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Strict ESS for n -species systems

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Abstract

A system of n asexual populations is considered where both intra- and interspecific frequency-dependent game conflicts with lack of information take place. The concept of a strict n -species ESS is introduced which implies local asymptotic stability of the replicator dynamics of pure phenotypes. The dynamical concept of strict stability is also introduced which turns out to be equivalent to the strict n -species ESS concept. The above notions are also related to similar concepts considered in the literature for the same biological situation. © 2000 Elsevier Science Ireland Ltd. All rights reserved.

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1. Introduction

Maynard Smith and Price (1973) introduced the concept of evolutionarily stable strategy (ESS) for the single-species case: a strategy is called ESS if in the course of selection, rare mutants cannot invade the population, provided the overwhelming majority of the individuals stick to this strategy. This definition primarily concerns asexual populations. The question arises, what about n species?

This paper starts out from the following biological situation: within each of the n populations there is a symmetric game-theoretical conflict, and between any two of the n populations an asymmetric game is played. It is also supposed that, both within the species and between them, there is a selection for the same behavioural phenotypes, and an individual cannot change its strategy according to the species its actual opponent belongs to. (The latter means that either each 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, figuring

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in the individual pay-offs with the same weight. The main goal of the present paper is to find an appropriate definition of an evolutionarily stable strategy for this situation.

Below we briefly review the most important papers on the subject. Hofbauer and Sigmund (1988) (p. 138) proved that, for two species asymmetric (bimatrix) games, there is no mixed ESS. Selten (1980) obtained a similar result for a very general class of asymmetric games. These results also motivate our definition of a strict n -species ESS given in Section 2, since for special interspecific pay-off matrices there will exist a mixed strict ESS. The reason for the latter existence is the lack of full information in the game.

For the two-species case, the problem raised in the present paper has been thoroughly studied by two authors. In his definition of ESS, Taylor (1979) requires the sum of the average fitness of the resident subpopulations to be greater than that of the mutant ones. This definition of ESS implies its dynamical stability.

The definition of two-species ESS given by Cressman (1992) (pp. 31–57) and Cressman (1996) requires that at least for one of the species the average fitness of the mutants is less than that of the residents of the same species. This definition still guarantees the asymptotic stability of the rest point of the replicator dynamics describing the variation of pure strategies. The author noticed that for a similar *multi-species* ESS definition this implication does not hold. A strict variant of this concept, to be studied below will guarantee the corresponding implication.

The biological foundation of our approach to the multi-species ESS concept is threefold. First, the mutants must be unable to invade their own species. Second, the presence of various species substantially increases the degree of freedom of perturbations of the system. Third, our multi-species ESS definition should be in accordance with the basic results of the asymmetric evolutionary game theory.

As is well-known, an asymptotically stable rest point of the pure strategy replicator dynamics is not necessarily an ESS. The question naturally arises: what kind of dynamical stability concept will be equivalent to the ESS? Cressman (1990)

pointed out that, for the single-species case, the so-called strong stability is equivalent to the ESS (see also Hines, 1980; Akin, 1982). Following Cressman we shall also give a so-called strict stability concept for the multi-species case which will be equivalent to our multi-species ESS concept.

For an overview, we shall relate our approach to the results obtained by Taylor and Cressman for similar biological situations.

2. Strict n -species ESS

Below we shall give a definition requiring uninvadability by mutants not only for the whole system but also for each species. This strict version of n -species ESS will allow a system to continue to evolve by successful mutants appearing in one of the species.

Species i is supposed to have m_i pure strategies and the elements of the simplex S_{m_i} are interpreted as distributions of the above pure strategies. Put

$\mathbf{S} = \times_{i=1}^n S_{m_i}$ and let $\mathbf{A}^{ij} \in R^{m_i \times m_j}$ be the pay-off matrix of species i in its conflict with species j .

