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Quantities that Frequency-Dependent  
Selection Maximizes

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# Quantities that Frequency-Dependent Selection Maximizes

Carlo Matessi<sup>1</sup> and Kristan A. Schneider<sup>2</sup>

## Abstract

We consider a model of frequency-dependent selection, to which we refer as the *Wildcard Model*, that accommodates as particular cases a number of diverse models of biologically specific situations. Two very different particular models (Lessard, 1984; Bürger, 2005; Schneider, 2006), subsumed by the Wildcard Model, have been shown in the past to have a Lyapunov functions (LF) under appropriate genetic assumptions. We show that the Wildcard Model: (i) in continuous time is a generalized gradient system for one locus, multiple alleles and for multiple loci, assuming linkage equilibrium, and its potential is a Lyapunov function; (ii) the LF of the particular models are special cases of the Wildcard Model's LF; (iii) the LF of the Wildcard Model can be derived from a LF previously identified for a model of density- and frequency- dependent selection due to Lotka-Volterra competition, with one locus, multiple alleles, multiple species and continuous-time dynamics (Matessi and Jayakar, 1981). We extend the LF with density and frequency dependence to a multilocus, linkage equilibrium dynamics.

## 1 Introduction

Frequency-dependent selection has been invoked in the explanation of many important evolutionary phenomena. These include the evolution of behavioral traits, the maintenance of genetic variation, and disruptive selection with its possible consequences of ecological character displacement, reproductive isolation and, eventually, speciation (Maynard Smith, 1966, 1982; Bulmer, 1974, 1980; Matessi and Jayakar, 1976, 1981; Clark, 1979; Slatkin, 1979, 1980; Felsenstein, 1981; Abrams, 1986, 1987; Asmussen and Basnayake, 1990; Dieckmann and Doebeli, 1999; Bürger et al., 2006; Schluter, 2000; Turelli

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et al., 2001; Gavrillets, 2003, 2004). Frequency-dependent selection occurs if the fitness of a particular phenotype depends on the frequency of its own and other phenotypes in the population. Many mechanisms causing frequency dependence are known, including intraspecific competition, systems of mimicry, host-parasite or predator-prey interactions, aposematic and cryptic coloration, or the evolution of self-incompatibility (cf. Matessi and Cori, 1972; Ayala and Campell, 1974; Clarke and Partridge, 1988). In general, frequency dependence occurs if changes in the population composition affect the biotic or abiotic environment that induces selection on this population.

Population-genetics theory has included frequency-dependent selection since its conception (Fisher, 1930), but concrete studies remained sporadic (e.g., Wright, 1948). A pioneer work by Haldane and Jayakar (1963) established it as a powerful mechanism for the maintenance of polymorphism in natural populations. Moreover, for the first time in population genetics it showed the possibility of permanent, more or less regular oscillations, a feature that is intimately engrained in this selective mechanism (e.g., Matessi and Cori, 1972; Gavrillets and Hastings, 1995). After the discovery of the impressive and unexpected amount of polymorphism at the molecular level in natural populations (Lewontin and Hubby, 1966), and during the intense debates over the causes of its maintenance, frequency-dependent selection has been often indicated as a most likely source of this phenomenon (e.g., Kojima and Yarbrough, 1967). Subsequently, the theory of one-locus models under frequency- (and density-) dependent selection has been the subject of a more systematic study (e.g., Clarke, 1972; Cockerham et al., 1972; Matessi and Jayakar, 1976, 1981; Asmussen, 1983; Asmussen and Basnayake, 1990), whereas the theory of multilocus models was limited to the study of much less general models (e.g., Bürger, 2005; Schneider, 2006).

Lately, the evolutionary consequences of frequency-dependent selection have been investigated mainly within the framework of population game theory (e.g., Maynard Smith, 1982; Hofbauer and Sigmund, 1998) and, more recently, also within what has been called adaptive dynamics theory (Dieckmann, 1997; Geritz et al., 1998; Doebeli and Dieckmann, 2000). Common to approaches within these frameworks is, with few exceptions, a lack of genetics, i.e., they usually assume asexual reproduction and monomorphic populations. Simple genetics has been incorporated in some ecological models, often, however, resting on a number of assumptions that are not completely specified or justified. In most cases computer simulations have been performed, but only little analytical theory has been developed. However, there are a few exceptions that either allow for more genetic details

(Lessard, 1984; Matessi et al., 2001; Kopp and Hermisson, 2006; Matessi and Gimelfarb, 2006), or provide analytical results for multilocus genetics (Schneider, 2007).

A well known and disappointing feature of frequency-dependent selection is that the mean fitness is in general not maximized, i.e., it is not a Lyapunov function, not even for selection at a single locus for which ‘Fisher’s Fundamental Theorem of Natural Selection’ holds for constant (frequency-independent) selection (although recent work, Schneider, 2008, establishes some conditions under which mean-fitness maximization occurs). On the other hand, alternative maximization principles for frequency-dependent selection have been found in a few cases: Matessi and Jayakar (1976, 1981) were one of the first to provide a global Lyapunov function for a general one-locus multiallele, multispecies model of frequency- and density- dependent selection in continuous time. Lessard (1984) established a Lyapunov function for the discrete-time, one-locus, multiallele dynamics resulting from a two-phenotype selection model where fitness depends on the payoffs from random pairwise contests. More recently, Bürger (2005) proved, for a particular model of selection on a continuous trait due to intraspecific competition, that a Lyapunov function exists in continuous time when the selected trait is genetically determined by multiple additive diallelic loci, under a so called linkage-equilibrium approximation. In particular, it was proved that the underlying system of differential equations forms a Shashahani gradient system. These results have been further generalized to multiple additive alleles by Schneider (2006).

In this paper we will consider a model of frequency-dependent selection that is sufficiently broad to accommodate many models of this type of selection which are present in the literature. We will refer to it as the *Wildcard Model*. In spite of their biological diversity, the models of Lessard (1984) and of Bürger (2005) and Schneider (2006) turn out to be particular cases of the Wildcard Model. Assuming one-locus, multiallele genetics, we will show that the continuous-time dynamics of the Wildcard Model forms a generalized gradient system. The potential of such a gradient system is therefore a Lyapunov function for the Wildcard Model. Moreover, it subsumes, as particular cases, the Lyapunov functions already identified for the Lessard and the Bürger-Schneider models, which, from their biological interpretation, would superficially appear to be very different. We then consider the relationships between the Lyapunov function of our model and that found by Matessi and Jayakar (1981) for density- and frequency-dependent selection due to scramble competition, represented by a Lotka-Volterra interaction model. We show that the former can be derived from the latter. Finally, we consider a multilocus, multi-

allele model and, assuming approximate linkage equilibrium, we show that the Lyapunov function of the Wildcard Model works also in this case. Moreover, we find that the form of density-dependence in the Matessi-Jayakar model and its Lyapunov function can be generalized to some extent.

Our results generalize all of the above mentioned models to some extent. In order to be able to precisely appreciate these generalizations, it is necessary first to briefly review these models and, if appropriate, also the results that have been previously established. This approach will guide us throughout this article to enforce our intuition for the various biological situations to which our Wildcard Model is applicable, and in particular how it is related to concrete evolutionary situations.

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## 2 Wildcard Model and Particular Cases

### 2.1 The Wildcard Model

The frequency-dependent selection model that we consider assumes that the fitness of an individual of type  $x \in X$ , where  $X$  is the set of all types, is given by the following function of population composition:

$$W_x = W_x(\mathbf{q}) = S_x + \sum_y A_{x,y} q_y + C(\mathbf{q}), \text{ with } A_{x,y} = A_{y,x} \text{ for all } x, y \in X, \quad (1)$$

where  $q_x$  is the frequency of type  $x$  in the population, so that the vector  $\mathbf{q} = (q_x)_{x \in X}$  represents the population composition;  $S_x$  is a frequency-independent component of fitness;

$A_{x,y}$  is the effect that individuals of type  $y$  have on the fitness of individuals of type  $x$ ; such an effect is assumed to be the same as that of type  $x$  on type  $y$ . Finally, the function  $C(\mathbf{q})$  is arbitrary and represents any effect on fitness that may vary with the population composition but is the same for all types.

It should be mentioned that (1) has a similar structure as the pairwise-interaction model of frequency-dependent selection which is commonly studied in the theoretical literature, e.g., Schutz et al. (1968), Allard and Adams (1969), Cockerham et al. (1972), Asmussen and Basnayake (1990), Altenberg (1991), Gavrillets and Hastings (1995), Asmussen et al. (2004), Trotter and Spencer (2008), Schneider (2008). However, the pairwise interaction model assumes  $C \equiv 0$  and, in general, does not require the symmetry conditions  $A_{x,y} = A_{y,x}$ .

Assuming that the different types correspond to the genotypes of a single diploid locus with  $n$  alleles,  $\mathcal{A}_1, \dots, \mathcal{A}_n$ , with respect to which matings occur at random, the dynamics in discrete generations of the allele frequencies,  $\mathbf{p} = (p_1, \dots, p_n)$ , under the selection regime (1) is then given by the following system of recursion equations:

$$p'_i = p_i \frac{\bar{W}_i(\mathbf{p})}{\bar{W}(\mathbf{p})} \quad \text{for } i \in \{1, \dots, n\}, \quad (2a)$$

where the marginal fitness of allele  $i$ ,  $\bar{W}_i(\mathbf{p})$ , and the population mean fitness,  $\bar{W}(\mathbf{p})$ , are

$$\bar{W}_i(\mathbf{p}) = \sum_{j=1}^n S_{ij} p_j + \sum_{j,k,l=1}^n A_{ij,kl} p_j p_k p_l + C(\mathbf{p}) \quad (2b)$$

$$\bar{W}(\mathbf{p}) = \sum_{i=1}^n \bar{W}_i(\mathbf{p}) p_i = \sum_{i,j=1}^n S_{ij} p_i p_j + \sum_{i,j,k,l=1}^n A_{ij,kl} p_i p_j p_k p_l + C(\mathbf{p}). \quad (2c)$$

Note that, since we assume that the effect of a gene does not depend on the parent by which it is transmitted, i.e., a lack of genomic imprinting, it follows that  $S_{ij} = S_{ji}$  and  $A_{ij,kl} = A_{ji,kl} = A_{ij,lk} = A_{ji,lk}$ .

