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# Many species partial adaptive dynamics

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## Abstract

A system of  $n$  asexual populations is considered in which both intra- and interspecific frequency-dependent matrix game conflicts with a lack of information are involved and the weak perturbation condition is satisfied (mutation is a very rare event and selection is quick). A new partial adaptive game dynamics is proposed that takes into account that the mutants interact not only with the residents but among themselves as well. It is also shown that if the Nash equilibrium (NE) is totally mixed and the interaction matrices are Replicator-Lyapunov stable (RL-stable), then the NE is an asymptotically stable point of these new dynamics. © 2002 Elsevier Science Ireland Ltd. All rights reserved.

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## 1. Introduction

The basic idea of evolutionary stability is that rare mutants are always worse off than residents (Maynard Smith, 1982). According to the Darwinian theory, a mutant phenotype is able to invade into the population under the influence of natural selection if this mutant phenotype has a fitness greater than the average over the whole population. Thus, the relative advantage function can be introduced in a natural way: the relative advantage of a mutant is defined as the average fitness of these mutants minus the average fitness of the whole population. This paper emphasises the fundamentality of the relative advantage function.

First of all, the sign of this function determines whether or not a mutant phenotype spreads. Second, based on the relative advantage there is a possibility to extend the notion of evolutionary stable strategies (ESS) from single species to an arbitrary number of interacting species. Third, Hofbauer and Sigmund (1990, 1999) introduced an adaptive dynamics based on the relative advantage and they proved that an evolutionarily stable state is an asymptotically stable rest point of this dynamics. Another adaptive dynamics (Geritz et al., 1998; Kisdi, 1999) is based on the following principle: a mutant can spread into the population if it is successful against the residents. In the present paper, a slightly different dynamics will be introduced taking into account that the mutant must compete not only with the residents but with the same type of mutants as well.

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The main object of this paper is to introduce a new dynamics in which the Nash equilibrium (NE) is a locally asymptotically stable point in a class of game.

## 2. Replicator-Lyapunov stability

The main result of this paper is based on the notion of Replicator-Lyapunov-stability (RL-stability) (see Garay and Varga, 2000; Cressman et al., 2001). Other concepts for  $n$ -species frequency-dependent interaction are not discussed. RL-stability relates to the following biological situation. Within each of  $n$  asexual populations there is a symmetric game-theoretical conflict, and the game is asymmetric between any two populations. It is also supposed that, both within and between species, there is selection for the same behavioural phenotypes and individuals cannot modify their strategy to comply with the opponent species. The latter condition means that either every individual has a fixed behavioural phenotype or the individuals have no information on their actual opponents. The individuals of each species have several possible pure strategies. The fitnesses are supposed to be frequency-dependent and the fitness components resulting from different types of conflicts are additively superimposed, contributing to the individual payoffs with the same weight, and all evolutionary game theoretical conflicts can be described by matrix games. Throughout this paper we suppose that mutation is a very rare event and selection is ‘quick’. This means that there is enough time for the fitter phenotypes to eliminate the less-fit ones, before new mutants perturb the system again. This weak perturbation condition guarantees that only two phenotypes may coexist for each species at a time.

Now I introduce some notations. Species  $i \in \overline{1, n}$  is supposed to have  $m_i$  pure strategies and the elements of the simplex  $S_{m_i}$  are interpreted as distributions of those strategies. Denote by  $A^{ij} \in \mathbb{R}^{m_i \times m_j}$  the payoff matrix of species  $i$  in its conflict with species  $j$ . For each  $j \in \overline{1, n}$  fix a strategy  $p^{j*} \in S_{m_j}$  and let  $\varepsilon_j \in [0, 1]$  be the time-dependent relative frequency of the individuals of

species  $j$  using the strategy  $p^{j*} \in S_{m_j}$ . (So  $1 - \varepsilon_j$  is the relative frequency of the mutants,  $p^j \in S_{m_j} \setminus \{p^{j*}\}$  users, in the  $j$ th species.) For brevity, let  $p := (p^1, p^2, \dots, p^n) \in \prod_{i=1}^n S_{m_i}$ ,  $S := \prod_{i=1}^n S_{m_i}$ .