A state is considered uninvadable if rare mutants cannot perturb the system in such a way that at least in one of the populations the fitness of the mutants exceeds that of the residents of the same population, provided the perturbation is small enough. Formally we give the following:

Definition 1. $\mathbf{p}^* = (\mathbf{p}^{1*}, \mathbf{p}^{2*}, \dots, \mathbf{p}^{n*}) \in \mathbf{S}$ is called a strict n -species ESS if, for each $\mathbf{p} = (\mathbf{p}^1, \mathbf{p}^2, \dots, \mathbf{p}^n) \in \mathbf{S} \setminus \{\mathbf{p}^*\}$ and $i \in \overline{1, n}$ with $\mathbf{p}^i \neq \mathbf{p}^{i*}$, there exists $0 < \varepsilon_{\mathbf{p}}^i < 1$ such that for all $0 < \varepsilon^i < \varepsilon_{\mathbf{p}}^i$ we have

$$\mathbf{p}^i \left(\sum_{j=1}^n \mathbf{A}^{ij} \mathbf{x}^j \right) < \mathbf{p}^{i*} \left(\sum_{j=1}^n \mathbf{A}^{ij} \mathbf{x}^j \right) \quad (1)$$

where $\mathbf{x}^j = (1 - \varepsilon^j) \mathbf{p}^{*j} + \varepsilon^j \mathbf{p}^j$.

This definition is quite closely related to the Darwinian principle that the phenotype having a greater fitness will propagate. From the biological point of view, it is also important that the perturbations of the system are independent in two

senses: on the one hand, the mutations described by distributions \mathbf{p}^i are independent, on the other hand ‘mutation rates’ (perturbation magnitudes) given by ε^i vary independently.

We remark that for $n = 2$ in the case $\mathbf{A} = 0$ and $\mathbf{D} = 0$, Definition 1 reduces to that given by Hofbauer and Sigmund (1988) (p. 138) for asymmetric matrix games. If $\mathbf{B} = 0$ and $\mathbf{C} = 0$, we recover the definition of uninvadability equivalent to ESS for a single population, as defined by Maynard Smith. In this sense, Definition 1 can be considered as a combination of the two definitions cited above.

Now we give a simple equivalent reformulation of Definition 1.

Proposition 1. $\mathbf{p}^* \in \mathbf{S}$ is a strict n -species ESS if and only if the following conditions are satisfied:

1. equilibrium condition: for all $\mathbf{p} \in \mathbf{S}$ we have

$$\mathbf{p}^i \left(\sum_{j=1}^n \mathbf{A}^{ij} \mathbf{p}^{j*} \right) \leq \mathbf{p}^{i*} \left(\sum_{j=1}^n \mathbf{A}^{ij} \mathbf{p}^{j*} \right) \quad (i \in \overline{1, n}) \quad (2.1)$$

2. stability condition: if for some $i \in \overline{1, n}$ and $\mathbf{p} \in S_n \setminus \{\mathbf{p}^*\}$ in Eq. (2.1) equality holds then

$$\mathbf{p}^i \left(\sum_{j=1}^n \mathbf{A}^{ij} \mathbf{p}^j \right) < \mathbf{p}^{i*} \left(\sum_{j=1}^n \mathbf{A}^{ij} \mathbf{p}^j \right) \quad (2.2)$$

For an insight to the meaning of strictness we shall use another reformulation of the stability condition:

if for some $i \in \overline{1, n}$ and $\mathbf{p} \in S \setminus \{\mathbf{p}^*\}$ in relation (2.1) equality holds then

$$(\mathbf{p}^i - \mathbf{p}^{i*}) \mathbf{A}^{ii} (\mathbf{p}^i - \mathbf{p}^{i*}) < 0 \quad (3.1)$$

and

for $\mathbf{p}^i \in \text{int } S_{m_i} \setminus \{\mathbf{p}^{i*}\}$ we have

$$\begin{aligned} (\mathbf{p}^i - \mathbf{p}^{i*}) \mathbf{A}^{ij} (\mathbf{p}^j - \mathbf{p}^{j*}) &= 0 \\ (\mathbf{p}^i \in S_{m_j} \setminus \{\mathbf{p}^{j*}\}, i \neq j) \end{aligned} \quad (3.2a)$$

for $\mathbf{p}^i \in \text{bd } S_{m_i} \setminus \{\mathbf{p}^{i*}\}$ we have

$$\begin{aligned} (\mathbf{p}^i - \mathbf{p}^{i*}) \mathbf{A}^{ij} (\mathbf{p}^j - \mathbf{p}^{j*}) &\geq 0 \\ (\mathbf{p}^i \in S_{m_j} \setminus \{\mathbf{p}^{j*}\}, i \neq j) \end{aligned} \quad (3.2b)$$

