

On Equilibria of Evolutionary Dynamics

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ON EQUILIBRIA OF EVOLUTIONARY DYNAMICS

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Abstract

We investigate equilibria (i.e., rest points) of a wide class of evolutionary dynamics, describing changes in the composition of a population in a competitive environment in time. We introduce the non-trivial equilibrium and the evolutionary stable equilibrium, and compare these equilibria with several dynamical equilibrium concepts, and with equilibrium concepts from non-cooperative game theory. The issues of existence, uniqueness, multiplicity, (dynamical) stability, and computability of certain equilibria are addressed. A procedure is proposed to find non-trivial equilibria.

Keywords: Evolutionary dynamics, stability, non-trivial equilibrium, evolutionary stable equilibrium, nonlinear complementarity problem.

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1. Introduction

In evolutionary game theory interacting groups within a population play genetically determined, distinguishable strategies. To each group a payoff is awarded, representing the fitness of this group, i.e. a measure of potential to reproduce. This payoff depends not only on the strategy used by the group, but also on the strategies used by the other groups and on the state, being the distribution of the population over these groups. The states evolve over time and the evolution of the population shares of the groups is in accordance with their (relative) fitness (cf. Van Damme [1991]).

In evolutionary economics the market shares of interacting groups of economic agents, e.g. firms, countries or (more abstract) technologies, are regarded as a state and such states change over time as well. Economic agents choose certain long term strategies or actions, having an effect on their fitness, here their ability to compete and to increase their market shares. Again fitness of a group of agents depends not only on the actions chosen by that group itself, but also on the actions chosen by other groups and the distribution of the market shares among all groups (cf. Silverberg [1988]).

Assume that a population consists of a certain number, say $n+1$, of distinguishable subgroups. The relative fitness function then is the $(n+1)$ -dimensional vector function which for every state attributes to each subgroup its relative fitness, meaning the difference between the subgroup's fitness and the population-share-weighted average fitness of the population. We exploit mathematical similarities between excess demand functions for pure exchange economies, and relative fitness functions of the evolutionary approaches. A relative fitness function for a population with $n+1$ subgroups is namely formally equivalent to an excess demand function for a pure exchange economy with $n+1$ goods and normalized prices.

At a non-trivial equilibrium each subgroup with positive population share has highest relative fitness. Admissible evolutionary dynamics describe the changes in the composition of the population. The set of non-trivial equilibria is a non-empty subset of the equilibria of admissible evolutionary dynamics, and contains the set of stable equilibria. Non-trivial equilibria are shown to correspond with Nash equilibria in standard settings in evolutionary game theory. Mathematically, a non-trivial equilibrium is equivalent to an economic equilibrium for a pure exchange economy, whereas admissible

evolutionary dynamics may be interpreted as (simultaneous) Walrasian tâtonnement processes.

An evolutionary stable equilibrium is introduced, differing from the well-known evolutionary stable strategy. Any trajectory reaching a certain neighborhood of an evolutionary stable equilibrium, converges towards this equilibrium, and the Euclidean distance to the equilibrium strictly decreases monotonically along this trajectory. The issues of multiplicity and stability of equilibria of admissible evolutionary dynamics are addressed. Conditions are derived for uniqueness of an interior non-trivial equilibrium, implying either asymptotical stability, or unstability of this equilibrium, for all admissible dynamics.

Researchers interested in finding fixed points of evolutionary dynamics may encounter some problems when trying to compute such points. The dynamical system is generally nonlinear and even low-dimensional dynamical systems may display an astonishing degree of complexity. A procedure to find non-trivial equilibria is proposed. First all vertices of the unit simplex are checked. To find other, possibly interior, non-trivial equilibria a variable dimension restart algorithm may be employed. Such an algorithm converges towards an approximation of a non-trivial equilibrium for arbitrary relative fitness functions, starting in an arbitrary point of the unit simplex.

This paper is organized as follows. In Section 2 we give an overview of related work in the fields of evolutionary game theory, evolutionary economics, dynamical systems, and equilibrium programming. In Section 3 we define the main concepts used in this paper. We compare several equilibrium concepts, dynamic as well as game-theoretical equilibria. In Section 4 we make some remarks on the stability and number of dynamic equilibria in certain evolutionary settings. In Section 5 we give a procedure to find equilibria, suggesting an algorithm to approximate non-trivial equilibria of evolutionary dynamics. Section 6 concludes.

2. Related literature

To model evolutionary changes in the distribution of a population over its subgroups over time, several dynamics are proposed in literature. We refer to Nachbar

[1990] and Friedman [1991] for an overview and treatment of such dynamics. The replicator dynamics, introduced in game theory by Taylor and Jonker [1978], are used to such an extent that the concept of evolutionary dynamics seems to have become identified with them. Selection dynamics, Malthusian or Darwinian dynamics are some of the other names by which they are known. Maynard Smith and Price [1973] are to be credited for introducing the central concept in evolutionary game theory, namely the evolutionary stable strategy (ESS). Taylor and Jonker [1978] and Zeeman [1981] investigate some relations of the ESS-concept with several dynamic equilibrium concepts for the replicator dynamics.

Van Damme [1991] provides an excellent survey on evolutionary game theory. The main concepts there in connection with this paper are: equilibria of replicator dynamics, stability of dynamic equilibria, and symmetric Nash equilibria¹. For an overview of very recent research in evolutionary game theory we refer to Mailath [1992]. Hofbauer and Sigmund [1988] give an extensive treatment of dynamics in an evolutionary framework. Hirsch and Smale [1974] is our main point of reference with regard to non-linear differential equations and dynamical systems. Recent examples of evolutionary approaches in economics are Hirshleifer [1977], Nelson and Winter [1982], Iwai [1984], Silverberg [1988, 1989], and Verspagen [1992]. Articles by Hodgson [1993] and Foster [1993] draw attention to the fact that Alfred Marshall was interested in a biological analogy for economics as early as 1898.

Fixed points of evolutionary dynamics are of interest, since such points can be associated with equilibria in game theory (economics). Furthermore, in a bounded rationality framework, replicator-type dynamics are often interpreted as processes to motivate Nash-equilibrium-learning, or equilibrium selection in the presence of multiple Nash equilibria². Certain fixed points for a wide class of evolutionary dynamics are easily found and their number is always equal to the number of subgroups in the population. Unfortunately, all these fixed points may be dynamically unstable and finding interior fixed points or dynamically stable fixed points, may be difficult or even impossible. This

¹ A dynamic equilibrium is a fixed point of the (replicator) dynamics. Stability of a dynamic equilibrium means that if such a state is slightly perturbed, a trajectory is followed within a neighborhood close to that state from that moment on. A trajectory is a sequence of states generated by the dynamics. Asymptotic stability means that if such a state is perturbed slightly, the system converges back to it. See Hirsch and Smale (1974) or Section 3 for more formal definitions.

² See e.g. Crawford [1985], Selten [1990].

is a discouraging prospect since for most settings the stable equilibria of the dynamics are relevant with respect to realistic predictions. Additional problems arise when the number of groups within a population is large.