Definition 1: the  $n$ -species interaction system of matrices  $\{A^{ij}\}_{ij=1, \dots, n}$  is RL-stable if for some  $r \in \mathbb{R}^n$  (with  $r_i \geq 0$  for all  $i = 1, \dots, n$ ):

$$\sum_{i=1}^n r_i \xi^i \left( \sum_{j=1}^n A^{ij} \xi^j \right) < 0$$

for all  $\xi^i \in \mathbb{R}^{m_i} \setminus \{0\}$  with  $\sum_{k=1}^{m_i} \xi_k^i = 0$

First, I recall a few important statements on RL-stability (see Cressman et al., 2001). RL-stability implies that there is a unique NE. An  $n$ -species NE is a  $p^* \in S$  that satisfies  $p^i \sum_{j=1}^n A^{ij} p^{j*} \leq p^{i*} \sum_{j=1}^n A^{ij} p^{j*}$  for all  $i \in \overline{1, n}$ ;  $p^i \in S_{m_i}$ . If  $p^* \in \text{int} S$  then equality holds for each  $i \in \overline{1, n}$ . The central part of this concept is based on that RL-stability guarantees the asymptotic stability of the monomorphic and the polymorphic populations as well. In order to show the intuitive background of RL-stability let us consider an  $n$ -species system in which in the  $i$ -th species all resident individuals have  $p^* \in \text{int} S_{m_i}$  mixed phenotype. Now assume that arbitrary mutation occurs, i.e. individuals of  $\varepsilon^i \in (0, 1)$  part of the  $i$ -th species ‘replace’ the resident phenotypes by a new mutant phenotype  $p^i \in \text{int} S_{m_i} \setminus \{p^{i*}\}$ . In biological terms,  $\varepsilon^i$  is the mutation rate of the  $p^{i*} \rightarrow p^i$  mutation. After the mutation the state (the average phenotype) of the  $i$ -th species is  $x^i = (1 - \varepsilon^i) p^{i*} + \varepsilon^i p^i$ , thus the perturbation of mutation can be given by  $\xi^i = p^{i*} - x^i$ . If the  $n$ -species interaction system of matrices  $\{A^{ij}\}_{ij=1, \dots, n}$  is RL stable and  $p^* \in \text{int} S$  is a NE (implying  $p^i \sum_{j=1}^n A^{ij} p^{j*} = p^{i*} \sum_{j=1}^n A^{ij} p^{j*}$  for all  $i \in \overline{1, n}$ ;  $p^i \in S_{m_i}$ ), we have:

$$\sum_{i=1}^n r_i (p^{i*} - x^i) \left( \sum_{j=1}^n A^{ij} x^j \right) > 0$$

From the biological viewpoint, this inequality means that the ‘weighted relative advantage, of the resident state is positive. In this sense, therefore, RL-stability implies that the resident state is ‘better’ than the perturbed one.

### 3. Diagonally strictly concave games

In Section 5, a relationship between RL-stability and the classical game theory will be established. For this purpose, let us consider the definition of diagonally strictly concave (DSC) games given by Rosen (1965) and the following  $n$ -person game. The  $i$ -th player has  $m_i$  pure strategies, so the  $i$ -th player's mixed strategy is an element of the simplex  $S_{m_i}$ . Let  $h_i: \rightarrow R_+$  ( $i \in \overline{1, n}$ ) be the pay-off function of the  $i$ -th player. We also recall some basic concepts of the mathematical game theory. An  $x^* := (x^{1*}, x^{2*}, \dots, x^{n*}) \in S$  is said to be a strict NE if for all  $x^i \in S_{m_i} \setminus \{x^{i*}\}$  ( $i \in \overline{1, n}$ ) we have:

$$h_i(x^*) > h_i(x^{1*}, x^{2*}, \dots, x^i, \dots, x^{n*})$$

Let us suppose that each pay-off function is continuously differentiable, and for an arbitrary  $r \in R_+^n$  we introduce the notation:

$$f(x, r) := \begin{pmatrix} r_1 \nabla_1 h_1(x) \\ r_2 \nabla_2 h_2(x) \\ \vdots \\ r_n \nabla_n h_n(x) \end{pmatrix} \in R^m \quad (x \in S)$$

where  $\nabla_i h_i$  denotes the gradient of the pay-off function  $h_i$  (as a column vector) with respect to  $x^i \in S_{m_i}$ , and  $m := \sum_{i=1}^n m_i$ .