Whenever selection is sufficiently weak, namely the parameters  $S_{ij}$  are sufficiently close to one another and the same can be said of the parameters  $A_{ij,kl}$ , the system of recursion relations (2) can be approximated by a system of differential equations. More precisely, we can argue as follows. Let the duration of the time interval between successive generations be  $\tau$ , and the point of time at which the current generation is observed be  $t$ , so that the gene frequencies at the current generation can be indicated by  $\mathbf{p}(t)$  and those of the next generation by  $\mathbf{p}(t + \tau)$ . In addition, let the selection parameters be written as

$$S_{ij} = s + \tau s_{ij}, \quad A_{ij,kl} = a + \tau a_{ij,kl}, \quad C(\mathbf{p}) = c + \tau \gamma(\mathbf{p}). \quad (3)$$

Hence, we have

$$\frac{p_i(t + \tau) - p_i(t)}{\tau} = p_i(t) \frac{\bar{s}_i + \bar{a}_i - \bar{s} - \bar{a}}{s + a + c + \tau (\bar{s} + \bar{a} + \gamma(\mathbf{p}))} \quad \text{for } i \in \{1, \dots, n\},$$

where

$$\bar{s}_i = \sum_{j=1}^n s_{ij} p_j, \quad \bar{s} = \sum_{i=1}^n \bar{s}_i p_i, \quad \bar{a}_i = \sum_{j,k,l=1}^n a_{ij,kl} p_j p_k p_l, \quad \bar{a} = \sum_{i=1}^n \bar{a}_i p_i. \quad (4a)$$

Assuming without loss of generality that the scaling constant  $s + a + c$  has been incorporated into the  $s_{ij}$ ,  $a_{ij,kl}$  parameters and letting  $\tau \rightarrow 0$ , we obtain the system of differential equations

$$\dot{p}_i(t) = p_i(t) (\bar{w}_i - \bar{w}) \quad \text{for } i \in \{1, \dots, n\}, \quad (4b)$$

where

$$\bar{w}_i = s_i + a_i \quad \text{and} \quad \bar{w} = \bar{s} + \bar{a}. \quad (4c)$$

For the purposes of this paper we will refer to the model defined by (1) and (2) or (4) as the *Wildcard Model*, because it incorporates many particular models of frequency-dependent selection present in the literature, motivated by specific biological situations, of which we will recall some in this article.

## 2.2 Particular Cases

### 2.2.1 Random pairwise contests

#### The Lessard model

Lessard (1984) introduced a model of frequency-dependent selection resulting from random pairwise contests, to investigate the population genetics dynamics implicitly underlying basic principles and results of ‘population game theory’, and in particular the notion of *evolutionarily stable strategy (ESS)* (see Maynard Smith and Price, 1973). This model contemplates two phenotypes - or strategies such as, for example, manners of behavior -  $C_1$  and  $C_2$ , that determine the outcomes of interactions among pairs of individuals. The fitness payoff accruing to  $C_i$  individuals from interactions with  $C_j$  individuals is given by the matrix  $F = (F_{ij})_{i,j \in \{1,2\}}$ , which is not necessarily symmetric. Hence, if the population



consists of several types of individuals with different probabilities of expressing  $C_1$  or  $C_2$ , such that type  $x$  has frequency  $q_x$  and expresses  $C_1$  with probability  $h_x$  (and  $C_2$  with probability  $1 - h_x$ ), then the fitness of a type- $x$  individual is

$$\begin{aligned} W_x^{(L)} &= [\bar{h}F_{11} + (1 - \bar{h})F_{12}]h_x + [\bar{h}F_{21} + (1 - \bar{h})F_{22}](1 - h_x) \\ &= (F_{12} - F_{22})h_x + (F_{11} - F_{21} + F_{22} - F_{12})h_x\bar{h} + [\bar{h}F_{21} + (1 - \bar{h})F_{22}], \end{aligned} \quad (5a)$$

where  $\bar{h} = \sum_y h_y q_y$  is the overall frequency of strategy  $C_1$  in the population. Comparison of (1) and (5a) shows immediately that this model is a particular case of our Wildcard Model with

$$S_x = (F_{12} - F_{22})h_x, \quad (5b)$$

$$A_{x,y} = A_{y,x} = (F_{11} - F_{21} + F_{22} - F_{12})h_x h_y, \quad (5c)$$

$$C(\mathbf{q}) = \bar{h}F_{21} + (1 - \bar{h})F_{22}. \quad (5d)$$

### The Matessi-Gimelfarb-Gavrilets model

Like Lessard (1984), Matessi et al. (2001) and Matessi and Gimelfarb (2006) considered a model in which frequency-dependent selection results from random pairwise interactions. While Lessard (1984) assumed a discrete strategy set of two elements,  $C_1$ ,  $C_2$ , the other authors were interested in the case where the outcome of a confrontation depends on the respective value of some continuous trait of interacting individuals. If interactions with opponents of trait value  $y$  provide the fitness payoff  $f(x, y)$  to individuals of trait value  $x$ , then the fitness of these individuals is  $\sum_y f(x, y)q_y$ . In Matessi et al. (2001) and in Matessi and Gimelfarb (2006) the payoff function  $f(x, y)$  is assumed to be

$$f(x, y) = 1 + \alpha x^2 - (\alpha + \beta)yx + \beta y^2, \quad x, y \in \mathbb{R}. \quad (6)$$

Note that at the trait value  $x = 0$ , there is an *evolutionary singularity* (see Geritz et al., 1998) since  $\left. \frac{\partial f(x, y)}{\partial x} \right|_{x=y=0} = 0$ . Hence, with this choice, for any smooth payoff function  $F(x, y)$  the function  $f(x, y) - 1$  is the second order Taylor approximation of  $F(x, y) - F(x, x)$ , if all individuals in the population have trait values in the vicinity of the singularity. This particular point is *continuously stable*, namely evolution in the phenotypic space tends to proceed in its direction (see Eshel, 1983), provided

$$\alpha < \beta \quad \text{continuous stability condition} \quad (7a)$$

and is a *MEAST* (see Christiansen, 1991), or a continuously stable ESS (CSS, see Eshel, 1983), if

$$\alpha < \beta, \quad \alpha < 0 \quad \text{MEAST condition.} \quad (7b)$$

In such a case selection in the vicinity of zero is stabilizing. On the opposite, the singularity is a *PEAST* (see Christiansen, 1991), or a *branching point* (see Geritz et al., 1998), and selection in its vicinity is disruptive, if

$$\alpha < \beta, \quad \alpha > 0 \quad \text{PEAST condition.} \quad (7c)$$

Under (6) and either (7b) or (7c), the fitness of an individual of trait value  $x$  is

$$W_x^{(MG)} = 1 + \alpha x^2 - (\alpha + \beta) x \bar{x} + \beta (\bar{x}^2 + v), \quad (8a)$$

where  $\bar{x} = \sum_x x q_x$  and  $v = \sum_x (x - \bar{x})^2 q_x$  are respectively the mean and the variance of the trait values in the population. Comparison of (1) and (8a) shows that this model is a particular case of our Wildcard Model with

$$S_x = 1 + \alpha x^2, \quad A_{x,y} = A_{y,x} = -(\alpha + \beta) xy, \quad C(\mathbf{q}) = \beta (\bar{x}^2 + v). \quad (8b)$$

### 2.2.2 Intraspecific Competition. The Bürger-Schneider model

Bürger (2005) and Schneider (2006) formulated a model of density- and frequency-dependent selection, due to competition for limited resources, where the competitive abilities of individuals are determined by the size of some continuous trait. The explicit intent of this model was that of providing a unified weak-selection approximation to many and diverse models of this kind available in the literature (e.g., Roughgarden, 1972; Slatkin, 1979; Bulmer, 1974, 1980; Christiansen and Loeschcke, 1980; Bürger, 2002a,b). The formulation is based on a rather general model presented by Bulmer (1974), which is then approximated in the limit of overall selection strength tending to zero (Bürger, 2005; Schneider, 2006). The resulting model assigns to individuals of trait value  $x$  in a population of size  $N$  a fitness given by

$$W_x^{(BSdd)} = F(N) \left[ 1 - \sigma x^2 + \sigma \eta(N) (x - \bar{x})^2 + \varphi(N, \mathbf{q}) \right], \quad (9)$$

where the trait's mean is  $\bar{x}$ . Here,  $F(N)$  can be any non-negative, monotonically decreasing, continuously differentiable function that is suitable to represent the rate of increase of

a population as a function of its size, such as, for example, those employed in the Beverton-Holt or the Hassel model (e.g., Thieme, 2003, Chapter 9) of population regulation. The positive parameter  $\sigma$  is a direct measure of the strength of stabilizing selection. Furthermore,  $\eta(N) = -f \frac{NF'(N)}{F(N)}$ , where the positive parameter  $f$  is a measure of the strength of the frequency-dependent effect, resulting from intraspecific competition, relative to the strength,  $\sigma$ , of stabilizing selection implied by the resource distribution. Finally,  $\varphi(N, \mathbf{q})$ , which is independent of  $x$ , is an arbitrary positive function of the population size and of the composition of the population,  $\mathbf{q}$ .

This model, however, has been used more often (e.g., Bürger, 2005; Schneider, 2006, 2007) in its density-independent version, derived from (9) by assuming that the population size is constant. In such a case both  $F(N)$  and  $\eta(N)$  are positive constants and  $\varphi$  depends only on the population composition,  $\mathbf{q}$ , so that (9) can be rewritten as (Bürger, 2005; Schneider, 2006)

$$W_x^{(BS)} = 1 - \sigma x^2 + \sigma \eta (x - \bar{x})^2 + \varphi(\mathbf{q}) . \quad (10a)$$

Short- and long-term evolution due to frequency-dependent selection as prescribed by the selection regime of (10a) has been studied, mostly assuming continuous time, under a one-locus or multilocus genetic model, with multiple alleles per locus, assuming additivity and, in the multilocus case, quasi-linkage equilibrium (Bürger, 2005; Schneider, 2006, 2007). By rewriting (10a) as

$$W_x^{(BS)} = 1 + \sigma(\eta - 1)x^2 - 2\sigma\eta\bar{x}x + \sigma\eta\bar{x}^2 + \varphi(\mathbf{q}) \quad (10b)$$

we perceive it immediately as basically equivalent to the fitness function of the selection model of Matessi et al. (2001) and Matessi and Gimelfarb (2006), given by (8a), and therefore as a particular case of the Wildcard Model, (1). Table 1 summarizes the correspondences among the parameters of these two functions and also those of a fitness function derived from the model of Christiansen and Loeschcke (1980), to be discussed below (Section 3.2.2).

## 3 Optimization by frequency-dependent selection

### 3.1 The Wildcard Model

Both in the Lessard model, (5), and in the Bürger-Schneider model, (10), it has been found that certain quantitative population properties increase monotonically in the course

of frequency-dependent selection and attain a maximum at a population equilibrium. The existence of such global *Lyapunov functions* has been demonstrated, for the Lessard model, assuming one locus with multiple alleles and discrete time (Lessard, 1984), while for the Bürger-Schneider model multiple additive loci and alleles, linkage equilibrium and a continuous-time approximation have been assumed (Bürger, 2005; Schneider, 2006). Given the equivalence of the Bürger-Schneider model to the Matessi-Gimelfarb-Gavrilets model, the Lyapunov function possessed by the former is of course shared by the latter model.

The Lessard model and the Bürger-Schneider model are aimed to represent quite distinct biological situations. Hence, the biological meaning of their respective Lyapunov functions is also very different. The question then arises whether such optimizing properties are only due to special features, peculiar of each of these two models, or can instead be extended to whatever model has the structure of our Wildcard Model, (1). We can show that indeed a global Lyapunov function is admitted by this model, for a one locus, multiple allele system, at least in the continuous-time approximation, and (in Section 4) that it can be extended to multilocus, multiallele genetics, provided linkage equilibrium can be assumed to prevail.