Van der Laan *et al.* [1987] introduce a variable dimension restart algorithm (v.d.r.a.) to solve the nonlinear complementarity problem on the unit simplex (NLCP). The problem of finding a non-trivial equilibrium for a certain class of evolutionary dynamics is an NLCP. Several other v.d.r.a.'s to solve the NLCP have been developed since. The potential directions to leave the arbitrary starting point of such an algorithm, are called rays. Efficiency of an algorithm is measured by the number of steps it needs to perform to reach an approximation fulfilling a certain accuracy criterion. Research indicates that the $(2^{n+1}-2)$ -ray algorithm of Doup *et al.* [1987] is the most promising v.d.r.a. for the NLCP. We refer to Garcia and Zangwill [1981], Van der Laan and Talman [1987] and Doup [1988] for surveys on finding equilibria of (dynamical) systems of non-linear equations, and on variable dimension restart algorithms.

3. The evolutionary model

Consider the following model, where a population consists of $n+1$ distinguishable, interacting subgroups. The interaction of the subgroups has consequences on their respective abilities to reproduce. Fitness of a subgroup may be interpreted as a measure of ability to reproduce, determined by its genetically given behavior in combination with the composition of the population. Since behavior of the subgroups is predetermined, fitness can be analyzed as a function exclusively of the population shares of all subgroups. Therefore, let $x = (x_1, x_2, \dots, x_{n+1})^T \in S^n = \{y \in \mathbb{R}^{n+1} \mid \sum_j y_j = 1, y_i \geq 0 \text{ for all } i = 1, 2, \dots, n+1\}$ denote a vector of population shares, henceforth to be called a state. Let $E: S^n \rightarrow \mathbb{R}^{n+1}$ be a continuous function, attributing to every subgroup its fitness at each state, and let furthermore $I^{n+1} = \{1, 2, \dots, n+1\}$. States change over time subject to evolutionary dynamics, meaning that if a subgroup has above-average (below-average) fitness at a certain state, its population share increases (decreases).

The relative fitness function $f: S^n \rightarrow \mathbb{R}^{n+1}$ is given by

$$f_i(x) = E_i(x) - \sum_j x_j E_j(x) \quad \text{for all } i \in I^{n+1}, x \in S^n. \quad (1)$$

The relative fitness function f attributes for every state $x \in S^n$, to each subgroup $i \in I^{n+1}$, the fitness of the subgroup relative to the average fitness of the population weighted by the population shares of all subgroups, $\sum_j x_j E_j(x)$.

In the sequel we suppress time-notations whenever confusion is not likely. The inner product of $x, y \in \mathbb{R}^{n+1}$, is denoted by $x^T y$. For $x, y \in \mathbb{R}^{n+1}$ the (Euclidean) distance is $d_2(x, y) = [\sum_i (y_i - x_i)^2]^{1/2}$. Furthermore, $e(j)$, $j \in I^{n+1}$, is the vertex x of the unit simplex satisfying $x_j = 1$. For $z \in \mathbb{R}^{n+1}$, we write for example, $z \geq 0$, meaning $z_i \geq 0$ for all $i \in I^{n+1}$. Several proofs are omitted and may be found in the Appendix.

PROPOSITION 3.1. For every $x \in S^n$, $x^T f(x) = 0$.

Hence, for every evolutionary setting the relative fitness function f , satisfies continuity, which follows directly from the assumption that the function E is continuous, and $x^T f(x) = 0$ for all $x \in S^n$.

By reasoning conversely, the following question arises. Given a function $g: S^n \rightarrow \mathbb{R}^{n+1}$, satisfying continuity and $x^T g(x) = 0$ for all $x \in S^n$, can we construct an evolutionary setting, i.e., define a function $E: S^n \rightarrow \mathbb{R}^{n+1}$, such that the resulting relative fitness function is equal to g ? The answer is affirmative and the argument is straightforward. Take an arbitrary function $g: S^n \rightarrow \mathbb{R}^{n+1}$, satisfying continuity and $x^T g(x) = 0$ for all $x \in S^n$. Let a population consist of $n+1$ subgroups, and define the fitness of subgroup $i \in I^{n+1}$, at every state $x \in S^n$, by $E_i(x) = g_i(x) + c$, $c \in \mathbb{R}$. Then for the corresponding relative fitness function f , it holds that

$$f_i(x) = (g_i(x) + c) - \sum_j x_j (g_j(x) + c) = g_i(x) \quad \text{for all } i \in I^{n+1}, x \in S^n. \quad (2)$$

In deriving Equation (2), we used $x^T g(x) = 0$ and $\sum_j x_j = 1$, hence $\sum_j x_j (g_j(x) + c) = \sum_j x_j g_j(x) + \sum_j x_j c = 0 + c = c$.

COROLLARY 3.2. A relative fitness function $f: S^n \rightarrow \mathbb{R}^{n+1}$ is characterized by continuity and $x^T f(x) = 0$.

In a series of papers, Sonnenschein [1972, 1973], Mantel [1974], and Debreu [1974]³ showed for any continuous function f , satisfying $x^T f(x) = 0$ for all $x \in S^n$, and for any $\epsilon > 0$, that there exists an (aggregate or community) excess demand function f^* derived from a pure exchange economy with utility maximizing agents, which satisfies $f^*(x) = f(x)$ for all $x \in \{y \in S^n \mid y_i \geq \epsilon, \text{ for all } i \in I^{n+1}\}$.

As mentioned in the first paragraph of this section, states change over time essentially as a function of the composition of the population, since behavior of each subgroup is assumed to be predetermined. Let us consider a dynamic process represented by the following system of $n+1$ differential equations:

$$dx/dt = G(x) \quad \text{for all } x \in S^n, \quad (3)$$

where $dx/dt = (dx_1/dt, dx_2/dt, \dots, dx_{n+1}/dt) = (G_1(x), G_2(x), \dots, G_{n+1}(x))$, denoting the continuous-time change of the population share of each subgroup as a function of the composition of the population. Obviously, the function G in Equation (3) must fulfill certain criteria to be appropriate in the present model. In the sequel we place weak restrictions on dynamics in order to examine a rather large class 'evolutionary' dynamics. Hence, given a relative fitness function f , we call the function $G: S^n \rightarrow \mathbb{R}^{n+1}$, in Equation (3), **admissible** (with respect to f) if

- a) G is continuous,
- b) $\sum_i G_i(x) = 0$ for all $x \in S^n$,
- c) $x_i = 0$ implies $G_i(x) = 0$ for all $x \in S^n$, $i \in I^{n+1}$, and
- d) $x_i > 0$ implies $\text{sign } G_i(x) = \text{sign } f_i(x)$ for all $x \in S^n$, $i \in I^{n+1}$.

For every $y \in \mathbb{R}$, $\text{sign } y$ is defined as: $\text{sign } y = +1$ if $y > 0$, $\text{sign } y = 0$ if $y = 0$, $\text{sign } y = -1$ if $y < 0$. We call dynamics admissible (as evolutionary dynamics) if the function G in Equation (3) is admissible. We emphasize that in the remainder of this section, we do not place additional restrictions on the function G in Equation (3). Most notably, differentiability of the function G is not assumed. Somewhat different from our

³ Eric van Damme encouraged the author to prove the characterization above, which is in the spirit of Sonnenschein, Mantel and Debreu. Hans Peters and the author found the argument given.

nomenclature, Friedman [1991] calls dynamics fulfilling the first three conditions as well as piecewise differentiability, admissible, whereas dynamics that fulfil condition d, are called weak compatible.