Remark 1. For the sake of simplicity, put $n = 2$. Below we give a characterization of possi-

ble examples for two-species systems in which there exists a strict two-species ESS. For an *interior equilibrium* strategy pair $(\mathbf{p}^{1*}, \mathbf{p}^{2*})$, the fulfilment of (3.1) and (3.2a) is a consequence of the hypothesis that the magnitudes of perturbation within the single populations are independent of each other, and the individual pay-offs are linear with respect to the individual strategy choice. For such a $(\mathbf{p}^{1*}, \mathbf{p}^{2*})$, e.g. the condition

$$(\mathbf{p}^1 - \mathbf{p}^{1*}) \mathbf{A}^{12} (\mathbf{p}^2 - \mathbf{p}^{2*}) = 0 \quad ((\mathbf{p}^1, \mathbf{p}^2) \in S_{m_1} \times S_{m_2})$$

is equivalent to an interesting structural condition on the matrix \mathbf{A}^{12} . Indeed, for \mathbf{p}^2 fixed, letting \mathbf{p}^1 run over the m_1 -dimension canonical basic vectors, from the above equality we get

$$\begin{aligned} (\mathbf{A}^{12} (\mathbf{p}^2 - \mathbf{p}^{2*}))_i &= (\mathbf{A}^{12} (\mathbf{p}^2 - \mathbf{p}^{2*}))_j \\ (\mathbf{p}^2 \in S_{m_2}, i, j \in \overline{1, m_1}) \end{aligned}$$

or equivalently, with the same $c_{\mathbf{p}^2} \in \mathbf{R}$

$$\mathbf{A}^{12} (\mathbf{p}^2 - \mathbf{p}^{2*}) = c_{\mathbf{p}^1} \mathbf{1}^{m_1}$$

where $\mathbf{1}^{m_1} = (1, 1, 1, \dots, 1) \in \mathbf{R}^{m_1}$.

Now let \mathbf{p}^2 run over the m_2 -dimensional canonical basic vectors. Then for all $j \in \overline{1, m_2}$ with some $c_j \in \mathbf{R}$ we have

$$\mathbf{a}_j - \mathbf{A}^{12} \mathbf{p}^{2*} = c_j \mathbf{1}^{m_1}$$

where \mathbf{a}_j is the j th column of \mathbf{A}^{12} . For reasons of symmetry, a similar statement holds for the rows of \mathbf{A}^{12} . Hence there exist $b \in \mathbf{R}$, $\lambda = (0, \lambda_2, \lambda_3, \dots, \lambda_{m_2}) \in \mathbf{R}^{m_2}$, $\mu = (0, \mu_2, \mu_3, \dots, \mu_{m_1}) \in \mathbf{R}^{m_1}$ such that

$$\mathbf{A}^{12} = \begin{bmatrix} b & b + \lambda_2 & b + \lambda_3 & \dots & b + \lambda_{m_2} \\ b + \mu_2 & b + \lambda_2 + \mu_2 & b + \lambda_3 + \mu_2 & \dots & b + \lambda_{m_2} + \mu_2 \\ \cdot & \cdot & \cdot & \dots & \cdot \\ \cdot & \cdot & \cdot & \dots & \cdot \\ b + \mu_{m_1} & b + \lambda_2 + \mu_{m_1} & b + \lambda_3 + \mu_{m_1} & \dots & b + \lambda_{m_2} + \mu_{m_1} \end{bmatrix}$$

Conversely, suppose that \mathbf{A}^{12} is of the above form. Then it is not hard to see that for all $\mathcal{G} \in \mathbf{R}^{m_1}$ with

$\sum_i g_i = 0$ we get

$$\mathbf{A}^{12}g = \left(\sum_{i=1}^m c_i g_{i+1} \right) \mathbf{1}^{m_1}$$

Hence for all \mathbf{p}^1 and \mathbf{p}^2 , the equality of formula (3.2a) easily follows.

A necessary and sufficient condition of the same type can be obtained for \mathbf{A}^{21} to satisfy Eq. (3.2a), for all \mathbf{p}^1 and \mathbf{p}^2 .

