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concepts in evolutionary game theory**

**by**

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# Paul Samuelson's critique and equilibrium concepts in evolutionary game theory\*

Reinoud Joosten<sup>†</sup>

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## Abstract

We present two new notions of evolutionary stability, the truly evolutionarily stable state (*TESS*) and the generalized evolutionarily stable equilibrium (*GESE*). The *GESE* generalizes the evolutionarily stable equilibrium (*ESE*) of Joosten [1996]. An *ESE* attracts all nearby trajectories monotonically, i.e., the Euclidean distance decreasing steadily in time. For a *GESE* this property should hold for at least one metric. The *TESS* generalizes the evolutionarily stable strategy (*ESS*) of Maynard Smith & Price [1973]. A *TESS* attracts nearby trajectories too, but the behavior of the dynamics nearby must be similar to the behavior of the replicator dynamics near an *ESS*.

Both notions are defined on the dynamics and immediately imply asymptotical stability for the dynamics at hand, i.e., the equilibrium attracts all trajectories sufficiently nearby. We consider this the relevant and conceptually right approach in defining evolutionary equilibria, rather than defining a static equilibrium notion and search for appropriate dynamics guaranteeing its dynamic stability. Moreover, the *GESE* and the *TESS* take similar positions as the *ESE* and *ESS* do in relation to other equilibrium and fixed point concepts in general.

**Key words:** evolutionary stability, evolutionary game theory.

**JEL-Codes:** A12; C62; C72; C73; D83

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\*Just a few days before the completion of this paper, Paul Samuelson, one of the early-day greats in economics and winner of The Sveriges Riksbank Prize in Economic Sciences in Memory of Alfred Nobel, passed away. In Samuelson [1941] he proved an advocate of defining stability of an economic equilibrium in terms of the dynamics of a system of price adjustment, instead of the prevailing practice to define stability properties of economic equilibria on the underlying economic system à la Hicks [1939]. See also Negishi [1962] for a similar evaluation and interpretation of Samuelson's critique. The concepts to be presented in our contribution, do withstand the general point made by Samuelson's critique and we have argued before (Joosten [1996, 2006]) and will argue again, that the *ESS* concept of Maynard Smith & Price [1973] fails to do so.

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## 1 Introduction

Evolutionary game theory originated in mathematical biology where it has found applications in the modeling of transformations of populations with several interacting subgroups. It is therefore, not surprising that several of the field's central concepts have a strong biological flavor, even though evolutionary game theory has become quite independent from its biological roots. The top two among concepts with such a flavor are probably the evolutionarily stable strategy and the replicator dynamics.

Central in the tradition initiated by Darwin [1859], is the idea of *natural selection*, i.e., fitter subgroups increase their population shares at the expense of less fit ones. A subgroup's fitness depends on its genetically predetermined features, on those of the other subgroups, and on the composition of the population.

Maynard Smith & Price [1973] combined game theory with Darwinian reasoning to explain animal behavior, and introduced the evolutionarily stable strategy (*ESS*). Each *ESS* is a Nash equilibrium of the game at hand, and is stable in the following sense. If a population, being at an *ESS*, is invaded by a small group using a strategy different from the one used by the resident population, then the fitness of this invading group is strictly lower in the strategic environment which arises by their invasion, than the fitness of the original population. The latter property is commonly referred to as (the) uninvadability (condition).

Taylor & Jonker [1978] introduced the replicator dynamics into the model of Maynard Smith and Price. They proved that each Nash equilibrium is a fixed point, and almost every *ESS* is an asymptotically stable fixed point of these dynamics. So, the conceptualization of the *ESS* predates the first actual proof of dynamic stability under evolutionary (Darwinian) dynamics and the latter kind of stability is to be regarded as the relevant one in a truly evolutionary context.

The good news of an attractive equilibrium concept and associated dynamics for which it is an attractor, i.e., an asymptotically stable fixed point, spread rapidly to areas outside biology. Dynamics, called evolutionary nowadays, have been used in the social sciences to model a variety of topics related to changing entities<sup>1</sup>, e.g., to model learning or selection processes, market share or migration dynamics, cf., e.g., Cross [1983], Friedman & Rosenthal [1986], Hansen & Samuelson [1988], Friedman [1991], Silverberg *et al.* [1988].

