relatively simple case considered here: interaction between two species coevolving on a T&T basis when the target trait in each species is controlled by two loci. The proposed formulation of species genetic interactions allows us to model much more complex species communities in the same way. As an example, we present here a three-species model, including two competing hosts and one parasite. For the sake of simplicity in the example, the relationships of the competitors with each other and with the common parasite depend on the same two-locus traits. The parasite is a four-locus system, with two traits controlled by two different blocks of linked loci (Fig. 4). This system appears to obey the proposed rules of Box 1, and a broad spectrum of non-trivial dynamics can be found for different combinations of parameters.

4. Conclusions

This paper sheds new light on the problem of polymorphism maintenance in species coevolution mediated by selection for quantitative traits. The basic difference of this class of models is that it takes advantage of direct *Mendelian* formulation of the genetic variation of the foregoing traits (Hamilton *et al*., 1990; Preygel & Korol, 1990; Korol *et al*., 1994; Doebeli, 1996a, b, 1997). This is crucial when the objective is to reveal the conditions for polymorphism maintenance, and especially, recombination and sex evolution (Korol *et al.*, 1994; Doebeli, 1996a). Trait-based *Mendelian* models have also been used to analyse intraspecific competition (Loeschcke & Christiansen, 1984; Korol *et al.*, 1994; Doebeli, 1996a, b).

The conditions of polymorphism maintenance in this class of models remains a difficult question (Hamilton, 1993). We showed here that the conditions for polymorphism maintenance in interacting species could be deduced from the behavior of the isolated partners in stable and changing environments. These results establish a common basis for comparison of the two forms of temporarily varying selection, i.e. abiotic and biotic, as evolutionary factors. Consequently, this allows addressing such difficult questions as polymorphism maintenance or evolution of sex and recombination, that can not be considered properly in non-Mendelian models. The obtained results demonstrate a remarkable property of trait-dependent coevolution concerning the conditions for maintenance of genetic polymorphism: what seems to be more realistic, that is non-equal gene effects and deviation from purely additive within-locus gene action, promotes polymorphism.

We envisage that the proposed analysis of multi-species multilocus coevolution based on T&T interactions, together with the heuristic rules for polymorphism maintenance, may find wide applications in the genetics–ecology interface. It can be applied to many real systems where the ecological details of species interactions are known or may be recorded on the level of quantitative traits. We should note, however, the restrictions of the model. The major one is caused by the conditions when the central model assumption is valid, namely: that species interaction can be represented by an approximation where fitness depends only on the mean trait values. Clearly, this condition means that each individual of one species encounters during its life many individuals of the other species, and vice versa. We believe that such situations may be characteristic for systems like "pollinator–host plant", "herbivore–plants", "macroparasite (like insects)–hosts". Nevertheless, in spite of the foregoing limitations, such an approach is a more feasible task in contrast to detailed genetic analysis of the involved individual loci. Still, its advantage is that it allows to analyse species coevolution and polymorphism maintenance in direct *Mendelian* terms.

FIG. 2. Polymorphism maintenance under host–parasite interaction as dependent on the ratio of gene effects (*d*), selection intensities (σ) and recombination rates. The parameters of the host and parasite populations are denoted by indices *h* and *p*, correspondingly: (a) $r_h = r_p = 0.1$, (b) $r_h = 0.4$, $r_p = 0.01$. The results of computer simulations are presented and are based on iterations of the coevolutionary operator (2) with fitness functions (1). The selected traits of each of the partners were assumed to depend on two linked loci with effects $d_{Ap} + d_{Bp} = 6$ and $d_{Ah} + d_{Bh} = 6$, so that if d_{Ap} varies from 1 to 3, then the ratio of gene effects varies from 5 to 1 (clearly, equal gene effects correspond to the middle values of d, $d = 3$). For an enlarged scale see the inserted figure in the right upper corner of part (a) where the axes d_{Ap} and d_{Ah} are shown for the little blocks that comprise both parts, (a) and (b), of the figure. Each such block corresponds to the indicated combination of the parameters σ (parasite) and σ (host). The yellow color corresponds to loss of polymorphism in either of the interacting populations for at least one of the loci, whereas the blue indicates polymorphic fixation for both loci in each of the populations. The green area denotes complex behavior with polymorphism maintained in both partners for both loci; a complex attractor in the inserted figure in the right upper part is an example of such a behavior in the parasite part of the system. P_A and P_B in the insert are the frequencies of corresponding alleles at the loci controlling the selected trait.