Notice that the structural criteria just obtained for \mathbf{A}^{12} and \mathbf{A}^{21} are very easy to check, unlike the Haigh-type negative definiteness condition (Haigh, 1975) (see (3.1)).

Now, for a better understanding of Eq. (3.2a) in biological terms, let us consider the case of the presence of only asymmetric conflicts (i.e. $\mathbf{A}^{11} = \mathbf{0}$ and $\mathbf{A}^{22} = \mathbf{0}$), and let both species have two pure strategies (behavioural phenotypes). We also suppose that \mathbf{A}^{12} and \mathbf{A}^{21} satisfy the above structural criteria. Then for matrix \mathbf{A}^{12} for all $(\mathbf{p}^1, \mathbf{p}^2) \in S_{m_1} \times S_{m_2}$, we have $\mathbf{p}^1 \mathbf{A}^{12} \mathbf{p}^2 = b \mathbf{1}^{m_1} + \mu \mathbf{p}^1 + \lambda \mathbf{p}^2$. A possible interpretation of this equality is the following: the pay-off to the first species is a superposition of three components: a basic fitness, independent of both strategies, a fitness depending only on the own strategy choice and a fitness depending only on the strategy of the second species. (Under this condition $\mathbf{p}^1 \mathbf{A}^{12} \mathbf{p}^2$ does not depend on terms of the type $p_i^1 p_j^2$.) A similar observation is valid for the matrix \mathbf{A}^{21} .

Now, concerning the equilibrium, there are two possible cases:

1. All rows of \mathbf{A}^{12} , resp. \mathbf{A}^{21} are equal (which, in this case, is necessary for the existence of an internal equilibrium). Then any strategy pair is an equilibrium. Furthermore, for any fixed resident strategy pair, all mutant strategies provide the same fitness. There is no real game-theoretical situation, since none of the species can influence its own pay-off.
2. If not all rows of \mathbf{A}^{12} , resp. \mathbf{A}^{21} are the same then there is no interior equilibrium strategy pair. There may, however, exist a pure ESS pair, e.g. for

$$\mathbf{A}^{12} = \begin{pmatrix} 0 & c \\ d & d+c \end{pmatrix}, \quad \mathbf{A}^{21}$$

$$= \begin{pmatrix} 0 & e \\ f & f+e \end{pmatrix} \text{ with } c, d, e, f > 0$$

the pair $[(0, 1), (0, 1)]$ is an ESS.

The fact that, in case of existence of an interior strict n -species ESS the pay-off matrices must be rather particular, fits well to the results of Selten (1980) and Hofbauer and Sigmund (1988) (p. 138).

3. Replicator dynamics

In this section, concerning some basic theorems on ESS, we shall follow the train of thought of Hofbauer and Sigmund (1988) (pp. 121–128).

Theorem 1. $\mathbf{p}^* \in \mathbf{S}$ is a strict n -species ESS if and only if

$$\mathbf{x}^i \left(\sum_{j=1}^n \mathbf{A}^{ij} \mathbf{x}^j \right) < \mathbf{p}^{i*} \left(\sum_{j=1}^n \mathbf{A}^{ij} \mathbf{x}^j \right) \quad (i \in \overline{1, n}) \quad (4)$$

holds for all $\mathbf{x} = (\mathbf{x}^1, \mathbf{x}^2, \dots, \mathbf{x}^n) \in \mathbf{S} \setminus \{\mathbf{p}^*\}$ in some neighbourhood of \mathbf{p}^* in \mathbf{S} .

Proof. Let us suppose that \mathbf{p}^* is an n -species strict ESS. Define

$$C^i := \{ \mathbf{p}^i \in S_{m_i} \mid \exists k \in \overline{1, m_i}, \mathbf{p}_k^{i*} \neq 0 \text{ and } \mathbf{p}_k^i = 0 \} \\ (i \in \overline{1, n})$$

Then for all $\mathbf{x}^i \in S_{m_i} \setminus \{\mathbf{p}^{i*}\}$ with some $\mathbf{p}^i \in C^i$ and $\varepsilon^i \in]0, 1]$ we have

$$\mathbf{x}^i = (1 - \varepsilon^i) \mathbf{p}^{i*} + \varepsilon^i \mathbf{p}^i$$