Referring to (4), consider the function

$$\Lambda(\mathbf{p}) = 2\bar{s} + \bar{a}, \quad (11)$$

where  $\mathbf{p} = \mathbf{p}(t) = (p_1(t), \dots, p_n(t))$ . By virtue of the symmetries in the  $s_{ij}$  and  $a_{ij,kl}$  parameters we obtain

$$\frac{\partial \Lambda}{\partial p_i} = 4 \sum_{j=1}^n s_{ij} p_j + 4 \sum_{j,k,l=1}^n a_{ij,kl} p_j p_k p_l = 4(\bar{s}_i + \bar{a}_i) = 4\bar{w}_i. \quad (12)$$

Hence, the time derivative of  $\Lambda$  is

$$\dot{\Lambda}(\mathbf{p}) = \sum_{i=1}^n \frac{\partial \Lambda}{\partial p_i} \dot{p}_i = 4 \sum_{i=1}^n \bar{w}_i (\bar{w}_i - \bar{w}) p_i = 4 \sum_{i=1}^n (\bar{w}_i - \bar{w})^2 p_i, \quad (13)$$

which is always positive except at any equilibrium of (4), where it vanishes. Hence, under (4),  $\Lambda(\mathbf{p})$  increases in time and is maximized at the locally stable equilibria of the population. The above calculations show that (4) is even a generalized (Shashahani) gradient system (see e.g., Hofbauer and Sigmund, 1998; Bürger, 2000). Hence, we obtain the following

**Theorem 1.** *Consider the system (4). Moreover, let  $\Lambda = 2\bar{s} + \bar{a}$ , where  $\bar{s}$  and  $\bar{a}$  are given by (4a). Then (4) is a generalized gradient system with potential  $\frac{\Lambda}{4}$ . In particular  $\Lambda$  is an (increasing) global Lyapunov function for (4), and its time derivative vanishes only at the equilibrium points. Furthermore, every trajectory approaches the set of equilibria.*

We have to show now that the Lyapunov function,  $\Lambda$ , of the Wildcard Model includes the Lyapunov functions already identified for the Lessard and the Bürger-Schneider models as particular cases.

## 3.2 Lyapunov Functions Previously Found in the Particular Cases

### 3.2.1 The Lessard Model

Lessard (1984) has demonstrated that the one-locus, multiallele, discrete-time dynamics generated by his frequency-dependent selection model, (5), admits the following global Lyapunov function increasing across generations:

$$\Lambda^{(Ld)}(\mathbf{p}) = (F_{11} - F_{21} + F_{22} - F_{12}) |\bar{h} - h^*|, \quad (14)$$

where  $\mathbf{p} = (p_1, \dots, p_n)$  is the vector of allele frequencies,  $\bar{h}$  is the overall frequency of strategy  $C_1$  and

$$h^* = \frac{F_{12} - F_{22}}{F_{21} - F_{11} + F_{12} - F_{22}}$$

is the frequency of  $C_1$  at the unique mixed ESS of the population game with payoff matrix  $F$ , whenever such an ESS indeed exists, namely whenever

$$F_{12} - F_{22} > 0 \text{ and } F_{21} - F_{11} > 0.$$

Observe that if this condition is satisfied, then  $(F_{11} - F_{21} + F_{22} - F_{12}) < 0$ , which, by the (increasing) Lyapunov function (14) implies that  $|\bar{h} - h^*|$  decreases across generations, namely the population phenotypic composition approaches the ESS.

On the other hand the Lessard model, as we have seen, is a particular case of the Wildcard Model. Hence, it must admit, in continuous time, the global Lyapunov function  $\Lambda$ , (11), in the particular version appropriate to its specific parametrization. But in order to derive this version of  $\Lambda$  it is required that we first represent the parameters of the

model in the form suitable to the continuous-time (i.e., weak-selection) approximation. In analogy to (3) we write  $F_{ij} = f + \tau f_{ij}$ . This yields

$$h^* = \frac{f_{12} - f_{22}}{f_{21} - f_{11} + f_{12} - f_{22}} \quad , \quad \Lambda^{(Ld)} = \tau (f_{11} - f_{21} + f_{22} - f_{12}) |\bar{h} - h^*| \quad (15a)$$

which, by (3) and (5b) - (5d) entails

$$S_{ij} = \tau (f_{12} - f_{22}) h_{ij} \quad , \quad (15b)$$

$$A_{ij,kl} = \tau (f_{11} - f_{21} + f_{22} - f_{12}) h_{ij} h_{kl} \quad , \quad (15c)$$

$$C(\mathbf{p}) = f + \tau [\bar{h} f_{21} + (1 - \bar{h}) f_{22}] \quad . \quad (15d)$$

Hence, by applying this parametrization to the general Lyapunov function  $\Lambda$  of (11) it results in

$$\Lambda(\mathbf{p}) = (f_{11} - f_{21} + f_{22} - f_{12}) (\bar{h}^2 - 2\bar{h}h^*) \quad .$$

Considering that adding a constant to a Lyapunov function obviously cannot change its nature, we may conclude that the particular version of the general Lyapunov function appropriate to the Lessard model in continuous time is

$$\Lambda^{(Lc)}(\mathbf{p}) = \Lambda(\mathbf{p}) + (f_{11} - f_{21} + f_{22} - f_{12}) h^{*2} = (f_{11} - f_{21} + f_{22} - f_{12}) (\bar{h} - h^*)^2 \quad , \quad (16)$$

which is clearly equivalent to the discrete time Lyapunov function  $\Lambda^{(Ld)}$ , of (14) or (15a), originally identified by Lessard (1984). We can therefore assert the following

**Corollary 1.** *The continuous-time version of the two-phenotype model of Lessard is a particular case of the Wildcard Model (4). Hence, it forms a generalized gradient system. Moreover, since  $\Lambda^{(Lc)}$  given by (16) differs from  $\Lambda$  given by (11) only by a constant,  $\Lambda^{(Lc)}/4$  is a potential function of this system. Thus, the global (increasing) Lyapunov function  $\Lambda^{(Lc)}$  can be regarded as a particular case of  $\Lambda$ .*

### 3.2.2 The Bürger-Schneider model

Bürger (2005) and Schneider (2006) have demonstrated that the continuous-time dynamics induced by their frequency-dependent selection model, (10b), on a single locus with multiple additive alleles, or even on multiple additive loci with multiple alleles, is governed by an increasing global Lyapunov function, that in the one locus case is

$$\Lambda^{(BS)}(\mathbf{p}) = (\eta - 1) v - \bar{x}^2 \quad , \quad (17)$$

where the trait's mean and variance are respectively  $\bar{x}$  and  $v$ . Note that if selection near the evolutionary singularity at  $x = 0$  is stabilizing, i.e., if  $\eta < 1$ , the implication of this Lyapunov function is that the population variance of the selected trait,  $v$ , tends to be minimized. If, instead, selection is disruptive, i.e.,  $\eta > 1$ , the population variance tends to be maximized. In either cases the mean trait tends to the singular trait value of zero.

Again, since the Bürger-Schneider model is a particular case of the general model, it must also admit the general Lyapunov function  $\Lambda$ , (11), so that we expect  $\Lambda^{(BS)}$  to be a particular version of  $\Lambda$ . Indeed, since

$$s_{ij} = \sigma (\eta - 1) x_{ij}^2, \quad a_{ij,kl} = -2\sigma\eta x_{ij}x_{kl} \quad (18a)$$

by computing  $\Lambda$ , subject to this prescription we find

$$\Lambda(\mathbf{p}) = 2\sigma(\eta - 1)v - 2\sigma\bar{x}^2 = 2\sigma\Lambda^{(BS)}(\mathbf{p}). \quad (18b)$$

Hence, we have

**Corollary 2.** *The one-locus, multiallele version of the Bürger-Schneider model in continuous time is a particular case of the Wildcard Model (4). Hence, it is a generalized gradient system. Its potential is  $\frac{\sigma}{2}\Lambda^{(BS)}$ , where  $\Lambda^{(BS)}$  is given by (17), which, in particular is a global (increasing) Lyapunov function. Thus,  $\Lambda^{(BS)}$  can be regarded as a particular case of  $\Lambda$ , given by (11).*

Note that the statement of the above corollary is more general than the results of Bürger (2005) and Schneider (2006) for the one-locus case, since it is not limited by the restriction to additive alleles.

Also, from the correspondence between the Bürger-Schneider and the Matessi-Gimelfarb-Gavrilets models and from (17) we immediately obtain

**Corollary 3.** *The one-locus multiallele dynamics in continuous time driven by the Matessi-Gimelfarb-Gavrilets frequency-dependent selection model form a generalized gradient system. Its potential function is given by  $\frac{\beta-\alpha}{4}\Lambda^{(MG)}$ , where*

$$\Lambda^{(MG)}(\mathbf{p}) = \frac{2\alpha}{\beta - \alpha}v - \bar{x}^2 \quad (19)$$

*is an increasing global Lyapunov function.*

### 3.3 An ancestor of the Lyapunov function of the Wildcard Model

#### 3.3.1 The Matessi-Jayakar model

Matessi and Jayakar (1981) analyzed density- and frequency-dependent selection, arising from scramble competition for limited resources, by means of a Lotka-Volterra fitness model applied to a system of multiple species with a single locus and multiple alleles per species. In the case of just one species, the fitness that this model assigns to individuals of type  $x$  in a population of size  $N$  is

$$W_x^{(MJ)} = 1 + r \left( K_x - N \sum_y B_{x,y} q_y \right), \quad B_{x,y} = B_{y,x}, \quad (20a)$$

where  $r$  is the intrinsic rate of increase of the population,  $K_x/B_{x,x}$  is the carrying capacity the population would have if it consisted only of individuals of type  $x$ , and  $B_{x,y}/B_{x,x}$  is the intensity of competition between types  $x$  and  $y$ .

We again assume that a single locus with  $n$  alleles determines the types. Accordingly, with discrete time, the changes occurring to a population in one generation are described by the following system of recurrence equations

$$N' = N [1 + r (\bar{K} - N\bar{B})], \quad (20b)$$

$$p'_i = p_i \frac{1 + r (\bar{K}_i - N\bar{B}_i)}{1 + r (\bar{K} - N\bar{B})}, \quad (20c)$$

for  $i \in \{1, \dots, n\}$ , where  $p_i$  is the frequency of  $i$ -th allele while

$$\bar{K}_i = \sum_{j=1}^n K_{ij} p_j, \quad \bar{K} = \sum_{i=1}^n \bar{K}_i p_i, \quad \bar{B}_i = \sum_{j,k,l=1}^n B_{ij,kl} p_j p_k p_l \quad \text{and} \quad \bar{B} = \sum_{i=1}^n \bar{B}_i p_i. \quad (20d)$$

If the intrinsic rate of increases,  $r$ , is small enough a continuous-time approximation can be made - even without assuming that differences among genotypes are very slight - transforming (20) into the following system of differential equations (Matessi and Jayakar, 1981)

$$\dot{N}(t) = \rho N(t) [\bar{K} - N(t)\bar{B}], \quad (21a)$$

$$\dot{p}_i(t) = \rho p_i(t) [\bar{K}_i - N(t)\bar{B}_i - \bar{K} + N(t)\bar{B}], \quad (21b)$$



for  $i \in \{1, \dots, n\}$ , where  $r = \tau\rho$ , and  $\tau$  is the duration of the time interval between successive generations, that by tending to zero transforms (20) into (21). Matessi and Jayakar (1981) have demonstrated that (21) admits the following global Lyapunov function

$$\Psi^{(MJ)}(\mathbf{p}, N) = 2\bar{K}N - \bar{B}N^2 \quad (22)$$

By comparing (20) - (21) to (1) - (4) we immediately notice that these two models would be essentially the same were it not for the density dependence in (20a). Correspondingly, it is clear that there is a close relation among the respective Lyapunov functions  $\Psi^{(MJ)}(\mathbf{p}, N)$ , (22), and  $\Lambda(\mathbf{p})$ , given by (11); so close that one would ask how the latter could be derived from the former.