FIG. 3. Polymorphism maintenance under host–parasite interaction as dependent on dominance deviations (*h*), selection intensities (σ) and recombination rates: (a) $r_h = 0.25$, $r_p = 0.01$, (b) $r_h = r_p = 0.01$. The selected traits of each of the partners were assumed to depend on two linked loci with effects $d_{Ap} = d_{Bp}$ and $d_{Ah} = d_{Bh}$, and within each of the systems one locus manifests some dominant effect ($h_{Ap} \neq 0$ and $h_{Ah} \neq 0$) whereas the second locus is purely additive ($h_{Bp} = 0$ and $h_{Bh} = 0$). Values of h_{Ap} from -0.5 to $+0.5$ correspond to a range from full dominance of the allele reducing the trait to full dominance of the opposite allele; (c) in an enlarged scale the axes h_{Ap} and h_{Ah} are shown for the little blocks that comprise both parts, (a) and (b), of the figure. The colors here correspond to those of Fig. 2. In Fig. 3(d) we show an example of a limit cycle in the host population.

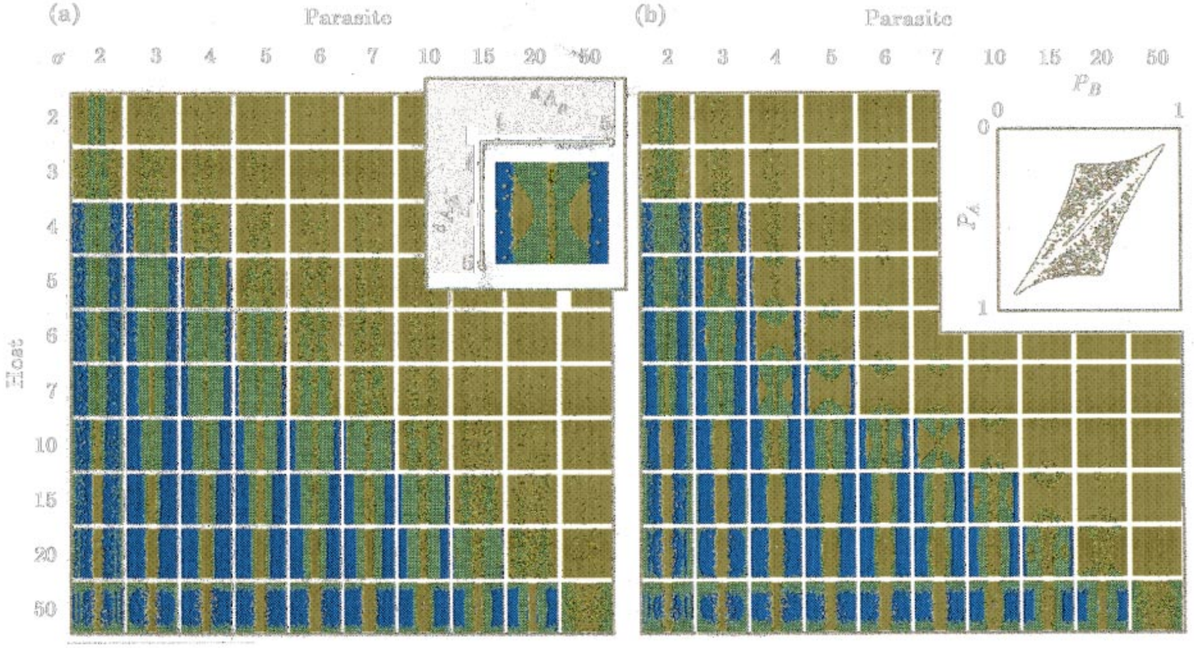

FIG. 2

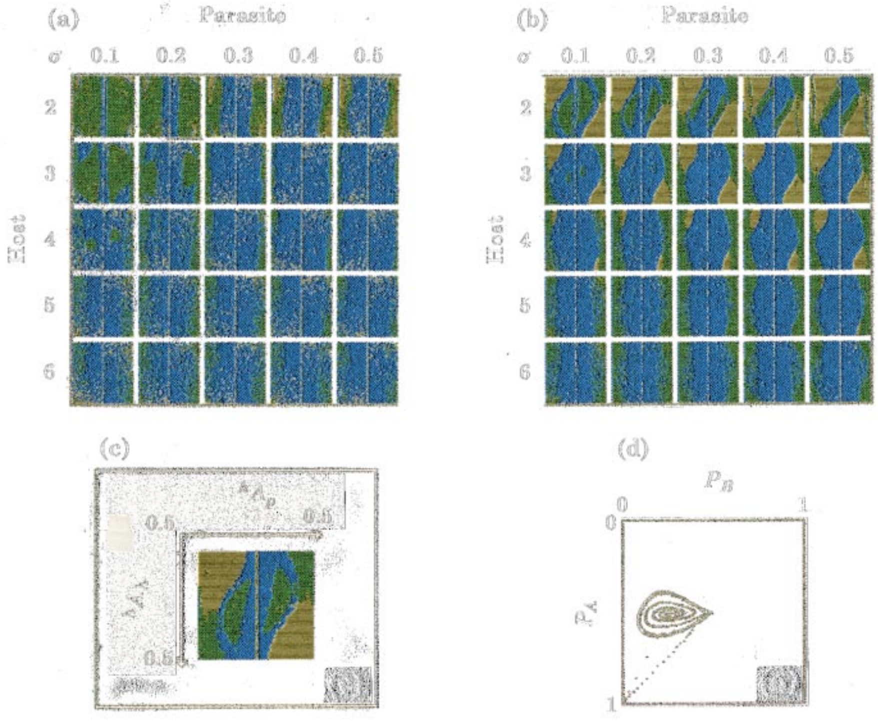

FIG. 3

Figs 2 & 3. (*Caption opposite*)