Fix an index set $I \subset \overline{1, n}$ and put

$$C_I := \times_{i \in I} C^i$$

Now for each $i \in I$ define a function $\tilde{e}_I^i: C_I \rightarrow \mathbf{R}$ by

$$\tilde{e}_I^i(\mathbf{p}) = \begin{cases} \frac{(\mathbf{p}^{i*} - \mathbf{p}^i) \sum_{j \in I} \mathbf{A}^{ij} \mathbf{p}^{j*}}{(\mathbf{p}^{i*} - \mathbf{p}^i) \sum_{j \in I} \mathbf{A}^{ij} \mathbf{p}^j}, & \text{if } (\mathbf{p}^{i*} - \mathbf{p}^i) \sum_{j \in I} \mathbf{A}^{ij} \mathbf{p}^j \leq 0 \\ 1 & \text{otherwise} \end{cases}$$

This function is clearly continuous and strictly positive because \mathbf{p}^* is a strict n -species ESS. Since the function

$$\hat{\varepsilon}_I: C_I \rightarrow]0, 1], \hat{\varepsilon}_I(\mathbf{p}): = \min_{i \in I} \{\tilde{\varepsilon}_I^i(\mathbf{p})\}$$

is continuous, it attains a positive minimum $\bar{\varepsilon}_I$. Let ε_0 be the minimum of the numbers $\bar{\varepsilon}_I$ where I runs over all non-empty subsets of $\overline{1, n}$. It is easy to check that inequality (Eq. (4)) holds for all $\mathbf{x} \neq \mathbf{p}^*$ from the ε_0 -neighbourhood of \mathbf{p}^* . The converse implication is straightforward.

We notice that inequality (4) holds for each single species. This means that in case of any sufficiently small perturbation of the system, the average pay-off of each species is less than the pay-off of the resident strategy of the same species.

An important consequence of Theorem 1 is the following.

Theorem 2. If \mathbf{p}^* is a strict n -species ESS, then \mathbf{p}^* is a locally asymptotically stable rest point of

$$\dot{x}_k^i = x_k^i [e_k^i - \mathbf{x}^i] \left[\sum_{j=1}^n \mathbf{A}^{ij} \mathbf{x}^j \right] \quad (i \in \overline{1, n}, k \in \overline{1, m_i}) \quad (5)$$

where e_k^i is the k th basic vector of \mathbf{R}^{m_i}

The proof of the above theorem is an easy generalisation of the one-species case treated in Hofbauer and Sigmund (1988) (p. 127). Dynamics (5) is a straightforward extension of the two-species replicator dynamics introduced and studied by Schuster et al. (1981).

Remark 2. For the asymptotic stability of \mathbf{p}^* with respect to dynamics Eq. (5), the following condition is sufficient.

Taylor's condition: For all $\mathbf{x} = (\mathbf{x}^1, \mathbf{x}^2, \dots, \mathbf{x}^n) \in \mathbf{S} \setminus \{\mathbf{p}^*\}$ in some neighbourhood of \mathbf{p}^* we have

$$\sum_i \mathbf{x}^i \left(\sum_{j=1}^n \mathbf{A}^{ij} \mathbf{x}^j \right) < \sum_i \mathbf{p}^{i*} \left(\sum_{j=1}^n \mathbf{A}^{ij} \mathbf{x}^j \right) \quad (6)$$

This is an obvious generalisation of Taylor's two-species ESS requirement (Taylor, 1979).

4. Strict stability

Now from Cressman (1990), we recall the

concept of strong stability for single-species models with m pure strategies: $\mathbf{q}^* \in S_m$ is called *strongly stable* if, for all $k \in \mathbf{N}$ and $\mathbf{q}^1, \mathbf{q}^2, \dots, \mathbf{q}^k \in S_m$, the following holds: if \mathbf{q}^* is a convex combination of $\mathbf{q}^1, \mathbf{q}^2, \dots, \mathbf{q}^k$, then \mathbf{q}^* is a locally asymptotically stable equilibrium of the mean strategy evolution determined by

$$\dot{\varepsilon}_i = \varepsilon_i [(\mathbf{q}^i - \mathbf{y}) \mathbf{A} \mathbf{y}] \quad (i \in \overline{1, k}) \quad (7)$$