Well-known admissible dynamics are the replicator dynamics, given by $G_i(x) = x_i f_i(x)$ for all $i \in I^{n+1}$, $x \in S^n$ in Equation (3). Replicator dynamics possess several attractive properties, which may have contributed to their popularity. Recently however, several papers investigate wider classes of dynamics, e.g. Nachbar [1990], Friedman [1991], Samuelson and Zhang [1992]. Similarly, Dow [1986] investigates economic adjustment mechanisms, called profit-responsive adjustment processes.

For dynamics represented by an admissible function G , a state $y \in S^n$ is a fixed point if $G(y) = 0$. At a fixed point changes in the composition of the population due to evolutionary influences, come to a rest. A fixed point $y \in S^n$ is stable if for any (open) neighborhood $U \subseteq S^n$ of y , a neighborhood $V \subseteq U$ of y exists such that any trajectory starting in V remains in U . A stable fixed point $y \in S^n$ is asymptotically stable if additionally a neighborhood $W \subseteq S^n$ of y exists such that all trajectories starting in a point of W converge towards y . See also Hirsch and Smale [1974]. A powerful tool for the analysis of dynamical stability properties of points is Lyapunov's (second) method. We use this method on several occasions in the sequel and we refer to Hirsch and Smale [1974] for a treatment of this elegant method. Furthermore, Lyapunov's method can be generalized directly to examine the dynamical properties or stability of certain sets of points (cf. e.g., Uzawa [1961], Hofbauer and Sigmund [1988]).

Rather than invoking some Brouwer-type fixed point argument, we show directly in the following that existence of fixed points is guaranteed for arbitrary relative fitness functions and admissible dynamics. Furthermore, the lower bound for the number of fixed points is equal to the number of subgroups of the population.

PROPOSITION 3.3. For admissible dynamics, each vertex of the unit simplex is a fixed point.

Given a relative fitness function f , $y \in S^n$ is a non-trivial equilibrium⁴ if $f(y) \leq 0$.

⁴ Hofbauer and Sigmund [1988] call such a point a saturated fixed point in a similar framework.

A non-trivial equilibrium y is strict if $f_j(y) = 0$ for precisely one $j \in I^{n+1}$. Finding such a state $y \in S^n$ for which $z(y) \leq 0$ for a continuous function $z: S^n \rightarrow \mathbb{R}^{n+1}$ satisfying $x^T z(x) = 0$ for all $x \in S^n$, is called the non-linear complementarity problem (NLCP) with respect to z . Finding a non-trivial equilibrium (NTEP) for f , is an NLCP with respect to f . At a non-trivial equilibrium every group with positive population share has average fitness. There exists no group, not even a group with population share equal to zero, with above-average-fitness. Any group with below-average-fitness has population share equal to zero.

In the following propositions, we show that every non-trivial equilibrium is a fixed point of all admissible evolutionary dynamics, that at least one non-trivial equilibrium exists for arbitrary relative fitness functions, and that each strict non-trivial equilibrium is asymptotically stable for admissible dynamics. If a boundary of the unit simplex acts as a repeller, there exists a certain (positive) threshold value such that certain subgroups have population shares at least equal to this threshold value as time goes to infinity, provided these subgroups have nonzero population shares to begin with.

PROPOSITION 3.4. Given the relative fitness function f , for all dynamics determined by an admissible function G , $f(y) \leq 0$ implies $G(y) = 0$.

PROPOSITION 3.5. There exists at least one non-trivial equilibrium for every relative fitness function.

PROPOSITION 3.6. For admissible dynamics every strict non-trivial equilibrium is asymptotically stable.

Proof: Let $f: S^n \rightarrow \mathbb{R}^{n+1}$ be a relative fitness function, let $G: S^n \rightarrow \mathbb{R}^{n+1}$ be admissible, let $y \in S^n$ be a strict non-trivial equilibrium.

By definition there exists some $j \in I^{n+1}$ satisfying $0 = f_j(y) > \max_{i \neq j} f_i(y)$, then Proposition 3.1 leads to:

$$0 = \sum_i y_i f_i(y) = y_j f_j(y) + \sum_{i \neq j} y_i f_i(y) = \sum_{i \neq j} y_i f_i(y) \leq \sum_{i \neq j} y_i \max_{i \neq j} f_i(y) = (1 - y_j) \max_{i \neq j} f_i(y) \leq 0. \text{ This implies } y_j = 1.$$

Since f is continuous, an $\epsilon > 0$ and a $\delta > 0$ exist, satisfying $f_i(u) < -\epsilon$ for all

$i \neq j$ and all $u \in U = \{x \in S^n \mid 1 - x_j < \delta\}$.

Furthermore, $G(y) = 0$ by Proposition 3.3, and $u \in U \setminus \{y\}$ implies

$$\text{sign } G_i(u) \leq 0 \text{ for all } i \neq j, \quad (4)$$

$$\text{sign } G_j(u) > 0. \quad (5)$$

For all $u \in U \setminus \{y\}$ it holds that $f_i(u) < -\epsilon$ for all $i \neq j$, therefore $\text{sign } G_i(u) = -1$ if $u_i > 0$, $\text{sign } G_i(u) = 0$ if $u_i = 0$, which proves (4).

Proposition 3.1 leads to $f_j(u) = -\sum_{i \neq j} u_i f_i(u)/u_j$, hence $f_j(u) > 0$ for all $u \in U \setminus \{y\}$.

Since $u_j > 0$, $\text{sign } G_j(u) > 0$, which proves (5).

Let $V: U \rightarrow \mathbb{R}$ be defined by $V(x) = (x_j - 1) - \sum_{i \neq j} x_i$ for all $x \in U$.

Obviously, $V(x) \leq 0$ for all $x \in U$. Since $\partial V(x)/\partial x_j = 1$ and $\partial V(x)/\partial x_i = -1$ for all $i \neq j$, it follows that $dV(x)/dt = \sum_k \partial V(x)/\partial x_k G_k(x) = G_j(x) - \sum_{i \neq j} G_i(x)$.

Hence, $dV(y)/dt = 0$, and $dV(x)/dt > 0$ for all $x \in U \setminus \{y\}$, since by (4) and (5) for all $u \in U \setminus \{y\}$, $G_j(u) > 0$ and $G_i(u) \leq 0$ for all $i \neq j$.

This means that V is a strict Lyapunov-function on U , and y is asymptotically stable (cf. Hirsch and Smale [1974]). ■

PROPOSITION 3.7. If there exists a set $K \subseteq I^{n+1}$ such that $x_k = 0$ implies $f_k(x) > 0$ for all $k \in K$, then there exists $\delta > 0$ satisfying $\lim_{t \rightarrow \infty} \inf x(t) \geq \delta$ for all $k \in K$.

Proof: Let $f: S^n \rightarrow \mathbb{R}^{n+1}$ be a relative fitness function, let $G: S^n \rightarrow \mathbb{R}^{n+1}$ be admissible, and let $K \subseteq I^{n+1}$ satisfy $f_k(x) > 0$, whenever $x_k = 0$ for all $k \in K$.

Let, furthermore, $S(K) = \{x \in S^n \mid x_k = 0, \text{ for some } k \in K\}$.

Since f is continuous, there exists $\delta_k > 0$ for each $k \in K$, such that $x_k < \delta_k$ implies $f_k(x) > 0$.