Indeed, from a purely formal point of view, (11) can be immediately obtained from (22) by simply assuming that the population size,  $N$ , is a constant,  $N \equiv N_0$ . Hence, by deleting the differential equation (21a) from (21),  $\Psi^{(MJ)}$  and  $\Lambda$  become identical, by the obvious switch of notation

$$N_0 K_{ij} = s_{ij}, \quad N_0^2 B_{ij,kl} = -a_{ij,kl}. \quad (23)$$

This point of view, although formally correct, has the weakness that it destroys the biological meaning of the Matessi-Jayakar model, (20) - (21), because a model in which competition for limited resources keeps the population size constant would be biologically inconceivable.

However, we can put forward a second argument that leaves intact the biology of (20) - (21) while producing  $\Lambda$  as an ‘approximation’ of  $\Psi^{(MJ)}$ . This argument is rooted in the approach taken by Christiansen and Loeschke (1980) to analyze evolutionary consequences of competition for limited resources, starting from Lotka-Volterra-like equations exactly of the same form as (20). To this model the authors add two assumptions. The first is implicitly justified by a ‘singular perturbation’ argument (e.g., Hoppensteadt, 1974). Namely it is stipulated that the population size changes much more rapidly than the population composition. This is reasonable if selection is sufficiently weak relative to the intrinsic rate of increase. Hence, it can be assumed that, on the slow time scale of the population-composition dynamics, it is always very close to the equilibrium value corresponding to the current value of the allele frequencies. The second assumption is that the carrying capacity parameters,  $K_x$ , and the competition parameters,  $B_{x,y}$ , (20a), are determined by the value of a continuous phenotypic trait, according to

$$K_x = \exp[-\theta x^2] \quad \text{and} \quad B_{x,y} = \exp[-\vartheta(x-y)^2]. \quad (24a)$$

In addition Christiansen and Loeschcke (1980) concentrate mostly on the case where all individuals have trait values close to zero. A situation that entails weak selection and justifies the further approximation that

$$K_x \simeq 1 - \theta x^2 \quad \text{and} \quad B_{x,y} \simeq 1 - \vartheta (x - y)^2 . \quad (24b)$$

In order to show the kinship of the two Lyapunov functions,  $\Psi^{(MJ)}$  and  $\Lambda$ , we follow the lead of Christiansen and Loeschcke (1980) and therefore, first, replace (21a) by

$$N(t) = \hat{N}(\mathbf{p}(t)) = \frac{\bar{K}}{\bar{B}} . \quad (25a)$$

Next, we assume there is a small number  $\varepsilon$  such that

$$\bar{K}_i = k_0 + \bar{k}_i \varepsilon + o(\varepsilon) , \quad \bar{K} = k_0 + \bar{k} \varepsilon + o(\varepsilon) , \quad \bar{k}_i = \sum_{j=1}^n k_{ij} p_j , \quad \bar{k} = \sum_{i=1}^n \bar{k}_i p_i , \quad (25b)$$

$$\bar{B}_i = b_0 + \bar{b}_i \varepsilon + o(\varepsilon) , \quad \bar{B} = b_0 + \bar{b} \varepsilon + o(\varepsilon) , \quad \bar{b}_i = \sum_{j,k,l=1}^n b_{ij,kl} p_j p_k p_l , \quad \bar{b} = \sum_{i=1}^n \bar{b}_i p_i . \quad (25c)$$

Finally, resting on these assumptions we can immediately conclude with

**Result 1.** (i) *The system of differential equations (21) can be approximated by*

$$N(t) = \hat{N}(\mathbf{p}(t)) = \frac{\bar{K}}{\bar{B}} \quad (26a)$$

$$\dot{p}_i(t) = \rho p_i(t) [\bar{K}_i - N_0 \bar{B}_i - \bar{K} + N_0 \bar{B}] , \quad (26b)$$

for  $i \in \{1, \dots, n\}$ , where  $N_0 = k_0/b_0$ .

(ii) *The function  $\Psi^{(MJ)}(\mathbf{p}, N)$  of (22) can be approximated by*

$$\Psi_0^{(MJ)}(\mathbf{p}) = 2N_0 \bar{K} - N_0^2 \bar{B} . \quad (26c)$$

(iii) *By changing notation according to (23), it is seen that the system (26b) and the function  $\Psi_0^{(MJ)}(\mathbf{p})$  coincide exactly with the system (4b) and its global Lyapunov function  $\Lambda(\mathbf{p})$ , (11), respectively.*

### 3.3.2 The Christiansen-Loeschcke model

Having recalled above some of the assumptions that characterize the model of Christiansen and Loeschcke (1980), we have the opportunity to uncover another tread of the network

connecting a variety of apparently unrelated models of frequency-dependent selections. In fact, it is easy to verify that, by its very assumptions, (24b) and (25a), this model reduces to a density-independent selection model equivalent to the models of Matessi et al. (2001), Matessi and Gimelfarb (2006), (8a), and of Bürger (2005), Schneider (2006), (10b). To see this it suffices to substitute (24b) and (25a) into the fitness function (20a), which coincides exactly with the basic model from which Christiansen and Loeschke (1980) start. In this substitution only the terms that are up to second order in the trait values are to be retained, because all trait values in the population are assumed to be very close to zero. In this way we find that the fitness function resulting from the assumptions of Christiansen and Loeschke (1980) is

$$W_x^{(CL)} = 1 + (\vartheta - \theta) x^2 - 2\vartheta x\bar{x} + (\vartheta + \theta) (\bar{x}^2 + v) - 2\vartheta v, \quad (27a)$$

where  $\bar{x}$  and  $v$  are respectively the mean and the variance of the trait values in the population. The parameters  $\vartheta$  and  $\theta$  depend on the variances of the (Gaussian) resource spectrum,  $V_R$ , and the individual's (Gaussian) resource utilization distribution,  $V_U$ , assumed to be the same for all individuals that, depending on their genotype, vary only in the modal position of their utilization distributions. More specifically, the relation among these parameters is

$$\theta = \frac{r}{2V_R + 2V_U}, \quad \vartheta = \frac{r}{4V_U}. \quad (27b)$$

**Table 1:** The correspondence between the Christiansen-Loeschke (CL), the Matessi-Gimelfarb-Gavrilets (MG) and the Bürger-Schneider (BS) model is shown. In the table,  $\bar{x}$ ,  $v$  and  $\mathbf{q}$  denote the mean trait value, the variance of trait values, and the distribution of types, respectively. The parameters are described in the main text. Moreover, their admissible range is shown and the condition under which selection is stabilizing in the respective models. If the respective condition is violated selection is disruptive.

generic formula: $W_x = 1 + Ax^2 + Bx\bar{x} + C(\mathbf{q})$					
model	$A$	$B$	$C(\mathbf{q})$	range	stabilizing selection
CL	$\vartheta - \theta$	$-2\vartheta$	$(\vartheta + \theta)(\bar{x}^2 + v) - 2\vartheta v$	$\vartheta, \theta > 0$	$\vartheta < \theta$
MG	$\alpha$	$-(\alpha + \beta)$	$\beta(\bar{x}^2 + v)$	$\alpha < \beta$	$\alpha < 0$
BS	$\sigma(\eta - 1)$	$-2\sigma\eta$	$\sigma\eta\bar{x}^2 + \varphi(\mathbf{q})$	$\sigma, \eta > 0$	$\eta < 1$

From (27a) it is immediately obvious that  $W_x^{(CL)}$  is essentially equivalent to the fitness functions  $W_x^{(MG)}$ , of (8a), and  $W_x^{(BS)}$ , of (10b). Table 1 summarizes the correspondences among the parameters of these three functions. We also conclude that the global Lyapunov function associated to the one-locus, multiple-allele dynamics in continuous time, generated by frequency-dependent selection with the Christiansen-Loeschke fitness function  $W_x^{(CL)}$ , (27), is

$$\Lambda^{(CL)}(\mathbf{p}) = \frac{\vartheta - \theta}{\theta} v - \bar{x}^2. \quad (28)$$

This Lyapunov function directly informs us that, in the Christiansen-Loeschke model, selection is stabilizing and phenotypic variance,  $v$ , (the variance among the positions of individual utilization distributions on the resource axis) tends to be minimized when the width of the resource spectrum,  $V_R$ , is smaller than that of the individual utilization distribution,  $V_U$ . In the opposite case selection is disruptive and the phenotypic variance tends to be maximized. In both cases the mean of the positions of individual utilizations on the resource axis tends to the modal point of resources abundance.

## 4 Multiple Loci

Concerning the genetic assumptions, so far we have assumed a single locus with multiple alleles. In this section we want to generalize the results of the previous sections to the case of multiple multiallelic loci under a linkage equilibrium approximation. Furthermore, based on the motivation of the last section, we will introduce a density-dependent version of our model.

Before we formulate our model and generalize our results to multiple loci we need some preliminaries. In the next section we will briefly summarize the multilocus notation that we will use.

### 4.1 The Multilocus Multiallele Framework

For the multilocus dynamics we use the notation introduced by Nagylaki (1993) and Nagylaki et al. (1999). As before, we assume a randomly mating diploid population under viability selection. Now, we consider  $n$  loci instead of just one, where on locus  $k$  the  $m_k$  alleles  $\mathcal{A}_{i_k}^{(k)}$  can occur ( $i_k \in \{1, \dots, m_k\}$ ). The multi-index  $\mathbf{i} = (i_1, \dots, i_n)$  is used as an abbreviation for the gamete  $\mathcal{A}_{i_1}^{(1)} \mathcal{A}_{i_2}^{(2)} \dots \mathcal{A}_{i_n}^{(n)}$ ; its frequency is denoted by  $p_{\mathbf{i}}$ .