Definition 2: the function  $f$  is called DSC if there exists an  $r \in R_+^n$  such that for each  $z, y \in S$ ,  $z \neq y$  the following relation holds

$$(z - y)f(y, r) + (y - z)f(z, r) > 0$$

However, this definition is rather difficult to check, therefore, in practice the following sufficient (almost necessary) condition is used:

- (I) Let us denote by  $F(x, r)$  the Jacobian matrix of  $f(x, r)$  with respect to  $x \in S$ . If for some  $r \in R_+^n$ , the matrix  $F(x, r) + F^T(x, r)$  is negative definite for all  $x \in S$  then the game is DSC.

It is not hard to see that if a game is DSC then the payoff functions are partially strictly concave in its variables. According to Rosen's theorem any DSC game has a unique NE. In order to find Nash equilibria, we can use the following sufficient condition:

- (II) If for some  $r \in R_+^n$  and a point  $x^* \in S$  the condition  $\max\{f(x^*, r)(x - x^*), x \in S\} = 0$  satisfies then  $x^* \in S$  is a NE. Condition (II) implies that if  $x^* \in S$  satisfies  $\nabla_i h_i(x^*) = 0$  then it is a NE. On the other hand, for DSC games, under condition (I) the unique NE, guaranteed by Rosen's theorem, is strict.

### 4. Partial-adaptive dynamics

Let us consider the following dynamics

$$\dot{x}^j := x^j(e_j^i - x^i)\nabla_i h_i(x) \quad (1)$$

where  $x^j$  is the  $j$ -th coordinate of the vector  $x^i \in S_{m_i}$  and  $e_j^i$  is the  $j$ -th vertex of the simplex  $S_{m_i}$ . Observe that the uniquely existing NE of the DSC game is a rest point of dynamics (1). In order to motivate our choice of dynamics heuristically I make the following remark. Let us suppose that, replaying the game many times, the players can only slightly change their strategies from game to game. Then, each player has a good chance to estimate the strategies of the others. Due to the fact that the payoff functions are partially strictly concave, knowing their previous choices of strategies, the players can optimise their payoffs unambiguously in the new game.

Theorem: if  $x^*$  is a NE of a DSC game, then it is an asymptotically stable rest point of the dynamics (1), globally in intS.

Proof: it is obvious, that an interior NEP is a rest point. With a fixed  $r \in R_+^n$  figuring in the definition of DSC game, the function:

$$L: R_+^m \rightarrow R, \quad L(x) = \sum_{i=1}^n r_i \sum_{j=1}^{m_i} x_j^{i*} \log x_j^i$$

is a Lyapunov function. Indeed,  $L(x) < 0$  in  $S \setminus \{x^*\}$  and its derivative with respect to (1) is the following:

$$\begin{aligned} & \sum_{i=1}^n r_i \sum_{j=1}^{m_i} x_j^i (e_j^i - x^i) \nabla_i h_i(x) \\ &= \sum_{i=1}^n r_i \left[ \sum_{j=1}^{m_i} x_j^{i*} e_j^i \nabla_i h_i(x) - x^i \nabla_i h_i(x) \sum_{j=1}^{m_i} x_j^{i*} \right] \\ &= \sum_{i=1}^n r_i (x^{i*} - x^i) \nabla_i h_i(x) \end{aligned}$$

Since  $\nabla_i h_i(x^{i*}) = 0$ , for all  $x \in S \setminus \{x^*\}$  we have:

$$\sum_{i=1}^n r_i(x^{i*} - x^i)(\nabla_i h_i(x) - \nabla_i h_i(x^*)) > 0$$

This inequality is obtained from the definition of DSC, with the choice  $y = x$ ,  $z = x^*$ .