Take $0 < \delta < \min \{\delta_k \mid k \in K\}$, and $U = \{p \in S^n \mid p_k \leq \delta \text{ for all } k \in K\}$.

Let $V: U \rightarrow \mathbb{R}^{n+1}$ be given by $V(x) = \min_{k \in K} x_k$ for all $x \in U$.

Clearly, $V(u) = 0$ for all $u \in S(K)$, $V(u) > 0$ for all $u \in U \setminus S(K)$.

Furthermore $dV(x)/dt = \sum_j \partial V(x)/\partial x_j dx_j/dt = G_{i^*}(x)$, where $i^* \in K$ is some index satisfying $x_{i^*} = \min_{k \in K} x_k$.

Hence $dV(u)/dt = 0$ for all $u \in S(K)$, whereas $dV(u)/dt > 0$ for all $u \in U \setminus S(K)$.

Since V strictly increases in time in $U \setminus S(K)$, for each trajectory $\{z(t)\}_{t \geq 0}$ with

$z(0) \in U \setminus S(K)$, there exists $t^* \geq 0$ such that $V(z(t^*)) = \delta$.

From the above it follows then that $dV(z(t^*))/dt > 0$, hence the trajectory leaves U . This completes the proof, since no trajectory will reach U from $S^n \setminus U$. ■

The proposition above implies more than just 'not becoming extinct'. It means that there exists a threshold value, $\delta > 0$, such that if the system is subjected to an incidental shock smaller than δ , then no group in such a set K will become extinct. We do not specifically model such shocks in this paper, but one can think of real-life systems where a shock may be caused by some environmental catastrophe or an invasion of the system. Furthermore, each non-trivial equilibrium y , satisfies $y_k \geq \delta$ for all $k \in K$. If the condition of Proposition 3.7 holds for $K = I^{n+1}$, this is sufficient for permanence of the system (cf. Amann and Hofbauer [1985], Hofbauer and Sigmund [1988]). A permanent system is invadable for any group of mutants, moreover the effects of such an invasion are persistent in the sense that no invading group of mutants is driven out in the limit.

For given relative fitness function and admissible dynamics, let ASE, SE, NTE, SNTE, FP denote the sets of all asymptotically stable equilibria, stable equilibria, non-trivial equilibria, strict non-trivial equilibria, and fixed points respectively. It is clear that $NTE \subset FP$ and $SNTE \subset ASE$ by Propositions 3.4 and 3.6, and that $ASE \subset SE$. Stability need not imply asymptotical stability, hence $SE \not\subset ASE$. Obviously, $ASE \not\subset SNTE$, since an asymptotically stable equilibrium need not be a vertex of the unit simplex. In the following we establish a connection between non-trivial equilibria and stable equilibria for admissible dynamics.

PROPOSITION 3.8. For any relative fitness function and for admissible dynamics, it holds that $SE \subset NTE$.

Proof: Let $f: S^n \rightarrow \mathbb{R}^{n+1}$ be a relative fitness function, let $G: S^n \rightarrow \mathbb{R}^{n+1}$ be admissible.

For $SE = \emptyset$, the proposition holds trivially, assume therefore $SE \neq \emptyset$.

Suppose $y \in SE$ and $y \notin NTE$, then $f_j(y) > 0$ and $y_j = 0$ for some $j \in I^{n+1}$.

Since f is continuous, an $\epsilon > 0$ and a $\delta > 0$ exist such that $f_j(x) > \epsilon$ for all $x \in U$, where $U = \{u \in S^n \mid \max_i |u_i - y_i| < \delta, i \in I^{n+1}\}$.

Let $\{z(t)\}_{t \geq 0}$ be a trajectory with $z(0) \in U$ and let $z_j(0) = \alpha > 0$.

Since $z_j(0) = \alpha$ and $f_j(z(0)) > \epsilon$, it follows that $\text{sign } G_j(z(0)) = +1$, implying $G_j(z(0)) > 0$. Furthermore, $z_j(t) > z_j(0)$ and $G_j(z(t)) > 0$ while $z(t) \in U$.

Then $\{z_j(t)\}_{t \geq 0}$ increases monotonically while $z(t) \in U$.

Hence, there exists $k > 0$ such that $\max_i |z_i(k) - y_i| = \delta$, $i \in I^{n+1}$, thus $z(k) \notin U$.

This contradicts $y \in \text{SE}$, because for U no neighborhood $V \subseteq U$ of y exists such that a trajectory $\{z(t)\}_{t \geq 0}$ with $z(0) \in V$ and $z_j(0) > 0$ remains in U . ■

That $\text{NTE} \not\subseteq \text{SE}$ follows easily, namely any unstable interior fixed point is a non-trivial equilibrium.

Another interesting set of points is the set of limit points. We call a point, say y , a limit point if there exists a trajectory $\{z(t)\}_{t \geq 0} \subset S^n$, such that $z(0) \neq y$ and $\lim_{t \rightarrow \infty} z(t) = y$. From the continuity of admissible dynamics combined with the compactness of S^n , it follows that such a limit point y is a fixed point of admissible dynamics, and furthermore that $y \in S^n$. If y is a limit point in the relative interior of S^n , then y is a non-trivial equilibrium, since all interior fixed points of admissible dynamics are non-trivial equilibria. Furthermore, the proof of Proposition 3.8 implies that a fixed point in the boundary of the unit simplex not being a non-trivial equilibrium, is not reached by any trajectory starting from the relative interior of the unit simplex. Therefore, each limit point for a trajectory starting in the relative interior of the unit simplex, which is located in a boundary of the unit simplex, is a non-trivial equilibrium. Summarizing, the set of limit points for trajectories starting in the interior of the unit simplex, is a subset of the set of non-trivial equilibria. While each asymptotically stable equilibrium is a limit point by definition, it is not clear what the connection between stable equilibria and limit points is in general. It is namely fairly easy to construct examples where a stable equilibrium is not a limit point and vice versa. For a graphical illustration we refer to Figure 3.1.

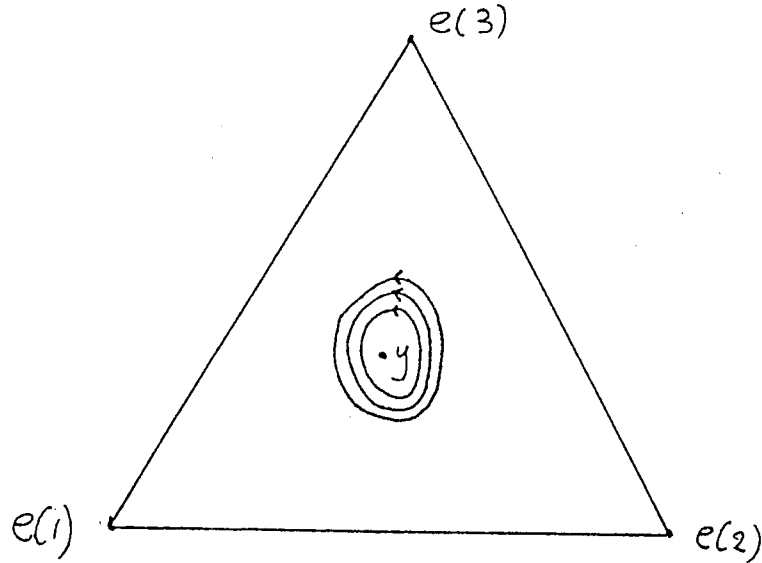
Taylor and Jonker [1978] and Zeeman [1981], connect the main concept in evolutionary game theory, the evolutionary stable strategy (state), with dynamic equilibrium concepts for the replicator dynamics. In the following, the relative fitness function f is given by