Collectively, these frequencies form the vector  $\mathbf{p}$  of gamete frequencies, which are elements of the simplex  $\mathcal{S}_{m_1 \dots m_n}$ . The frequency of  $\mathcal{A}_{i_k}^{(k)}$  is given by

$$p_{i_k}^{(k)} = \sum_{\mathbf{i}}^{(k)} p_{\mathbf{i}}. \quad (29)$$

The above sum runs over all multi-indices  $\mathbf{i}$  with the  $k$ th component fixed as  $i_k$ . We denote the gene-frequency vector  $(p_{i_k}^{(k)})$  by  $\boldsymbol{\rho} \in \mathcal{S} := \mathcal{S}_{m_1} \times \dots \times \mathcal{S}_{m_n}$ . The fitness of genotype  $\mathbf{i}\mathbf{j}$  is denoted by  $W_{\mathbf{i}\mathbf{j}}$ , and since we assume a lack of genomic imprinting  $W_{\mathbf{i}\mathbf{j}} = W_{\mathbf{j}\mathbf{i}}$  holds for all  $\mathbf{i}, \mathbf{j}$ . The marginal fitness of gamete  $\mathbf{j}$  is given by

$$\bar{W}_{\mathbf{j}} = \sum_{\mathbf{i}} W_{\mathbf{i}\mathbf{j}} p_{\mathbf{i}}, \quad (30)$$

and the mean fitness of the population is

$$\bar{W} = \sum_{\mathbf{i}\mathbf{j}} W_{\mathbf{i}\mathbf{j}} p_{\mathbf{i}} p_{\mathbf{j}}. \quad (31)$$

Let  $I, J$  be a nontrivial decomposition of the set  $M = \{1, \dots, n\}$ , i.e.,  $I \cup J = M$  and  $I \cap J = \emptyset$  normalized by  $1 \in I$ . We denote by  $r_I$  the recombination probability between the sets of loci  $I$  and  $J$ . Throughout we assume  $r_I > 0$  for every  $I$ . Thus, the dynamics of the gametic frequencies are given by the following recurrence relations,

$$p'_{\mathbf{i}} = p_{\mathbf{i}} \frac{\bar{W}_{\mathbf{i}}}{\bar{W}} - D_{\mathbf{i}}, \quad (32)$$

where

$$D_{\mathbf{i}} = \frac{1}{\bar{W}} \sum_{\mathbf{j}} \sum_I r_I (W_{\mathbf{i}\mathbf{j}} p_{\mathbf{i}} p_{\mathbf{j}} - W_{\mathbf{i}_I \mathbf{j}_J} p_{\mathbf{i}_I} p_{\mathbf{j}_J}) \quad (33)$$

is a measure for linkage disequilibrium for gamete  $\mathbf{i}$ . In the above formula,  $\mathbf{i}_I \mathbf{j}_J$  signifies the vector with  $k$ th component  $i_k$  if  $k \in I$  and  $j_k$  if  $k \in J$ .

The allele frequencies in the next generation are

$$p_{i_k}^{(k)'} = \frac{p_{i_k}^{(k)} W_{i_k}^{(k)}}{\bar{W}}, \quad (34)$$

where the marginal fitness,  $W_{i_k}^{(k)}$ , of allele  $\mathcal{A}_{i_k}^{(k)}$  is defined by

$$p_{i_k}^{(k)} W_{i_k}^{(k)} := \sum_{\mathbf{i}}^{(k)} p_{\mathbf{i}} \bar{W}_{\mathbf{i}}. \quad (35)$$

The *linkage-equilibrium manifold*, or *Wright manifold*, is given by

$$\mathcal{L}_0 = \{\mathbf{p} : p_{\mathbf{i}} = p_{i_1}^{(1)} p_{i_2}^{(2)} \dots p_{i_n}^{(n)} \text{ for all } \mathbf{i}\}. \quad (36)$$

We assume that there is no position effect, i.e.,  $W_{\mathbf{ij}} = W_{i_1 j_1, i_2 j_2, \dots, i_n j_n}$  for every  $\mathbf{i}, \mathbf{j}$ , and  $I$ . Therefore, it follows immediately that  $D_{\mathbf{i}} = 0$  for every  $\mathbf{p} \in \mathcal{L}_0$ , and we have  $\mathcal{L}_0 \subseteq \{\mathbf{p} \mid D_{\mathbf{i}} = 0 \text{ for every } \mathbf{i}\}$ . Equality holds in the absence of selection (see Nagylaki et al., 1999).

Fitnesses are frequency dependent and if population regulation is added to the model, they depend also on the population size,  $N$ . In such a situation the population size changes according to the following recursion relation:

$$N' = N\bar{W}. \quad (37)$$

In the following we will assume linkage equilibrium, in which case it is sufficient to consider the dynamics of allele frequencies (34) instead of the dynamics of gamete frequencies (32). Additionally, in analogy to the one-locus case of previous sections, we will assume weak selection and therefore the discrete-time dynamics (34) and (37) will be approximated by a continuous-time dynamics. Hence, our results will hold for any model of weak selection which can be accurately approximated by the linkage-equilibrium dynamics. In other words, our results hold if there exists an invariant manifold (the *quasi linkage-equilibrium manifold*) sufficiently close to the linkage-equilibrium manifold, where the dynamics behave almost as if they are in linkage equilibrium, which is reached by every trajectory within a few generations. Of course the linkage-equilibrium approximation will not be accurate for any given model. The applicability of such an approximation will heavily depend on the concrete model, i.e., the concrete expressions of the fitnesses, the strength of selection relative to recombination etc.

As in the previous sections, we will concentrate on our Wildcard Model, (1), and also introduce a density-dependent modification of this model, which slightly generalizes the Matessi-Jayakar model (20a).

## 4.2 The Density-Independent Model

Now, we are able to formulate the multilocus version of our Wildcard Model. In analogy to the single locus case we assume that the phenotypes under selection are identified with their genotypic configuration at the  $n$  loci under consideration. Since we are dealing with

a continuous-time approximation, according to an argument analogous to that in Section 2.1, the fitness of the genotype  $\mathbf{ij}$  appropriate for the differential equations is given by

$$w_{\mathbf{ij}} = s_{\mathbf{ij}} + \sum_{\mathbf{k,l}} a_{\mathbf{ij,kl}} p_{\mathbf{k}} p_{\mathbf{l}} + \gamma(\boldsymbol{\rho}). \quad (38)$$

Here, the parameters are defined in a way similar to (3). In particular, the frequency-independent fitness component,  $s_{\mathbf{ij}}$ , satisfies  $s_{\mathbf{ij}} = s_{\mathbf{ji}}$ . Moreover, the parameters  $a_{\mathbf{ij,kl}}$  of the frequency-dependent term must satisfy

$$a_{\mathbf{ij,kl}} = a_{\mathbf{ji,kl}} = a_{\mathbf{ij,lk}} = a_{\mathbf{ji,lk}}$$

for all  $\mathbf{i}, \mathbf{j}, \mathbf{k}, \mathbf{l}$ . As in the one-locus case we assume that an individual  $\mathbf{ij}$  is affected by an individual  $\mathbf{kl}$  in the same way as  $\mathbf{kl}$  is affected by  $\mathbf{ij}$ , which implies

$$a_{\mathbf{ij,kl}} = a_{\mathbf{kl,ij}}$$

for all  $\mathbf{i}, \mathbf{j}, \mathbf{k}, \mathbf{l}$ . Moreover,  $\gamma(\boldsymbol{\rho})$  is a function that depends only on the frequency distribution of alleles and is the same for all genotypes. We mention here that all our results hold if  $\gamma(\boldsymbol{\rho})$  in (38) is replaced by  $\varphi_{\mathbf{ij}}$  for all  $\mathbf{i}, \mathbf{j}$ , which are arbitrary functions of the allele frequencies  $\boldsymbol{\rho}$  satisfying  $\varphi_{\mathbf{ij}} = \varphi_{\mathbf{ji}}$  and

$$\gamma(\boldsymbol{\rho}) := \sum_{\mathbf{j}} \varphi_{\mathbf{ij}}(\boldsymbol{\rho}) p_{\mathbf{j}} = \sum_{\mathbf{j}} \varphi_{\mathbf{kj}}(\boldsymbol{\rho}) p_{\mathbf{j}} \quad \text{for all } \mathbf{i}, \mathbf{k}.$$

The marginal fitness of gamete  $\mathbf{i}$  is then given by

$$\bar{w}_{\mathbf{i}} = \sum_{\mathbf{j}} s_{\mathbf{ij}} p_{\mathbf{j}} + \sum_{\mathbf{j,k,l}} a_{\mathbf{ij,kl}} p_{\mathbf{j}} p_{\mathbf{k}} p_{\mathbf{l}} + \gamma(\boldsymbol{\rho}),$$

and the mean fitness is given by

$$\bar{w} = \sum_{\mathbf{i,j}} s_{\mathbf{ij}} p_{\mathbf{i}} p_{\mathbf{j}} + \sum_{\mathbf{i,j,k,l}} a_{\mathbf{ij,kl}} p_{\mathbf{i}} p_{\mathbf{j}} p_{\mathbf{k}} p_{\mathbf{l}} + \gamma(\boldsymbol{\rho}). \quad (39a)$$

The dynamics under linkage equilibrium then become

$$\dot{p}_{i_k}^{(k)} = p_{i_k}^{(k)} (w_{i_k}^{(k)} - \bar{w}) \quad \text{for } 1 \leq i_k \leq m_k, 1 \leq k \leq n, \quad (39b)$$

where

$$w_{i_k}^{(k)} = \sum_{\mathbf{i}}^{(k)} \bar{w}_{\mathbf{i}} \prod_{\substack{l=1 \\ l \neq k}}^n p_{i_l}^{(l)} = \sum_{\mathbf{i}}^{(k)} \prod_{\substack{l=1 \\ l \neq k}}^n p_{i_l}^{(l)} \sum_{\mathbf{j}} s_{\mathbf{ij}} p_{\mathbf{j}} + \sum_{\mathbf{i}}^{(k)} \prod_{\substack{l=1 \\ l \neq k}}^n p_{i_l}^{(l)} \sum_{\mathbf{j,k,l}} a_{\mathbf{ij,kl}} p_{\mathbf{j}} p_{\mathbf{k}} p_{\mathbf{l}} + \gamma(\boldsymbol{\rho}) \quad (39c)$$

Note that (39b) is independent of  $\gamma(\boldsymbol{\rho})$ .

We are now able to generalize the results of the corresponding one-locus model to the multilocus model in linkage equilibrium.

**Theorem 2.** *Consider the system (39). Moreover, let*

$$\Lambda(\boldsymbol{\rho}) := 2\bar{s} + \bar{a},$$

where

$$\bar{s} = \sum_{\mathbf{i}, \mathbf{j}} s_{\mathbf{i}\mathbf{j}} p_{\mathbf{i}} p_{\mathbf{j}} \quad \text{and} \quad \bar{a} = \sum_{\mathbf{i}, \mathbf{j}, \mathbf{k}, \mathbf{l}} a_{\mathbf{i}\mathbf{j}, \mathbf{k}\mathbf{l}} p_{\mathbf{i}} p_{\mathbf{j}} p_{\mathbf{k}} p_{\mathbf{l}}.$$

Then, the system (39b) is a generalized gradient system with potential  $\Lambda/4$ , i.e.,

$$\dot{p}_{i_k}^{(k)} = \frac{p_{i_k}^{(k)}}{4} \left( \frac{\partial \Lambda}{\partial p_{i_k}^{(k)}} - \sum_{j_k=1}^{m_k} p_{j_k}^{(k)} \frac{\partial \Lambda}{\partial p_{j_k}^{(k)}} \right) \quad \text{for} \quad 1 \leq i_k \leq m_k, 1 \leq k \leq n.$$

In particular,  $\Lambda$  is a global Lyapunov function for the set of equilibria, i.e.,  $\dot{\Lambda}(\boldsymbol{\rho}) \geq 0$  and  $\dot{\Lambda}(\hat{\boldsymbol{\rho}}) = 0$  if and only if  $\hat{\boldsymbol{\rho}}$  is an equilibrium.