Originally, replicator dynamics were used in a metaphorical ('as if') man-

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<sup>1</sup>We refer to Witt [2008a] for a critical review on methods in evolutionary modeling in the social sciences in general, and Witt & Cordes [2007] for a more specific one. Evolutionary game theory has been quite passive in the more conceptual discussions in evolutionary economics, e.g., as between champions of Universal Darwinism (e.g., Hodgson & Knudsen [2006]) and opponents (e.g., Cordes [2006], Buenstorf [2006], Vromen [2004, 2006]). Yet, it can not be accused of shallowly accepting analogies or metaphors, as we will see.

ner, and formal justifications for replicator or other dynamics were lacking. Since approximately a decade ago, several contributions appeared tackling the justification theme, cf., e.g., Börgers & Sarin [1997], Schlag [1998,1999], Fudenberg & Levine [1998], Hofbauer & Sigmund [1998], Sethi [1998], Brenner [1999], Sandholm [2007]. Partial support for the value of these dynamics for modeling may be found in the experimental literature, e.g., Bush & Mosteller [1955], Roth & Erev [1995], Erev & Roth [1997], Cheung & Friedman [1997], Camerer & Ho [1999].

From the combined ‘justification’ and experimental literatures we may conclude that evolutionary dynamics may be used for modeling purposes in the social sciences indeed, but that the *replicator dynamics* are far from compelling outside biology. So, we must investigate wider classes of dynamics as plausible candidates for the formal modeling of evolving entities. The field has proven to be quite fertile and alternative classes of evolutionary dynamics have been proposed<sup>2</sup>, cf., e.g., Friedman [1991], Swinkels [1993], Ritzberger & Weibull [1995], Samuelson & Zhang [1992], Joosten [1996], Joosten & Roorda [2009], Harper [2009a,2009b].

Friedman [1991] defined the class of weakly compatible evolutionary dynamics which in the terminology of Joosten [1996] imply that the angle between the relative fitness vector and the vector representing the dynamics is never obtuse. Joosten [1996] introduced sign-compatible dynamics which imply that the population share of each non-extinct subgroup increases (decreases, stays the same) provided its relative fitness is positive (negative, or zero, respectively). Moreover, weakly sign-compatible dynamics were defined as dynamics such that the population share of at least one non-extinct subgroup having above-average fitness increases. Sign-compatible dynamics are both weakly compatible and weakly sign-compatible. A prominent example of sign-compatible dynamics is the replicator dynamics. The best-response dynamics of Matsui [1992], a deterministic version of the dynamics of Gilboa & Matsui [1991], are both weakly compatible and weakly sign-compatible, but not sign-compatible. Weak sign-compatibility need not imply weak compatibility, nor vice versa.

The theme of expanding the class of plausible evolutionary dynamics was taken up enthusiastically, as we have seen. Yet, the vast majority of work in evolutionary game theory remains faithful to its central equilibrium concept, the *ESS*. This is rather astonishing since the notion is defined essentially as a static concept, its dynamic stability only guaranteed for a small subclass in the rich classes of evolutionary dynamics just mentioned (see e.g., Hofbauer [2000], Lahkar & Sandholm [2008], Joosten & Roorda

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<sup>2</sup>We focus on deterministic dynamics (on a population level) and relevant equilibrium concepts. Readers interested in work using stochastic evolutionary dynamics requiring new types of equilibrium concepts dealing with this stochasticity, are referred to e.g., Gilboa & Matsui [1991], Fudenberg & Harris [1992], Kandori *et al.* [1993], Young [1993], Binmore & Samuelson [1994], Vega-Redondo [1996].

[2008] for examples). Furthermore, the *ESS* lacks, as do the replicator dynamics, a motivation outside the biological realm where it is quite unclear how to interpret the uninvadability condition.<sup>3</sup> Progress seems connected to finding new dynamics for which the *ESS* is an asymptotically stable fixed point, rather than coming up with viable alternatives to the *ESS*.

Friedman [1991] took an elegant but quite rigorous approach by defining all asymptotically stable fixed points of evolutionary dynamics as evolutionary equilibria (*EE*). No restrictions were posed on the dynamics or on the type of asymptotic stability, i.e., the behavior of the dynamics nearby. The *ESS* is not necessarily an *EE*, except for the replicator dynamics and a class of related dynamics; not even for the replicator dynamics every *EE* is an *ESS* (cf., e.g., Taylor & Jonker [1978], Weissing [1991]).