$$f_k(x) = e(k)^T A x - x^T A x \text{ for all } x \in S^n, k \in I^{n+1}, \quad (6)$$

where A denotes an $(n+1) \times (n+1)$ -matrix. For the bimatrix game (A, A^T) where $A^T_{ij} = A_{ji}$ for all $i, j \in I^{n+1}$, the mixed strategy combination (y, y) , $y \in S^n$, is a symmetric Nash equilibrium if $y^T A x \leq y^T A y$ for all $x \in S^n$. Furthermore, $y \in S^n$ is an evolutionary stable strategy if $x \in S^n$, then $x^T A y \leq y^T A y$, and additionally if $x \neq y$ and $x^T A y = y^T A y$, then $x^T A x < y^T A x$.

PROPOSITION 3.9. For every non-trivial equilibrium, y , of the relative fitness function given by (6), (y, y) is a Nash equilibrium of the corresponding bimatrix game, (A, A^T) .

a)



b)

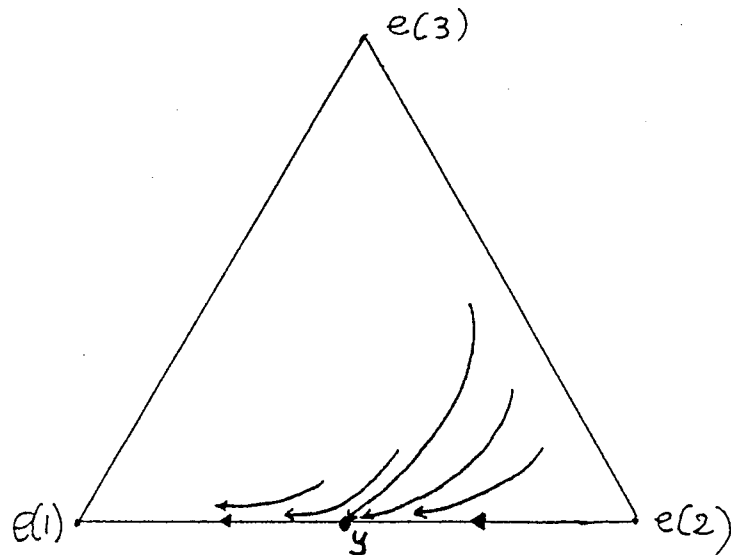


Figure 3.1. In graph a) $y \in \text{NTE}$, $y \in \text{SE}$, $y \notin \text{LP}_{\text{int}}$, $y \notin \text{ASE}$. In graph b) $y \in \text{NTE}$, $y \notin \text{SE}$, $y \in \text{LP}_{\text{int}}$.

Let ESS and SNE denote the sets of points of the unit simplex associated with respectively all evolutionary stable strategies and symmetric Nash equilibria in the symmetric bimatrix game (A, A^T) . Let ASE, SE, (S)NTE and FP denote the sets of all asymptotically stable, stable, and (strict) non-trivial equilibria and fixed points for the relative fitness function given by (6) combined with admissible dynamics. Let LP_{int} be the set of all limit points of trajectories starting in the relative interior of the unit simplex for admissible dynamics. Nachbar [1990] showed for replicator dynamics that $LP_{\text{int}} \subseteq SNE$, and this result was generalized in this section for admissible dynamics. $ASE \not\subseteq ESS$ for admissible dynamics (cf. Taylor and Jonker [1978]). Every strict non-trivial equilibrium corresponds with a symmetric strict Nash equilibrium, hence, $SNTE \subseteq ESS$ (cf. Van Damme [1991]). Taylor and Jonker [1978] established $ESS \subseteq ASE$ for replicator dynamics, however this need not hold for all admissible dynamics.

COROLLARY 3.10. For the relative fitness function given by (6) and for admissible dynamics, it holds that

- 1) $SNTE \subseteq ASE \subseteq SE \subseteq NTE = SNE \subseteq FP$,
- 2) $SNTE \subseteq ESS$,
- 3) $LP_{\text{int}} \subseteq NTE = SNE$.

Van Damme [1991] characterizes an evolutionary stable strategy (ESS) in a symmetric bimatrix game (A, A^T) . This characterization translates into our notations as follows. The strategy $y \in S^n$ is an ESS, if and only if there exists a neighborhood $U \subset S^n$ of y such that

$$y^T f(x) > 0 \quad \text{for all } x \in U \setminus \{y\}, \quad (7)$$

where the relative fitness function f is given by (6). It is tempting to generalize this directly for arbitrary relative fitness functions. However, although it can be shown that there exists no non-trivial equilibrium in $U \setminus \{y\}$ if (7) holds for U , it should be noted that asymptotical stability is not necessarily implied for all admissible dynamics. Therefore, a dynamic characterization of an evolutionary stable state must be given in terms of the dynamics of the system (cf. Bomze and Van Damme [1992]).

In this context the following concept may be useful. We call a non-trivial equilibrium $y \in S^n$, an evolutionary stable equilibrium if and only if there exists a neighborhood $U \subset S^n$ of y satisfying

$$y^T G(x) > x^T G(x) \quad \text{for all } x \in U \setminus \{y\}. \quad (8)$$

Let ESE be the set of all evolutionary stable equilibria. In the following we prove that $\text{SNTE} \subset \text{ESE} \subset \text{ASE}$, for a given relative fitness function and given admissible dynamics.

PROPOSITION 3.11. If, for a non-trivial equilibrium y and for admissible dynamics G , there exists a neighborhood U such that (8) holds, then y is asymptotically stable for G .

Proof: Let y be a non-trivial equilibrium and let G be admissible. Let $U \subset S^n$ be a neighborhood of y such that (8) holds.

Let $V: S^n \rightarrow \mathbb{R}$ be defined by $V(x) = -\frac{1}{2} \sum_i (y_i - x_i)^2$.

Obviously, $V(x) < 0$ for all $x \in U \setminus \{y\}$, and $V(y) = 0$. Furthermore,

$$dV(x)/dt = \sum_i \partial V(x)/\partial x_i dx_i/dt = \sum_i (y_i - x_i) G_i(x) = \sum_i y_i G_i(x) - \sum_i x_i G_i(x) = y^T G(x) - x^T G(x).$$

Hence $dV(x)/dt > 0$ for all $x \in U \setminus \{y\}$, and $dV(y)/dt = 0$.

This means that V is a strict Lyapunov-function on U , hence y is asymptotically stable (cf. Hirsch and Smale [1974]). ■

With respect to the dynamic behavior of the system in the neighborhood of an evolutionary stable equilibrium y , we can say the following. For every trajectory $\{z(t)\}_{t \geq 0}$ satisfying $z(k) \in W = \{x \in U \mid 0 \leq d_2(x, y) < r\}$ for some $k \geq 0$, it follows from the proof above, that $d_2(z(t_2), y) < d_2(z(t_1), y)$ for all $t_2 > t_1 \geq k$, since $d_2(x, y) = [-2V(x)]^{1/2}$ for all $x \in S^n$. Hence, the Euclidean distance to y decreases strictly and monotonically over time along any trajectory starting in or reaching W .