where $\mathbf{y} = \sum_i \varepsilon_i \mathbf{q}^i$

The strength of this concept is shown by the following result: $\mathbf{q}^* \in S_m$ is strongly stable if and only if \mathbf{q}^* is an ESS (Hines, 1980; Akin, 1982; Cressman, 1992). In this statement, strong stability can be replaced by the following condition. For all $\mathbf{q} \in S_m$, $\mathbf{q} \neq \mathbf{q}^*$, the rest point 1 is locally asymptotically stable for the dynamics

$$\dot{\varepsilon} = \varepsilon [(\mathbf{q}^* - \mathbf{y}) \mathbf{A} \mathbf{y}] \quad (8)$$

where $\mathbf{y} = \varepsilon \mathbf{q}^* + (1 - \varepsilon) \mathbf{q}$ (Cressman, 1990). It is easy to see that uninvadability of \mathbf{q}^* implies that the right-hand side of dynamics (8) is positive for all $\mathbf{y} \in S_m$, $\mathbf{y} \neq \mathbf{q}^*$ in the neighbourhood of \mathbf{q}^* . The above reasoning motivates the following:

Definition 2. A $\mathbf{p}^* = (\mathbf{p}^{1*}, \mathbf{p}^{2*}, \dots, \mathbf{p}^{n*}) \in \mathbf{S}$ is called strictly stable if for all fixed $\mathbf{p} = (\mathbf{p}^1, \mathbf{p}^2, \dots, \mathbf{p}^n) \in \mathbf{S} \setminus \{\mathbf{p}^*\}$, and for all

$$\varepsilon \in \prod_{i=1}^n [0, 1]$$

close enough to the point $\mathbf{1}^n = (1, 1, \dots, 1) \in \mathbf{R}^n$ with $\varepsilon \neq \mathbf{1}^n$, the right-hand side of the dynamical system

$$\dot{\varepsilon}_i = \varepsilon_i [\mathbf{p}^{i*} - \mathbf{x}^i] \left[\sum_{j=1}^n \mathbf{A}^{ij} \mathbf{x}^j \right] \quad (i \in \overline{1, n}) \quad (9)$$

is positive where $\mathbf{x}^i = \varepsilon_j \mathbf{p}^{j*} + (1 - \varepsilon_j) \mathbf{p}^j$.

Theorem 3. A $\mathbf{p}^* \in \mathbf{S}$ is a strict n -species ESS if and only if it is strictly stable.

The proof is an easy generalisation of Cressman (1990), Section 2.

5. Overview

The intuitive concept of evolutionary stability, at the same time, also means the terminal state of phenotypic selection. The basic idea of ESS for one species is that, roughly speaking, a mutant is always worse off than a resident. This principle can be extended to the case of n species in two ways.

1. *Uninvadability approach*: in the case of any small perturbation (low-rate mutation), the fitness of the mutants should be less than that of the residents of the same species (see Definition 1).
2. *Dynamical approach*: in the case of any small perturbation the mutants should die out, according to an appropriate dynamics.

The dynamical approach, in certain species, may allow the existence of mutants having a fitness greater than that of the resident one (both fitnesses taken in the perturbed state of the population). The main point is that, in the long run, the mutants should die out, provided the perturbation is small. Thus this approach weakens the requirement of uninvadability within the given species, having in mind the long-term dynamical behaviour of the system in consideration. The question is how a compromise between these two approaches could be given in order to 'render therefore unto Caesar the things which are Caesar's; and unto God the things that are God's'.

Let us start out from the biological situation of classical ESS theory, supposing that the mutation is a very rare event and the selection is quick. This means that there is enough time for the fitter phenotypes to eliminate the less fit one, before new mutants perturb the system again.

The following compromise type definition is based on Cressman's insightful strong stability concept (Hines 1980; Akin 1982; Cressman 1996):

Definition 3. A $\mathbf{p}^* \in \mathbf{S}$ is said to be *evolutionarily dynamically stable*, if for all $\mathbf{p} \in \mathbf{S} \setminus \{\mathbf{p}^*\}$, $\mathbf{1}^n = (1, 1, \dots, 1) \in \mathbf{R}^n$ is an asymptotically stable rest point of the system

$$\dot{\varepsilon}_i = \varepsilon_i [\mathbf{p}^{i*} - \mathbf{x}^i] \left[\sum_{j=1}^n \mathbf{A}^{ij} \mathbf{x}^j \right] \quad (i \in \overline{1, n}) \tag{10}$$

where $\mathbf{x}^j := \varepsilon_j \mathbf{p}^{j*} + (1 - \varepsilon_j) \mathbf{p}^j \quad (j \in \overline{1, n})$.