**Proof.** We need to derive the partial derivatives  $\frac{\partial \Lambda}{\partial p_{i_k}^{(k)}}$ . First, note that we have

$$\frac{\partial p_{\mathbf{j}}}{\partial p_{i_k}^{(k)}} = \delta_{i_k, j_k} \prod_{\substack{l=1 \\ l \neq k}}^n p_{j_l}^{(l)},$$

where  $\delta$  denotes the Kronecker- $\delta$ . Now, straightforward calculations yields

$$\begin{aligned} \frac{1}{4} \frac{\partial \Lambda}{\partial p_{i_k}^{(k)}} &= \frac{1}{2} \sum_{\mathbf{i}, \mathbf{j}} s_{\mathbf{i}\mathbf{j}} \left( \frac{\partial p_{\mathbf{i}}}{\partial p_{i_k}^{(k)}} p_{\mathbf{j}} + \frac{\partial p_{\mathbf{j}}}{\partial p_{i_k}^{(k)}} p_{\mathbf{i}} \right) \\ &\quad + \frac{1}{4} \sum_{\mathbf{i}, \mathbf{j}, \mathbf{k}, \mathbf{l}} a_{\mathbf{i}\mathbf{j}, \mathbf{k}\mathbf{l}} \left( \frac{\partial p_{\mathbf{i}}}{\partial p_{i_k}^{(k)}} p_{\mathbf{j}} p_{\mathbf{k}} p_{\mathbf{l}} + \frac{\partial p_{\mathbf{j}}}{\partial p_{i_k}^{(k)}} p_{\mathbf{i}} p_{\mathbf{k}} p_{\mathbf{l}} + \frac{\partial p_{\mathbf{k}}}{\partial p_{i_k}^{(k)}} p_{\mathbf{i}} p_{\mathbf{j}} p_{\mathbf{l}} + \frac{\partial p_{\mathbf{l}}}{\partial p_{i_k}^{(k)}} p_{\mathbf{i}} p_{\mathbf{j}} p_{\mathbf{k}} \right) \\ &= \sum_{\mathbf{i}, \mathbf{j}} s_{\mathbf{i}\mathbf{j}} \frac{\partial p_{\mathbf{i}}}{\partial p_{i_k}^{(k)}} p_{\mathbf{j}} + \sum_{\mathbf{i}, \mathbf{j}, \mathbf{k}, \mathbf{l}} a_{\mathbf{i}\mathbf{j}, \mathbf{k}\mathbf{l}} \frac{\partial p_{\mathbf{i}}}{\partial p_{i_k}^{(k)}} p_{\mathbf{j}} p_{\mathbf{k}} p_{\mathbf{l}} \\ &= \sum_{\mathbf{i}}^{(k)} \sum_{\mathbf{j}} s_{\mathbf{i}\mathbf{j}} p_{\mathbf{j}} \prod_{\substack{l=1 \\ l \neq k}}^n p_{i_l}^{(l)} + \sum_{\mathbf{i}}^{(k)} \sum_{\mathbf{j}, \mathbf{k}, \mathbf{l}} a_{\mathbf{i}\mathbf{j}, \mathbf{k}\mathbf{l}} p_{\mathbf{j}} p_{\mathbf{k}} p_{\mathbf{l}} \prod_{\substack{l=1 \\ l \neq k}}^n p_{i_l}^{(l)} \\ &= w_{i_k}^{(k)} - \gamma(\boldsymbol{\rho}). \end{aligned}$$



From the above we obtain

$$\dot{p}_{i_k}^{(k)} = p_{i_k}^{(k)} \left( \frac{1}{4} \frac{\partial \Lambda}{\partial p_{i_k}^{(k)}} - \sum_{j_k=1}^{m_k} \frac{1}{4} \frac{\partial \Lambda}{\partial p_{j_k}^{(k)}} p_{j_k}^{(k)} \right),$$

which immediately proves the first statement.

Now, applying the chain rule gives

$$\begin{aligned} \frac{1}{4} \dot{\Lambda} &= \frac{1}{4} \frac{d\Lambda}{dt} = \frac{1}{4} \sum_{k=1}^n \sum_{i_k=1}^{m_k} \frac{\partial \Lambda}{\partial p_{i_k}^{(k)}} \dot{p}_{i_k}^{(k)} = \sum_{k=1}^n \sum_{i_k=1}^{m_k} (w_{i_k}^{(k)} - \gamma(\boldsymbol{\rho})) (w_{i_k}^{(k)} - \bar{w}) p_{i_k}^{(k)} \\ &= \sum_{k=1}^n \sum_{i_k=1}^{m_k} (w_{i_k}^{(k)} - \bar{w})^2 p_{i_k}^{(k)} \geq 0. \end{aligned}$$

Moreover, we have  $\dot{\Lambda} = 0$  if and only if  $w_{i_k}^{(k)} = \bar{w}$  or  $p_{i_k}^{(k)} = 0$ , i.e., if and only if  $w_{i_k}^{(k)} = \bar{w}$  whenever  $p_{i_k}^{(k)} \neq 0$ . In other words, we have  $\dot{\Lambda} = 0$  only at an equilibrium. Thus,  $\Lambda$  is a global Lyapunov function for the set of equilibria. □

From similar considerations as in the previous section and from straightforward multilocus formulations of the particular models we immediately obtain the following

**Corollary 4.** *Corollaries 1 - 3 remain valid for underlying multilocus, multiallele genetics if a linkage-equilibrium approximation can be assumed.*

Note that Bürger (2005) and Schneider (2006) in the proofs of the existence of a gradient system in their model assumed additive genetics, i.e., no dominance or epistasis, an assumption that is not required by our more general result (Corollary 4). However, using the additivity assumption Bürger (2005) and Schneider (2006) were able to prove that the trajectories in their model indeed converge to a quasi-linkage equilibrium if selection is sufficiently weak compared with recombination. It is yet unknown to what extent the linkage-equilibrium approximation is valid if the additivity assumption is relaxed, as in our model. Thus, to apply our more general results to a concrete model one has first to ascertain the validity of the linkage-equilibrium approximation.

### 4.3 The Density-Dependent Model

Here, we shall formulate a model which is slightly more general than the Matessi-Jayakar model (see Section 3.3.1) with underlying multilocus genetics. We will refer to it as the

density-dependent version of the Wildcard Model. It assumes that the fitness of genotype  $\mathbf{i}\mathbf{j}$  is given by

$$w_{\mathbf{i}\mathbf{j}} = s_{\mathbf{i}\mathbf{j}} + f(N) \sum_{\mathbf{k},\mathbf{l}} a_{\mathbf{i}\mathbf{j},\mathbf{k}\mathbf{l}} p_{\mathbf{k}} p_{\mathbf{l}}, \quad (41)$$

where  $s_{\mathbf{i}\mathbf{j}}$ , and the  $a_{\mathbf{i}\mathbf{j},\mathbf{k}\mathbf{l}}$ 's are as in the density-independent case, hence have the same interpretation, and we impose the same relations. Moreover,  $f(N)$  is some differentiable function of the population size satisfying  $f(N), f'(N) > 0$  or  $f(N), f'(N) < 0$  for all admissible values of  $N$ . Note, that (41) is similar to (1) or (38), but it does not allow for an arbitrary function  $\gamma$ .

The marginal fitness of gamete  $\mathbf{i}$  is then given by

$$\bar{w}_{\mathbf{i}} = \sum_{\mathbf{j}} s_{\mathbf{i}\mathbf{j}} p_{\mathbf{j}} + f(N) \sum_{\mathbf{j},\mathbf{k},\mathbf{l}} a_{\mathbf{i}\mathbf{j},\mathbf{k}\mathbf{l}} p_{\mathbf{j}} p_{\mathbf{k}} p_{\mathbf{l}},$$

the mean fitness is given by

$$\bar{w} = \sum_{\mathbf{i},\mathbf{j}} s_{\mathbf{i}\mathbf{j}} p_{\mathbf{i}} p_{\mathbf{j}} + f(N) \sum_{\mathbf{i},\mathbf{j},\mathbf{k},\mathbf{l}} a_{\mathbf{i}\mathbf{j},\mathbf{k}\mathbf{l}} p_{\mathbf{i}} p_{\mathbf{j}} p_{\mathbf{k}} p_{\mathbf{l}}, \quad (42a)$$

and the marginal fitness of allele  $\mathcal{A}_{i_k}^{(k)}$  is given by

$$w_{i_k}^{(k)} = \sum_{\mathbf{i}}^{(k)} \prod_{\substack{l=1 \\ l \neq k}}^n p_{i_l}^{(l)} \sum_{\mathbf{j}} s_{\mathbf{i}\mathbf{j}} p_{\mathbf{j}} + f(N) \sum_{\mathbf{i}}^{(k)} \prod_{\substack{l=1 \\ l \neq k}}^n p_{i_l}^{(l)} \sum_{\mathbf{j},\mathbf{k},\mathbf{l}} a_{\mathbf{i}\mathbf{j},\mathbf{k}\mathbf{l}} p_{\mathbf{j}} p_{\mathbf{k}} p_{\mathbf{l}}. \quad (42b)$$

The continuous-time dynamics under weak selection and linkage equilibrium, is given by the following system of differential equations

$$\dot{p}_{i_k}^{(k)} = p_{i_k}^{(k)} (w_{i_k}^{(k)} - \bar{w}) \quad \text{for } 1 \leq i_k \leq m_k, 1 \leq k \leq n \quad (42c)$$

and

$$\dot{N} = N\bar{w}. \quad (42d)$$

The following theorem, a density-dependent analog of Theorem 2, extends the results of the corresponding one-locus results of Matessi and Jayakar (1981) to the multi-locus model with linkage equilibrium:

**Theorem 3.** Consider the system of differential equations (42). Let

$$\Psi(\boldsymbol{\rho}, N) := f(N)(2\bar{s} + f(N)\bar{a}),$$

where

$$\bar{s} = \sum_{\mathbf{i}, \mathbf{j}} s_{\mathbf{i}, \mathbf{j}} p_{\mathbf{i}} p_{\mathbf{j}} \quad \text{and} \quad \bar{a} = \sum_{\mathbf{i}, \mathbf{j}, \mathbf{k}, \mathbf{l}} a_{\mathbf{i}, \mathbf{j}, \mathbf{k}, \mathbf{l}} p_{\mathbf{i}} p_{\mathbf{j}} p_{\mathbf{k}} p_{\mathbf{l}}.$$

Then (42) is a generalized gradient system with potential  $\Psi$ , i.e.,

$$\dot{p}_{i_k}^{(k)} = \frac{p_{i_k}^{(k)}}{4f(N)} \left( \frac{\partial \Psi}{\partial p_{i_k}^{(k)}} - \sum_{j_k=1}^{m_k} p_{j_k}^{(k)} \frac{\partial \Psi}{\partial p_{j_k}^{(k)}} \right)$$

and

$$\dot{N} = N \frac{1}{2f'(N)} \frac{\partial \Psi}{\partial N}.$$

In particular  $\Psi$  is a global Lyapunov function for the set of equilibria, i.e.,  $\dot{\Psi}(\boldsymbol{\rho}, N) \text{ sign } f(N) \geq 0$  and  $\dot{\Psi}(\hat{\boldsymbol{\rho}}, \hat{N}) = 0$  if and only if  $(\hat{\boldsymbol{\rho}}, \hat{N})$  is an equilibrium.