PROPOSITION 3.12. For given relative fitness function f and admissible dynamics G , it holds that $\text{SNTE} \subset \text{ESE}$.

Proof: Let y be a strict non-trivial equilibrium, then from the proof of Proposition 3.6 it follows that there exists a neighborhood U such that (4) and (5) hold in $U \setminus \{y\}$. Let furthermore $y = e(j)$ for some $j \in I^{n+1}$, then for all $x \in U \setminus \{y\}$ it follows that $y_j - x_j > 0$, and $y_i - x_i \leq 0$ for all $i \neq j$. This implies $(y_j - x_j) G_j(x) > 0$, as well as $(y_i - x_i) G_i(x) \geq 0$ for all $i \neq j$. Hence, $(y - x)^T G(x) > 0$ for all $x \in U \setminus \{y\}$, which completes the proof. ■

COROLLARY 3.13. For any relative fitness function and given admissible dynamics, it holds that

- 1) $\text{SNTE} \subseteq \text{ESE} \subseteq \text{ASE} \subseteq \text{SE} \subseteq \text{NTE} \subseteq \text{FP}$,
- 2) $\text{LP}_{\text{int}} \subseteq \text{NTE}$.

4. Some remarks on multiplicity and stability of equilibria

This section deals with equilibria of admissible dynamics for a population with, as before, $n+1$ subgroups, under various conditions. Let $|S|$ denote the cardinality of the set S . We have shown that each vertex of the unit simplex is a fixed point of admissible dynamics, hence $|\text{FP}| \geq n+1$. At least one non-trivial equilibrium exists for arbitrary relative fitness functions, therefore $|\text{NTE}| \geq 1$. Corollary 3.13 leads to $0 \leq |\text{SNTE}| \leq |\text{ESE}| \leq |\text{ASE}| \leq |\text{SE}| \leq |\text{NTE}| \leq |\text{FP}|$.

The properties mentioned above hold for all admissible dynamics based on an arbitrary relative fitness function. In the remainder of this section, we describe some less general settings where additional statements can be made about the number of equilibria. In order to do this we make two side-steps. One leads to Hofbauer and Sigmund [1988], the other to Arrow, Block and Hurwicz [1959].

Hofbauer and Sigmund [1988] call a system of which the dynamics are given by a differentiable function $h: \mathbb{R}^{n+1} \rightarrow \mathbb{R}^{n+1}$, cooperative (competitive) on a set $G \subseteq \mathbb{R}^{n+1}$, if $\partial h_i(x)/\partial x_j \geq (\leq) 0$ for all $i \neq j$, $x \in G$. We call an evolutionary system **strongly cooperative (competitive)** if the relative fitness function f is differentiable at all $x \in S^n$, and if

$$\partial f_i(x)/\partial x_j > (<) 0 \text{ for all } i \neq j \text{ and all } x > 0. \quad (9)$$

Arrow, Block and Hurwicz [1959] consider the case that all goods in an economy are strong gross substitutes. Under some additional conditions it is shown that if all goods are strong gross substitutes, all equilibrium price vectors are positive. Moreover, they belong to the same ray, meaning that for each pair of equilibrium price vectors, one is a positive scalar multiple of the other and vice versa. We use these results in the following.

PROPOSITION 4.1. If the system is strongly cooperative, and if an equilibrium $y > 0$ exists, then y is the **unique** non-trivial equilibrium in the interior of S^n .

Proof: Let f be a relative fitness function, differentiable at all $x \in S^n$. Let $\partial f_i(x)/\partial x_k > 0$ for all $k \neq i$, $x > 0$. Let $y \in S^n$ satisfy $y > 0$ and $f(y) = 0$. Define for every $p \in \mathbb{R}^{n+1}$, $p > 0$, the function F by

$$F(p) = f(x(p)), \text{ where } x(p) \equiv p/(\sum_j p_j), j \in I^{n+1}. \quad (10)$$

For $p \in \mathbb{R}^{n+1}$, $p > 0$, F is continuous, $p^T F(p) = (\sum_j p_j) x(p)^T f(x(p)) = 0$, and F is positively homogeneous of degree zero, i.e. $F(\lambda p) = F(p)$ for every $\lambda > 0$.

F is differentiable, moreover $\partial F_i(p)/\partial p_k = (1/\sum_j p_j) \partial f_i(x(p))/\partial x_k(p) > 0$.

From Arrow, Block and Hurwicz [1959] it follows for a function fulfilling these conditions, that

- (a) there exists $q \in \mathbb{R}^{n+1}$, $q > 0$, satisfying $F(q) = 0$, and
- (b) if $F(p) = 0$ for some $p > 0$, then $p = \lambda q$ for some $\lambda > 0$.

Let $q > 0$ and $F(q) = 0$. Then $x(q) \in S^n$, and $F(q) = F(x(q)) = 0$.

Then $x(q) = y$, in view of b, which completes the proof. ■

For a strongly competitive evolutionary system with relative fitness function f , the system with relative fitness function $-f$ is strongly cooperative. Proposition 4.1 shows that if an interior equilibrium y exists for the system with relative fitness function $-f$, then y is the unique interior non-trivial equilibrium. Hence, y is the unique non-trivial equilibrium in

the interior of S^n for the relative fitness function f .

The following lemma is a straightforward adaptation of a theorem of Uzawa [1961] to the present framework.

LEMMA 4.2. If, for a strongly cooperative system, there exists an interior equilibrium y , then every trajectory of admissible dynamics starting in the interior of S^n converges to y .

If the conditions of Lemma 4.2 are fulfilled, then the non-trivial equilibrium in the interior of S^n is asymptotically stable. Conversely, if a system is strongly competitive, the interior non-trivial equilibrium is unstable. Uzawa [1961] shows furthermore, that if strong cooperativeness (strong competitiveness) is replaced by a weaker version formalized by $\partial f_i(x)/\partial x_j \geq (\leq) 0$ for all $i \neq j$ and for all $x > 0$ in Equation (9), uniqueness of the interior equilibrium need not hold. However, all trajectories for admissible dynamics starting in the interior of S^n converge to some interior equilibrium.

If, for a strongly cooperative system, it holds that $f_i(x) > 0$ whenever $x_i = 0$, then Proposition 3.7 can be used to show that every non-trivial equilibrium lies in the interior of S^n , whereas Proposition 4.1 implies that there exists only one equilibrium in the interior of S^n . By Lemma 4.2 this point is asymptotically stable, hence $|NTE| = |ASE| = 1$.

If, for a strongly competitive system, it holds that $f_i(x) < 0$ whenever $x_i = 0$, then Proposition 3.6 implies that every vertex of S^n is an asymptotically stable equilibrium. Proposition 4.1 and Lemma 4.2 show that exactly one interior equilibrium exists, which is unstable, and therefore $|NTE| > |ASE| \geq |SNTE| = n+1$.

5. Finding equilibria of admissible dynamics

Regardless of the specifications of the relative fitness function, the vertices of the unit simplex are fixed points of all admissible dynamics. We think that a procedure to find non-trivial or (asymptotically) stable equilibria, must include a check of the vertices in view of Proposition 3.6. Furthermore, we have seen that the existence of at least one

non-trivial equilibrium for arbitrary fitness functions is guaranteed. Finding or approximating such an equilibrium is difficult in general, since the system consists of $n+1$ variables and $n+1$ (generally) nonlinear equations, when there are $n+1$ subgroups in the population.