This definition is related to the uninvadability principle since the right-hand side of Eq. (10) is given on the basis of the inequalities Eq. (1). To each possible mutation a particular dynamics is given. The price of the compromise of Definition 3 is that, on the one hand, not all mutants are supposed to be worse off. On the other hand, the loss of the dynamical approach is that, instead of a single dynamics, an infinite family of them must be considered in terms of asymptotic stability.

We notice that Definition 3 is equivalent to the classical ESS, for $n = 1$ and to Cressman's two-species ESS, for $n = 2$ (Cressman, 1992, 1996, Theorem 3.2.4).

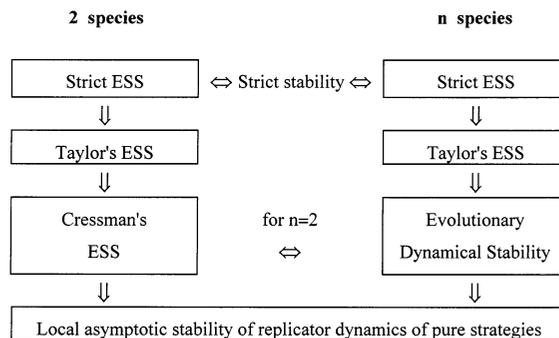
As it is seen, our definition is a weakening of Cressman's strong stability, since we supposed only the presence of two phenotypes. (Selection is quicker than mutation.) It is not clear if Definition 3 implies Cressman's strong stability concept, although for $n = 2$ in case of regular ESS it is proved in Cressman (1992) (p. 49). We also mention that, by taking a mutation within a single species, Definition 3 implies conditions of (3.1) (3.2a).

Following the proof of Theorem 2.5.2 of Cressman (1992), we obtain:

Theorem 4. If Taylor's condition (6) holds, then \mathbf{p}^* satisfies the requirements of Definition 3.

We remind that Taylor's condition (6) is a generalisation of the two-species ESS condition given by Taylor (1979).

Finally, for the sake of lucidity, we summarise the relations between the various evolutionary stability concepts in the scheme below.



6. Conclusions

From the above study of the strict n -species ESS, we can conclude the following.

1. Our strict version of n -species ESS is in harmony with the Darwinian principle that what has a greater fitness, will propagate. This concept, in particular cases, reduces to the uninvadability principles considered by Maynard Smith (1982) and Hofbauer and Sigmund (1988) for symmetric and asymmetric conflicts, respectively.
2. As we have mentioned in the Introduction there is no interior ESS in case of symmetric conflicts (Selten, 1980; Hofbauer and Sigmund, 1988) We can say that this fact, in general, remains valid for the strict n -species ESS of Definition 1, as well. An important difference is, however, that in very special interspecific conflicts there may be a totally mixed evolutionarily stable strategy. The reason for the existence of a mixed ESS is that the individuals either do not recognise their opponents having different strategy sets, or they are unable to choose their strategies depending on the strategy sets of their opponents.
3. The strict n -species ESS is in analogy with the one-species ESS theory from a dynamical point of view, too, since it guarantees the asymptotic stability of the replicator dynamics of pure strategies (while the inverse implication is not true). Furthermore, also in our case a strict stability concept can be given which is equivalent to the strict n -species ESS and is a natural extension of Cressman's insightful strong stability concept.

As we mentioned above, a totally mixed strict n -species ESS can exist, provided the interspecific pay-off matrices have a special structure (there is no real interspecific game–theoretical conflict). This fact offers a possibility for verification of the approach proposed by us. Indeed, suppose that there is an asymmetric conflict between two given species and there are symmetric conflicts within the species. It is also supposed that the standard

conditions of evolutionary game theory are satisfied; the individuals, however, either do not recognize the strategy set of their opponents, or they are not able to change their strategies. If under these circumstances mixed strategies are observed within each species then by estimating the pay-off matrices, their above mentioned special structure can be checked directly.

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