**Proof.** Similarly as in the proof of Theorem 2, straightforward calculation yields

$$\frac{1}{4} \frac{\partial \Psi}{\partial p_{i_k}^{(k)}} = f(N) w_{i_k}^{(k)}.$$

Moreover, we have

$$\begin{aligned} \frac{1}{4} \frac{\partial \Psi}{\partial N} &= \frac{f'(N)}{4} \left( 2 \sum_{\mathbf{i}, \mathbf{j}} s_{\mathbf{i}, \mathbf{j}} p_{\mathbf{i}} p_{\mathbf{j}} + 2f(N) \sum_{\mathbf{i}, \mathbf{j}, \mathbf{k}, \mathbf{l}} a_{\mathbf{i}, \mathbf{j}, \mathbf{k}, \mathbf{l}} p_{\mathbf{i}} p_{\mathbf{j}} p_{\mathbf{k}} p_{\mathbf{l}} \right) \\ &= \frac{f'(N)}{2} \bar{w}. \end{aligned}$$

The above derivations immediately yield the first statement.

By applying the chain rule we obtain

$$\begin{aligned} \dot{\Psi} &= \frac{d\Psi}{dt} = \frac{\partial \Psi}{\partial N} \dot{N} + \sum_{k=1}^n \sum_{i_k=1}^{m_k} \frac{\partial \Psi}{\partial p_{i_k}^{(k)}} \dot{p}_{i_k}^{(k)} \\ &= N \frac{f'(N)}{2} \bar{w}^2 + f(N) \sum_{k=1}^n \sum_{i_k=1}^{m_k} w_{i_k}^{(k)} (w_{i_k}^{(k)} - \bar{w}) p_{i_k}^{(k)} \\ &= N \frac{f'(N)}{2} \bar{w}^2 + f(N) \sum_{k=1}^n \sum_{i_k=1}^{m_k} (w_{i_k}^{(k)} - \bar{w})^2 p_{i_k}^{(k)}. \end{aligned}$$

Hence,  $\text{sign } f(N)\dot{\Psi} \geq 0$ . Moreover, we have  $\dot{\Psi} = 0$  if and only if  $\bar{w} = 0$  and  $w_{i_k}^{(k)} = \bar{w}$  provided  $p_{i_k}^{(k)} \neq 0$ . In other words, we have  $\dot{\Psi} = 0$  only at an equilibrium. This finishes the proof. □

We immediately obtain the following corollary

**Corollary 5.** *The multilocus, multiallele version of the Matessi-Jayakar model under the assumption of linkage equilibrium is a generalized gradient system. Its potential function is a global Lyapunov function and is given by*

$$\Psi^{(MJ)}(\boldsymbol{\rho}, N) = N(2\bar{K} - N\bar{B}).$$

We can further conclude

**Remark 1.** *The density-dependent version of the Christiansen-Loeschke model, i.e., the model without the singular-perturbation approximation, is a particular case of the Matessi-Jayakar model. Hence, Corollary 5 is also valid for the Christiansen-Loeschke model with obvious modifications.*

Note that the density-dependent version of the Bürger-Schneider model is not a particular case of our density-dependent Wildcard Model.

## 5 Discussion

In this article we studied a model of frequency-dependent selection (the Wildcard Model) at a single autosomal locus with arbitrarily many alleles. Initially, starting from a discrete-time formulation we switched to the continuous-time analog of the model, which can be regarded as an approximation if selection is weak. We proved that our model forms a generalized gradient system, for which the potential function  $\Lambda$  can be derived explicitly. In particular, this function is a global Lyapunov function. Moreover, as a consequence all trajectories approach the set of equilibria. If this is finite, every trajectory converges to an equilibrium. We were able to generalize these results to a density-dependent version of the Wildcard Model, which is a slightly more general version of the model introduced by Matessi and Jayakar (1981). Furthermore, under the assumption of linkage equilibrium, we generalized the results to multilocus, multiallele versions of the density-independent as well as of the density-dependent model. Our model, in both its density-independent and

density-dependent versions, subsumes and generalizes in some respects several other particular models, and hence admits many different interpretations. Furthermore, it extends to these other models the validity of our results concerning the Lyapunov function. In order for this to transpire most clearly and to show with the greatest precision in which directions our generalizations are effected it has been necessary in this paper to review some of these models in detail.

Christiansen and Loeschcke (1980) studied a model of intraspecific competition for a continuous, unimodal resource spectrum, which is a special case of the Wildcard Model. Their model, however, was derived from Lotka-Volterra-like equations. The competition model studied by Bürger (2005) and Schneider (2006, 2007) also is a special case of the Wildcard Model. Their model was derived as an approximation to, at the best of our knowledge, all models of intraspecific competition for a unimodal resource continuum that are available in the theoretical literature. Initially motivated by the model of Bulmer (1974, 1980), it approximates for instance the models of Roughgarden (1972), Slatkin (1979), Christiansen and Loeschcke (1980), Christiansen (1982) and Loeschcke and Christiansen (1984). Hence, these models can be approximately represented by our model.

Lessard (1984) studied a game theoretically motivated model. In his model individuals join one of two phenotypic pools - or pure strategies - with a certain probability based on their genotype. Although this is not a model of intraspecific competition it is also a special case of the Wildcard Model. Another model that is rooted in evolutionary game theory is that of Matessi et al. (2001), which was later studied by Matessi and Gimelfarb. They formulated a quadratic model to study stabilizing or disruptive selection near an evolutionary singularity, i.e., MEAST or PEAST, respectively (cf. Christiansen, 1991). This model, which has no biologically specific interpretation, can also be formulated in terms of our model.

A commonly studied model of frequency-dependent selection is the pairwise interaction model, e.g., Schutz et al. (1968), Allard and Adams (1969), Cockerham et al. (1972), Asmussen and Basnayake (1990), Altenberg (1991), Gavrilets and Hastings (1994), Asmussen et al. (2004), Trotter and Spencer (2008), Schneider (2008). The pairwise interaction model can be formulated in terms of our density-independent model, whereas the class of frequency- and density-dependent models studied by Asmussen (1983) are connected to our density-dependent model.

Since all of the above mentioned models can be represented, at least approximately, by

the Wildcard Model, the existence of a global Lyapunov function for each of them follows immediately. Note that Lyapunov functions were already established for the models of Matessi and Jayakar (1981), Lessard (1984) and Bürger (2005), Schneider (2006). These Lyapunov functions are all equivalent to ours. However, the Lyapunov function in the two-phenotype model of Lessard (1984) was established for discrete time.

Bürger (2005) and Schneider (2006) used the assumptions of additivity within and between loci to show the existence of a Lyapunov function for the density-independent version of their model. However, our results prove that for their model additivity is not required for the existence of a Lyapunov function in the one-locus case, and epistasis does not need to be excluded, as long as the assumption of linkage equilibrium is justified, in the multilocus case. The existence of a global Lyapunov function for the density-dependent version of the Bürger-Schneider model remains open, since this model is not a particular case of our density-dependent Wildcard Model. Christiansen and Loeschcke (1980) initially formulated their model with Gaussian resource utilization functions. However, for most of their analysis they assumed a quadratic approximation. Since their model is a special case of ours even in the Gaussian formulation, the results of this article are applicable, suggesting that more detailed analytical results might be feasible for this particular model. Furthermore, our results also apply to multilocus generalizations of the Christiansen and Loeschcke (1980) model, as studied for instance by Loeschcke and Christiansen (1984) in a two-locus context. Hence, for the latter model more analytical results could be feasible.

Lessard (1984) and Schneider (2007) used the existence of a global Lyapunov function to study the long-term evolution of their models by repeated occurrence and possible invasion of new mutations. Thus, our results might be used to study long-term evolution of a variety of models with different interpretations based on explicit short-term results. Thus, we conclude that our results have the potential to bridge the gap between traditional population genetic and evolutionary models based on dynamical systems (short-term evolution) and adaptive dynamics (long-term evolution) based on invasion dynamics.

Although our results are relevant for many models in the theoretical literature, they are restricted in several respects. First, the Wildcard Model is formulated in continuous instead of discrete time, which implies weak selection. However, most of the above mentioned models that are special cases of ours were formulated originally in discrete time. Hence, it would be desirable to prove similar results for this case. Since difference equations are usually more complicated than differential equations, it is uncertain

whether similar results can be proved. Second, the symmetry assumption of our model is crucial, i.e.,  $a_{ij,kl} = a_{kl,ij}$ . Since our results do not hold without this assumption, the biological scenarios that are covered by our results are constrained. For instance, our density-independent model is formally equivalent to the pairwise interaction model. However, because of the symmetry assumptions, our results do not cover situations like the rock-scissor-paper scenario, which is commonly studied in evolutionary game theory (cf. Hofbauer and Sigmund, 1998).

Note that multi-phenotype generalizations of the two-phenotype model of Lessard (1984) can be formulated with our model. However, in general, the symmetry assumption will be violated, unless the payoff matrix is symmetric. Therefore, our results cannot be applied to generalizations of the Lessard model, indicating that the results of Lessard (1984) cannot be generalized. Anyway, our model will cover multilocus generalizations of the two-phenotype model. Third, our model allows only for a very specific kind of density dependence. Although it is not very general, this kind of density dependence occurs frequently in the theoretical literature. Fourth, in the multilocus case the assumption of linkage equilibrium is crucial. Generalizing our assumptions to linkage disequilibrium seems infeasible. Thus, when applying our results to a particular multilocus model, one has to establish convergence to quasi-linkage equilibrium first. Especially if recombination is weak compared with selection, or for strong epistasis, convergence to quasi-linkage equilibrium has been disproved.

Summarizing, we studied population-genetic models of frequency-dependent selection with underlying one-locus or multilocus genetics, that may also allow for population regulation, which cover many particular models that have been studied in the theoretical literature so far. Although, these models superficially seem to be different and have completely different biological interpretations, they turn out to be different disguises of the model studied in this article. Our results are hence applicable to various evolutionary problems, and give hope that many of them can be tackled analytically. Especially the perspective of studying long-term evolution seems inviting for future research.