Simulation is quite popular in evolutionary game theory (e.g. Nachbar [1992], Hirshleifer and Martinez Coll [1992]) and evolutionary economics (e.g. Nelson and Winter [1982], Verspagen [1992]). However, simulation in order to find equilibria may be unpractical for a number of reasons. For large numbers of subgroups in a population, the simulated dynamics are less tractable and computational efforts become quite considerable. An additional difficulty is that admissible dynamics become very 'slow' near the boundaries of the unit simplex. It might therefore seem for long periods of time in the simulation, as if the system were converging to a certain point on such a boundary, while the equilibrium is located somewhere else. This phenomenon is termed **pseudo-convergence** in Nachbar [1992].

Furthermore, although the continuous-time dynamics may converge to a Nash(-type) equilibrium in the interior of the unit simplex, this need not be the case in simulation. In this context, Dekel and Scotchmer [1992] show that simulated dynamics approximating discrete-time replicator dynamics, may spiral outward to the boundary. Another problem which is related to the latter, is the problem of cycling, i.e., a certain sequence of points is repeated infinitely, without reaching an equilibrium. Firstly, detecting that the simulated dynamics cycle is not straightforward, and may require a rather large memory, since it may take many iterations before a sequence of points repeats itself, especially when the number of subgroups in the population is large. Secondly, there is the problem that simulated dynamics cycle, whereas the real dynamics converge to an equilibrium. In this context a recent paper by Weissing [1990] may serve as an illustration and a caveat. For relative fitness functions where continuous-time replicator dynamics exhibit (stable) limit cycles only for populations with four or more subgroups, Weissing shows existence of stable limit cycles already for three subgroups for discrete-time replicator dynamics. This implies that even if simulated evolutionary dynamics converge to a stable limit cycle from all interior points of the unit simplex, conclusions about the (non-)convergence of the real, i.e. continuous-time, evolutionary dynamics should not be based on the behavior of these simulated dynamics.

The force behind admissible dynamics is the relative fitness function. We have argued that such a function fulfills the requirements of an excess demand function for a pure exchange economy, namely continuity and a property which is known in economics as Walras' law. Continuing the analogy, admissible dynamics may be interpreted as a Walrasian tâtonnement process on the unit simplex (cf. Samuelson [1947], Uzawa [1961]). Many methods have been suggested to find equilibria of Walrasian tâtonnement processes, and they may also provide solutions to find certain equilibria of admissible dynamics for some relative fitness functions (e.g., Smale [1976]). However, the results of Saari and Simon [1978] and Saari [1985] suggest that, in order to find equilibria for dynamics based on **arbitrary** relative fitness functions, one should rely on Scarf-type algorithms (e.g., Scarf [1973]), and improvements (e.g., Eaves [1972], Todd [1976], Van der Laan and Talman [1979]).

One class of Scarf-type (simplicial) algorithms to solve the nonlinear complementarity problem, are the variable dimension restart algorithms (v.d.r.a.) originated by Van der Laan and Talman [1979]. Each algorithm in this class is globally convergent. An algorithm is called globally convergent in this context, if it converges to an approximation of an equilibrium for arbitrary excess demand (relative fitness) functions while being started from an arbitrary point of the unit simplex. A v.d.r.a. employs a simplicial subdivision of the unit simplex depending on the starting point of the algorithm. A piecewise linear path in a sequence of adjacent simplices of variable dimension, is generated connecting the starting point with an approximation of an equilibrium. When the accuracy of the approximation is not satisfactory, the algorithm is restarted in this point, using a finer simplicial subdivision. Thus a more accurate approximation is generally found. This procedure is repeated until a certain accuracy-level is reached. Several v.d.r.a.'s have been designed to solve the NLCP, which also solve the NTEP. The $(2^{n+1}-2)$ -ray algorithm of Doup *et al.* [1987] seems to be the most efficient for the NLCP. To describe such a v.d.r.a. with $2^{n+1}-2$ rays in detail would go beyond the scope of this paper. For $n = 2$, we give a graphic illustration of a path followed by this algorithm in Figure 5.1.

One might wonder if there does not exist a globally convergent algorithm to approximate an (asymptotically) stable equilibrium. To the best of our knowledge no such algorithm exists. Even if one were to be able to design an algorithm terminating

exclusively with an approximation of such an equilibrium, it may not terminate at all, since (asymptotically) stable equilibria need not exist (e.g., Scarf [1960]). Hence, this equilibrium concept is probably too restrictive for computational purposes. In this context, the non-trivial equilibrium seems to be useful for computational purposes. We have shown that the set NTE is never empty, and that NTE contains the sets SE and ASE. Furthermore, a non-trivial equilibrium can be approximated by a variable dimension restart algorithm under precisely the conditions which guarantee its existence.

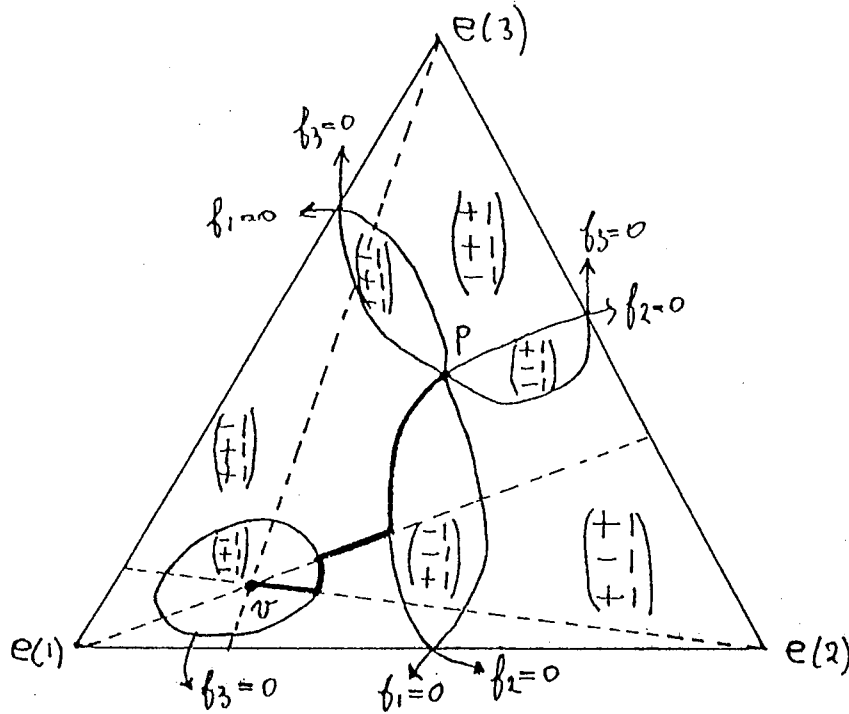


Figure 5.1. The algorithm approximately follows the heavy line from v to p . The rays leaving v are indicated by broken lines. Vector $(+1, -1, -1)^T$ denotes $(\text{sign } f_1(x), \text{sign } f_2(x), \text{sign } f_3(x))^T$ for all x of the corresponding set, whereas $f_i=0$ denotes a line of points where $f_i(x)=0$, $i=1,2,3$.