## 5. Application

To establish the relationship between the  $n$ -species game and the  $n$ -person DSC game, a game must be defined first. Let us fix a resident state, and let the ‘mutants’ be the players. Now we need the payoff functions. Let us start from the relative advantage function of a  $p^i$ -mutant over its population, which is defined as:

$$R(p^i, x) = (p^i - x^i) \left( \sum_{j=1}^n A^{ij} x^j \right) \quad (2)$$

where  $x^j = \mu_{pi} p^{j*} + (1 - \mu_{pi}) p^j$  is the perturbed state of the  $j$ -th species ( $j \in \overline{1, n}$ ),  $p^{j*} \in S_{m_j}$  is the resident phenotype and  $1 - \mu_{pi} \in [0, 1]$  denotes the amplitude of perturbation of  $p^j$ -mutant. Thus

$$R(p^i, x) = \mu_{pi} (p^i - p^{i*}) \left( \sum_{j=1}^n \mu_{pj} A^{ij} p^{j*} + \sum_{j=1}^n (1 - \mu_{pj}) A^{ij} p^j \right) \quad (3)$$

Hence, according to the tenet of Darwinian selection, a mutant spreads if and only if its relative advantage is positive because it needs a fitness higher than that of its competitors in the same species. The success of a given mutant depends on the phenotypes of all residents, the phenotypes and frequencies of all mutants (including itself). For a criterion of successfulness of a new mutant it is reasonable to fix a threshold frequency. (It is natural to assume that the threshold is higher than each mutation rate.) A given phenotype can coexist only if its relative frequency exceeds this threshold. If the populations are large enough, then the interaction between mutants must occur. Note that this idea is practically parallel with the notion of permanence in ‘ecological’ models.

Now let me point out a difference between the present and the earlier approaches (Hofbauer and Sigmund, 1990; Geritz et al., 1998; Kisdi, 1999). They, in the definition of the relative advantage, compare the mutants with the residents, while in my approach mutants play against the whole perturbed population. Technically, according to the approach of the quoted authors, in (2)  $p^i \in S_{m_i}$  and  $x^i \in S_{m_j}$  (the resident state) would vary independently, so (2) is linear in the mutant strategies and quadratic in the resident strategies. In my approach,  $x \in S$  is the perturbed population state resulting from the mutation, implying that (2) and consequently (3) are quadratic in the mutant and resident strategies as well. My approach appears in line with the original concept of uninvadability (see e.g. Maynard Smith’s definition of ESS 1982).

Since in the classical game theory the players are not populations, the mutation rates are not introduced. Thus in order to establish the relationship between the  $n$ -species game and the  $n$ -person DSC game we must neglect the ‘freedom’ of mutation rates. Let us fix an appropriate  $\mu \in ]0, 1[$ , and according the above assume that  $\mu_{pi} = \mu (p^i \in S_{m_i}, i \in \overline{1, n})$ . Now an  $n$ -person game of mutants will be introduced. Let the strategy set of  $i$ -mutants be  $S_{m_i}$ , the payoff function be the relative advantage of  $i$ -mutants over their perturbed population, for fixed  $\mu \in ]0, 1[$  and  $p^* \in S$ . It is easy to see the following.

Proposition: let us assume that the resident state is a totally mixed ( $p^* \in \text{int}S$ ) and the interaction system of matrices is RL-stable. Then, the game of mutants is DSC.

Now let  $h_i(p^i) = R(p^i, x) \in (i \in \overline{1, n})$ , with fixed  $\mu \in ]0, 1[$  and  $p^* \in S$ . For the game of mutants, the partial adaptive dynamics (1) introduced in Section 4 has the following concrete form:

$$\dot{p}_j^i = \mu p_j^i (e_j^i - p^i) \left( \sum_{j=1}^n A^{ij} p^{j*} + (1 - \mu) \sum_{j=1}^n A^{ij} [p^j - p^{j*}] + (1 - \mu) (A^{ii})^T [p^i - p^{i*}] \right) \quad (4)$$

which for a totally mixed equilibrium resident state,  $p^* \in \text{int}S$  reads

$$p_j^{i*} = \mu(1 - \mu)p_j^i(e_j^i - p^i) \left( \sum_{j=1}^n A^{ij}[p^j - p^{j*}] + (A^{ii})^T[p^i - p^{i*}] \right) \quad (5)$$

In the latter case, the whole evolution process does not depend on the threshold frequency. Using the Proposition and the Theorem we get the following.

Corollary: if the interaction system of matrices is RL-stable then a totally mixed NE is an asymptotically stable rest point of the partial-adaptive dynamics (7).

The dynamics (7) proposed above describes how the ‘mutants’ can choose their strategies in an optimal way at every moment. Finally, observe that the Proposition and the Corollary to it depend essentially on a very restrictive condition, namely, the equal frequency of mutants holds for all species. This condition, however, gives a possibility to establish the relationship between the notions of DSC game and RL-stability.

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