## References

- Abrams, P. A., 1986. Character displacement and niche shift analyzed using consumer-resource models of competition. *Theoret. Population Biol.* 29 (1), 107–160.
- Abrams, P. A., 1987. Alternative models of character displacement and niche shift. 2. displacement when there is competition for a single resource. *The American Naturalist* 130 (2), 271–282.  
URL <http://www.journals.uchicago.edu/doi/abs/10.1086/284708>
- Allard, R. W., Adams, J., 1969. Population studies in predominantly self-pollinating species. xiii. intergenotypic competition and population structure in barley and wheat. *The American Naturalist* 103 (934), 621–645.  
URL <http://www.journals.uchicago.edu/doi/abs/10.1086/282630>
- Altenberg, L., 1991. Chaos from linear frequency-dependent selection. *The American Naturalist* 138 (1), 51–68.  
URL <http://www.journals.uchicago.edu/doi/abs/10.1086/285204>
- Asmussen, M. A., 1983. Density dependent selection incorporating intraspecific competition. II. A diploid model. *Genetics* 103 (2), 335–350.
- Asmussen, M. A., Basnayake, E., 1990. Frequency-dependent selection: The high potential for permanent genetic variation in the diallelic, pairwise interaction model. *Genetics* 125 (1), 215–230.  
URL <http://www.genetics.org/cgi/content/abstract/125/1/215>
- Asmussen, M. A., Cartwright, R. A., Spencer, H. G., 2004. Frequency-dependent selection with dominance: a window onto the behavior of the mean fitness. *Genetics* 167 (1), 499–512.  
URL <http://www.genetics.org/cgi/content/abstract/167/1/499>
- Ayala, F. J., Campell, C. C., 1974. Frequency-dependent selection. *A Rev. Ecol. Syst.* 5, 115–138.
- Bulmer, M. G., 1974. Density-dependent selection and character displacement. *The American Naturalist* 108 (959), 45–58.  
URL <http://www.journals.uchicago.edu/doi/abs/10.1086/282884>



- Bulmer, M. G., 1980. The mathematical theory of quantitative genetics. The Clarendon Press. Oxford University Press, New York, oxford Science Publications.
- Bürger, R., 2000. The mathematical theory of selection, recombination, and mutation. Wiley Series in Mathematical and Computational Biology. John Wiley & Sons Ltd., Chichester.
- Bürger, R., 2002a. Additive genetic variation under intraspecific competition and stabilizing selection: A two-locus study. *Theor. Popul. Biol.* 61 (2), 197–213.
- Bürger, R., 2002b. On a genetic model of intraspecific competition and stabilizing selection. *The American Naturalist* 160 (5), 661–682, pMID: 18707515.  
URL <http://www.journals.uchicago.edu/doi/abs/10.1086/342813>
- Bürger, R., 2005. A multilocus analysis of intraspecific competition and stabilizing selection on a quantitative trait. *J. Math. Biol.* 50 (4), 355–396.
- Bürger, R., Schneider, K. A., M., W., 2006. The conditions for speciation through intraspecific competition. *Evolution*. 60 (11), 2185–2206.
- Christiansen, F. B., 1982. Natural selection related to the biotic natural selection related to the biotic environment. In: Jayakar, S. D., Zonta, L. (Eds.), *Evolution and the genetics of populations*. Vol. 29 of *Atti Ass. Genet. Ital.* pp. 85–102.
- Christiansen, F. B., 1991. On conditions for evolutionary stability for a continuously varying character. *The American Naturalist* 138 (1), 37–50.  
URL <http://www.journals.uchicago.edu/doi/abs/10.1086/285203>
- Christiansen, F. B., Loeschcke, V., 1980. Evolution and intraspecific exploitative competition. I. One-locus theory for small additive gene effects. *Theoret. Population Biol.* 18 (3), 297–313.
- Clark, B., 1979. The evolution of genetic diversity. *Proc. R. Soc. Lond. B* 205, 453–474.
- Clarke, B., 1972. Density-dependent selection. *The American Naturalist* 106 (947), 1–13.  
URL <http://www.journals.uchicago.edu/doi/abs/10.1086/282747>
- Clarke, B. C., Partridge, L. (Eds.), 1988. *Frequency-dependent selection*. Royal Society, London.

- Cockerham, C. C., Burrows, P. M., Young, S. S., Prout, T., 1972. Frequency-dependent selection in randomly mating populations. *The American Naturalist* 106 (950), 493–515.  
URL <http://www.journals.uchicago.edu/doi/abs/10.1086/282790>
- Dieckmann, U., 1997. Can adaptive dynamics invade? *Trends in Ecology and Evolution* 12, 128–131.
- Dieckmann, U., Doebeli, M., 1999. On the origin of species by sympatric speciation. *Nature* 400 (6742), 354–357.  
URL <http://dx.doi.org/10.1038/22521>
- Doebeli, M., Dieckmann, U., 2000. Evolutionary branching and sympatric speciation caused by different types of ecological interactions. *The American Naturalist* 156 (s4), S77–S101.  
URL <http://www.journals.uchicago.edu/doi/abs/10.1086/303417>
- Eshel, I., 1983. Evolutionary and continuous stability. *J. Theoret. Biol.* 103 (1), 99–111.
- Felsenstein, J., 1981. Skepticism towards santa rosalia, or why are there so few kinds of animals. *Evolution* 35, 124–138.
- Fisher, R. A., 1930. *The genetical theory of natural selection*. Oxford: Clarendon Press.
- Gavrilets, S., 2003. Models of speciation: what have we learned in 40 years? *Evolution* 57, 2197–2215.
- Gavrilets, S., 2004. *Fitness Landscapes and the Origin of Species*. Vol. 41 of *Monographs in Population Biology*. Princeton University Press.
- Gavrilets, S., Hastings, A., 1994. Maintenance of multilocus variability under strong stabilizing selection. *J. Math. Biol.* 32 (4), 287–302.
- Gavrilets, S., Hastings, A., 1995. Intermittency and transient chaos from simple frequency-dependent selection. *Proc Biol Sci.* 261 (1361), 233–8.
- Geritz, S. A. H., Kisdi, E., Meszéna, G., Metz, J. A. J., 1998. Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evol. Ecol.* 12, 35–57.

- Haldane, J., Jayakar, S., 1963. Polymorphism due to selection of varying direction. *J. Genet.* 58, 237–242.
- Hofbauer, J., Sigmund, K., 1998. *Evolutionary games and population dynamics*. Cambridge University Press, Cambridge.
- Hoppensteadt, F., 1974. Asymptotic stability in singular perturbation problems. II. Problems having matched asymptotic expansion solutions. *J. Differential Equations* 15, 510–521.
- Kojima, K., Yarbrough, K. M., 1967. Frequency-dependent selection at the esterase 6 locus in *Drosophila melanogaster*. *Proc. natn. Acad. Sci. U.S.A.* 57, 645–649.
- Kopp, M., Hermisson, J., 2006. Evolution of genetic architecture under frequency-dependent disruptive selection. *Evolution* 60, 1537–1550.
- Lessard, S., 1984. Evolutionary dynamics in frequency-dependent two-phenotype models. *Theor. Popul. Biol.* 25, 210–234.
- Lewontin, R. C., Hubby, J. L., 1966. A molecular approach to the study of genetic heterozygosity in natural populations. II. Amount of variation and degree of heterozygosity in natural populations of *Drosophila pseudoobscura*. *Genetics* 54 (2), 595–609.  
URL <http://www.genetics.org>
- Loeschcke, V., Christiansen, F. B., 1984. Evolution and intraspecific exploitative competition. II. A two-locus model for additive gene effects. *Theoret. Population Biol.* 26 (2), 228–264.
- Matessi, C., Cori, R., 1972. Models of population genetics of batesian mimicry. *Theoretical Population Biology* 3 (1), 41–68.  
URL <http://www.sciencedirect.com/science/article/B6WXD-4F1Y9N0-5B/2/45136c66d612d0e0bffc6127a24fc7cf>
- Matessi, C., Gimelfarb, A., 2006. Discrete polymorphisms due to disruptive selection on a continuous trait. I: The one-locus case. *Theor. Popul. Biol.* 69 (3), 283–295.
- Matessi, C., Gimelfarb, A., Gavrillets, S., 2001. Long-term buildup of reproductive isolation promoted by disruptive selection: How far does it go? *Selection* 2 2 (1-2), 41–64.

- Matessi, C., Jayakar, S. D., 1976. Models of density-frequency dependent selection for the exploitation of resources. I. Intraspecific competition. In: Population genetics and ecology (Proc. Conf., Israel, 1975). Academic Press, New York, pp. 707–721.
- Matessi, C., Jayakar, S. D., 1981. Coevolution of species in competition: a theoretical study. *Proc. Nat. Acad. Sci. U.S.A.* 78 (2, part 2), 1081–1084.
- Maynard Smith, J., 1966. Sympatric speciation. *The American Naturalist* 100 (916), 637–650.  
URL <http://www.journals.uchicago.edu/doi/abs/10.1086/282457>
- Maynard Smith, J., 1982. *Evolution and the Theory of Games*. Cambridge University Press.
- Maynard Smith, J., Price, G. R., 1973. The logic of animal conflict. *Nature* 246 (5427), 15–18.  
URL <http://dx.doi.org/10.1038/246015a0>
- Nagylaki, T., 1993. The Evolution of Multilocus Systems Under Weak Selection. *Genetics* 134 (2), 627–647.  
URL <http://www.genetics.org/cgi/content/abstract/134/2/627>
- Nagylaki, T., Hofbauer, J., Brunovský, P., 1999. Convergence of multilocus systems under weak epistasis or weak selection. *J. Math. Biol.* 38 (2), 103–133.
- Roughgarden, J., 1972. Evolution of niche width. *The American Naturalist* 106 (952), 683–718.  
URL <http://www.journals.uchicago.edu/doi/abs/10.1086/282807>
- Schluter, D., 2000. Ecological character displacement in adaptive radiation. *The American Naturalist* 156 (s4), S4–S16.  
URL <http://www.journals.uchicago.edu/doi/abs/10.1086/303412>
- Schneider, K. A., 2006. A multilocus-multiallele analysis of frequency-dependent selection induced by intraspecific competition. *J. Math. Biol.* 52 (4), 483–523.
- Schneider, K. A., 2007. Long-term evolution of polygenic traits under frequency-dependent intraspecific competition. *Theor. Popul. Biol.* 71 (3), 342–366.

- Schneider, K. A., 2008. Maximization principles for frequency-dependent selection I: the one-locus two-allele case. *Theoretical Population Biology* 74 (3), 251–262.  
URL <http://www.sciencedirect.com/science/article/B6WXD-4T5CGPC-1/2/9e95e3ed090323bbba5212cd2fe028e1>
- Schutz, W. M., Brim, C. A., Usanis, S. A., 1968. Intergenotypic competition in plant populations. i feedback systems with stable equilibria in populations of autogamous homozygous lines. *Crop. Sci.* 8, 61–66.
- Slatkin, M., 1979. Frequency- and density-dependent selection on a quantitative character. *Genetics* 93 (3), 755–771.
- Slatkin, M., 1980. Ecological character displacement. *Ecology* 61 (1), 163–177.  
URL <http://www.esajournals.org/doi/abs/10.2307/1937166>
- Thieme, H. R., 2003. *Mathematics in population biology*. Princeton Series in Theoretical and Computational Biology. Princeton University Press, Princeton, NJ.
- Trotter, M., Spencer, H. G., 2008. The Generation and Maintenance of Genetic Variation by Frequency-dependent Selection: Constructing Polymorphisms Under the Pairwise Interaction Model. *Genetics*, genetics.108.088880.  
URL <http://www.genetics.org/cgi/content/abstract/genetics.108.088880v1>
- Turelli, M., Barton, N., Coyne, J., 2001. Theory and speciation. *Trends in Ecology and Evolution* 16, 330–343.
- Wright, S., 1948. On the role of directed and random changes in gene frequency in the genetics of populations. *Evolution* 2, 279–294.