6. Conclusions

We have investigated an evolutionary model, relaxing several assumptions in literature with respect to the relative fitness functions and the population dynamics. We specified a class of dynamics, called admissible dynamics, and we defined an equilibrium concept for relative fitness functions, namely the non-trivial equilibrium. We showed that the set of non-trivial equilibria is nonempty for arbitrary relative fitness functions, and

that each non-trivial equilibrium is a fixed point for admissible dynamics. Furthermore, we demonstrated that every stable fixed point of admissible dynamics is a non-trivial equilibrium. For the 'traditional' game-theoretical evolutionary models a non-trivial equilibrium corresponds with a symmetric Nash equilibrium.

An 'evolutionary interpretation' of a non-trivial equilibrium is straightforward, namely that at a non-trivial equilibrium the composition of the population does not change over time, since every subgroup with positive population share has average fitness and every subgroup with below-average-fitness has population share equal to zero. At a non-trivial equilibrium no extinct subgroup has above-average fitness.

Furthermore, an evolutionary stable equilibrium was defined for given evolutionary dynamics. Such an equilibrium is an asymptotically stable equilibrium with attractive properties. Every trajectory starting in the neighborhood of an evolutionary stable equilibrium converges toward this equilibrium, and the Euclidean distance decreases strictly and monotonically over time along the trajectory.

There exist mathematical similarities between relative fitness functions and excess demand functions for pure exchange economies. A non-trivial equilibrium corresponds with an economic equilibrium, whereas admissible dynamics for a given relative fitness function correspond with a Walrasian tâtonnement process for an excess demand function of the same mathematical form. Since a parallel to the papers of Sonnenschein [1972, 1973], Mantel [1974] and Debreu [1974] is constructed in this paper for relative fitness functions, we should anticipate **any** dynamic process on the unit simplex as the outcome of admissible dynamics combined with **some** relative fitness function. Researchers trying to find dynamic equilibria, must therefore anticipate certain (computational) difficulties. It is known in economics, that multiple equilibria exist even in 'simple' cases (cf. Kehoe [1988]), and that tâtonnement-type dynamics based on excess demand functions, may possess stable limit cycles (cf. Scarf [1960]).

We proposed a two-step method to find non-trivial equilibria. First all vertices of the unit simplex are examined. We have shown that a strict non-trivial equilibrium is asymptotically stable and these equilibria are necessarily extreme points of the state space. To find other non-trivial equilibria and in particular interior non-trivial equilibria, variable dimension restart algorithms provide a solution. A variable dimension restart algorithm designed for the non-linear complementarity problem, converges to a non-

trivial equilibrium within a finite number of steps for arbitrary replicator dynamics under the conditions which guarantee existence of a non-trivial equilibrium. Variable dimension restart algorithms are quite efficient and for the problem considered the $(2^{n+1}-2)$ -ray algorithm of Doup *et al.* [1987] appears to be the most efficient in this class.

Having approximated a non-trivial equilibrium, further analysis on stability may be undertaken. We have defined an evolutionary stable equilibrium for which the conditions are readily checked. Each evolutionary stable equilibrium is an asymptotically stable equilibrium, but not conversely. Hence, if the check mentioned fails, the non-trivial equilibrium may still be (asymptotically) stable. Checking (asymptotical) stability usually either involves constructing a Lyapunov function in its neighborhood, or calculation of all eigenvalues of the matrix of partial derivatives of the dynamics at the equilibrium, provided these partial derivatives exist.

APPENDIX

Proofs of several propositions omitted above. The numbers refer to the propositions in the text.

Proof 3.1: Take $x \in S^n$, then $x^T f(x) = \sum_i x_i f_i(x) = \sum_i x_i (E_i(x) - \sum_j x_j E_j(x)) = \sum_i x_i E_i(x) - \sum_i x_i (\sum_j x_j E_j(x)) = \sum_i x_i E_i(x) - \sum_j x_j E_j(x) = 0.$ ■

Proof 3.3: Let $f: S^n \rightarrow \mathbb{R}^{n+1}$ be a relative fitness function and let $G: S^n \rightarrow \mathbb{R}^{n+1}$ be admissible. Let $x = e(i)$ for some $i \in I^{n+1}$, then $f_i(x) = E_i(x) - 1 E_i(x) - \sum_{j \neq i} 0 E_j(x) = 0$, hence $\text{sign } G_i(x) = G_i(x) = 0$. Furthermore, $x_j = 0$ for all $j \neq i$, which implies $G_j(x) = 0$ for all $j \neq i$. This leads to $G(x) = 0.$ ■

Proof 3.4: Let $f: S^n \rightarrow \mathbb{R}^{n+1}$ be a relative fitness function and let $G: S^n \rightarrow \mathbb{R}^{n+1}$ be admissible. Let $y \in S^n$ satisfy $f(y) \leq 0$. Then, from Proposition 3.1 it follows that for every $j \in I^{n+1}$ precisely one of the following situations occurs

- (a) $y_j > 0$ and $f_j(y) = 0$,
- (b) $y_j = 0$ and $f_j(y) \leq 0$.

Situation (a) implies $\text{sign } G_j(y) = \text{sign } f_j(y) = 0$, thus $G_j(y) = 0$. Situation (b) leads to $G_j(y) = 0$ since $y_j = 0$. Hence, $G(y) = 0.$ ■

Proof 3.5: Let $f: S^n \rightarrow \mathbb{R}^{n+1}$ be a relative fitness function and let F be the point-to-set mapping from S^n to the subsets of S^n , for every $x \in S^n$ defined by

$$F(x) = \text{conv}(\{e(j) \mid f_j(x) = \max_i f_i(x), i \in I^{n+1}\}).$$

Then F is upper-semicontinuous, and for every $x \in S^n$ the set $F(x)$ is nonempty, convex and compact. From Kakutani [1941], it follows that there exists $y \in S^n$, satisfying $y \in F(y)$. Let $c = \max_i f_i(y)$ and let $T = \{k \mid f_k(y) = c\}$. Since $y \in F(y)$ it follows that nonnegative numbers $\lambda_j, j \in T$, summing up to one, exist, such that

$$y = \sum_{j \in T} \lambda_j e(j).$$

Since $y_j = 0$ for all $j \notin T$, we obtain, using Proposition 3.1:

$$0 = \sum_{j \in T} y_j f_j(y) + \sum_{j \notin T} y_j f_j(y) = \sum_{j \in T} y_j f_j(y) = c (\sum_{j \in T} \lambda_j) = c.$$

Consequently, $\max_i f_i(y) = 0, i \in I^{n+1}$, which proves the proposition. ■

Proof 3.9: Let y be a non-trivial equilibrium for the relative fitness function f given by (6).

Let $T = \{j \mid f_j(y) = 0\}$. Since $y_j > 0$ leads to $f_j(y) = 0 = \max_i f_i(y)$, it follows that $y_j > 0$ implies $e(j)^T A y = \max_i e(i)^T A y, i \in I^{n+1}$.

Furthermore $j \notin T$ implies $e(j)^T A y < \max_i e(i)^T A y$, and $y_j = 0$.

By symmetry, (y, y) is a Nash equilibrium of the bimatrix game (A, A^T) . ■

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