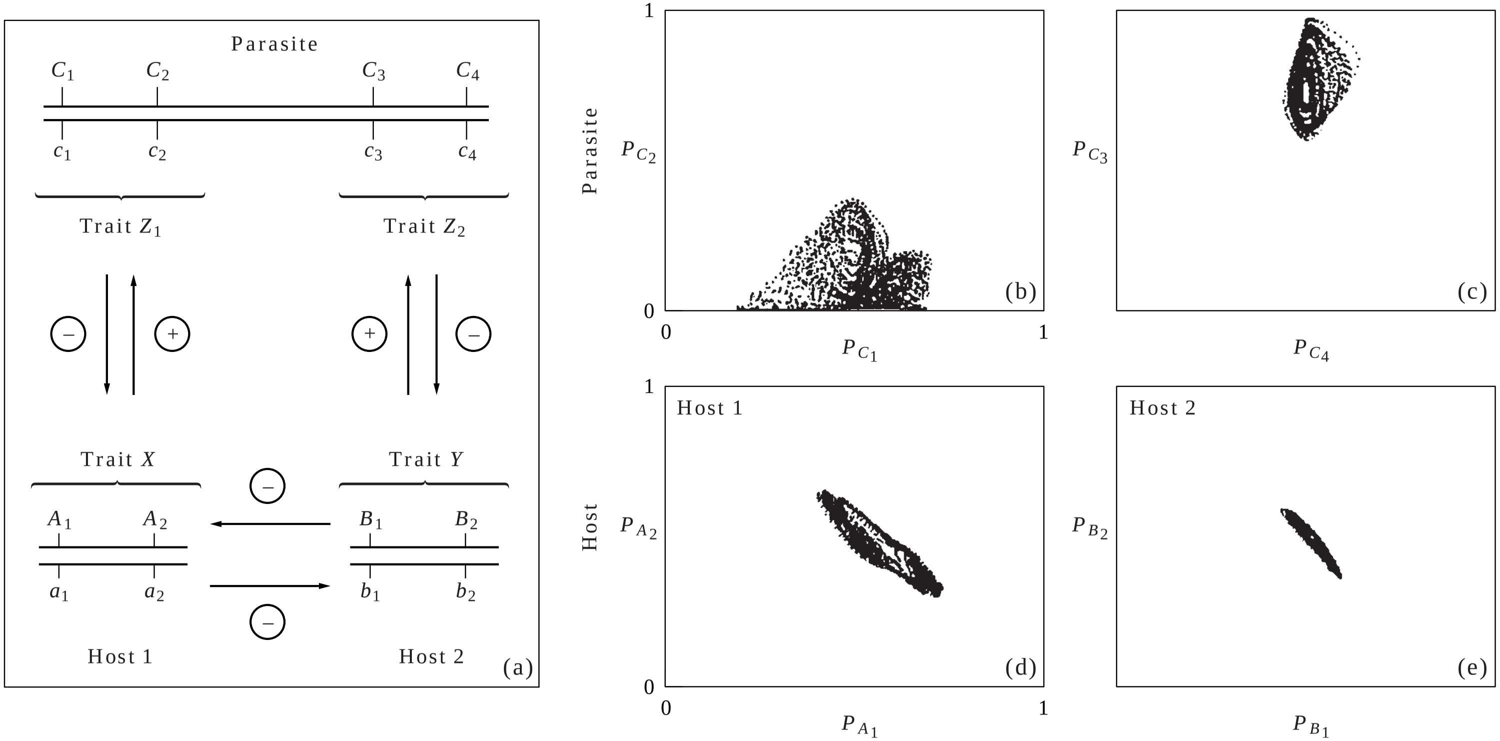

FIG. 4. Dynamic polymorphism in a system of three interacting species: two competing hosts and a common parasite. (a) The scheme of interactions in the community. We considered here a four-locus parasite whose traits Z_1 and Z_2 affect the fitness of the two two-locus hosts. The hosts traits X and Y affect simultaneously the parasite and the competitor. Clearly, the fitness of any genotype of a host grows with deviation of its trait values from the mean values of the corresponding traits values of the partner species populations; such dependencies are marked by minus-arrows. The opposite strategy, when fitness decreases with deviation from the mean value of the partner species is marked by plus-arrows. The coselection between the species is governed by the following fitness functions: for host 1: $w_{h_1} = \exp[(x-y)^2/\sigma_1^2 + (x-z_1)^2/\sigma_{12}^2]$, with $\sigma_{11} = 7$ and $\sigma_{12} = 20$; for host 2: $w_{h_2} = \exp[(x-y)^2/\sigma_{21}^2 + (x-z_2)^2/\sigma_{22}^2]$, with $\sigma_{21} = 6$, $\sigma_{22} = 30$; and for the parasite $w_p = \exp[-(z_1-x)^2/\sigma_3^2] + \exp[-(z_2-y)^2/\sigma_3^2]$, with $\sigma_3 = 1.5$. The effects of the trait loci were: $d_{A_1} = 1$ and $d_{A_2} = 3.5$ for host 1; $d_{B_1} = 1$ and $d_{B_2} = 2.5$ for host 2; and $d_{C_1} = 3$, $d_{C_2} = 1$, $d_{C_3} = 1$ and $d_{C_4} = 3$ for parasite. Recombination rates were equal in both hosts $r_{h_1} = r_{h_2} = 0.2$; within the parasite blocks $r_{p_1} = r_{p_3} = 0.1$, recombination between the blocks $r_{h_2} = 0.3$; (b)–(e) dynamics of allele frequencies at trait loci: the limiting sets (representing 5000 generations) of the population trajectories are shown, from generation #20 001 to 25 000; P_{A_i}, P_{B_i}, and P_{C_j} are the frequencies of trait enhancing allele at the trait loci ($i = 1,2$; $j = 1, \ldots, 4$); (b) the parasite loci in the first block; (c) dynamics of the parasite loci in the second block; (d) dynamics of the host 1 loci; (e) dynamics of the host 2 loci. Note, that the considered system represents complex limiting behaviour.

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