Joosten [1996] presented an evolutionary equilibrium concept directly based on dynamics, namely the evolutionarily stable equilibrium (*ESE*). The *ESE* was inspired by the *ESS* and by early work in economics by Arrow & Hurwicz [1958,1960a,b] and Arrow, Block & Hurwicz [1959]. On the one hand, the conditions defining *ESS* and *ESE* are very similar in mathematical form. Furthermore, an implication of *ESS* in biology happens to be mathematically equivalent to an implication of *WARP*, the Weak Axiom of Revealed Preference (Samuelson [1938]), in economics. Under *WARP* all trajectories under the price-adjustment process of Samuelson [1941] converge to the equilibrium and the Euclidean distance to it decreases monotonically over time along any such trajectory sufficiently close by. On the other, Samuelson's dynamics used by Arrow and coauthors do not yield dynamics applicable in an evolutionary framework. The *ESE* takes, so to speak, the consequence of *WARP* in the specific framework mentioned, namely *monotone convergence in the Euclidean distance for given dynamics*, as its *raison d'être*. Despite their technical and conceptual similarities, *ESS* and *ESE* coincide only for the a small class of evolutionary dynamics (see e.g., Joosten & Roorda [2008]).

Harper [2009a, 2009b] introduces an approach with respect to evolutionary dynamics and evolutionary equilibria inspired by information-geometric concepts, and concepts from statistical thermodynamics. In an original, unified approach he presents dynamics and equilibria in 'perfect' pairs. For instance, the so-called escort *ESS* is a suitable (static) evolutionary equilibrium concept for which the so-called escort replicator dynamics are precisely the dynamics for which it is an asymptotically stable fixed point. A particularly interesting (sub)class of escort dynamics is the class of *q*-deformed replicator dynamics. It turns out that two values of the scalar *q* yield well-known dynamics in evolutionary game theory; for *q* = 0 the deformed replicator dynamics are equal to the so-called orthogonal projection dynamics of

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<sup>3</sup>A rather successful interpretation is given e.g., by Witt [2008b, p.16 and onwards] in the context of social-cognitive (i.e., observational) learning.

Lahkar & Sandholm [2008], whereas for  $q = 1$  the deformed variant is actually equal to the standard version of the replicator dynamics. It remains unclear what the dynamic stability properties of, for instance, an escort *ESS* are if the perfect pair is broken up, i.e., alternative dynamics are taken.

Here, we present two novel evolutionary equilibrium concepts, namely the generalized evolutionarily stable equilibrium (*GESE*) and the truly evolutionarily stable state (*TESS*). The motivation of the new concepts is twofold. First, the notions are defined in terms of the behavior of the dynamics near the equilibrium. Most importantly, for these concepts asymptotic stability is guaranteed, but both put additional restrictions on the dynamics nearby. Second, the *GESE* and the *TESS* take very similar positions to the *ESE* and *ESS* with respect to other equilibrium or fixed point concepts for evolutionary dynamics.

The *GESE*-concept captures the main idea of monotone convergence to equilibrium as incorporated by the *ESE*, that for given dynamics all trajectories sufficiently nearby converge to the equilibrium approaching it monotonically for at least one distance function or metric. So, the distance to the equilibrium decreases monotonically over time measured by some (given) metric. Hence, every *ESE* is a *GESE* but not vice versa, and every *GESE* is an *EE*. For a huge number of formal results in geometry one can be quite imprecise as to which distance function one takes, for monotone convergence the metric is crucial. An equilibrium may attract all trajectories nearby monotonically in one metric, but not for another. By sticking to a definition based on one specific metric, as we did earlier in our definition of the *ESE* being a monotone attractor with respect to the Euclidean distance, one might be accused of introducing an undesirable arbitrariness. To deal with the latter aspect, we extend the scope of monotonicity to all metrics, not just the Euclidean or any other specific metric, in the sense described.

The *TESS*-notion is based on a refinement of asymptotic dynamic stability, too. Every *TESS* is asymptotically stable for the dynamics at hand, hence an *EE*, but not every asymptotically stable fixed point of a given dynamical system is a *TESS*. If applied to the ‘standard’ model in evolutionary game theory with replicator dynamics, our definition is equivalent to the *ESS*.<sup>4</sup> In the more general setting of Joosten [1996], our new definition of the *TESS* is equivalent to a *GESS* for the replicator dynamics, for other ones *TESS* and *GESS* need not coincide.

We demonstrate that the two novel concepts take similar yet distinct places in relation to other equilibrium and fixed point concepts, and quite similar to the one taken by the *ESS* in a standard evolutionary model using the replicator dynamics. We do not engage in any motivational attempts

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<sup>4</sup>Our major source of inspiration for the *TESS* was Weissing [1991], who deals with discrepancies between the *ESS* and the *EE* in the context of so-called generalized Rock-Scissor-Paper games, but whose approach seems unfeasible for more general traditional evolutionary games, let alone the generalizations introduced in Joosten [1996].

beyond a dynamic one and a positioning one with regards to other equilibrium notions. Clearly, the dynamics are the only aspect in common among the evolutionary approaches in the social sciences, which suggests that it is a ‘natural’ overarching motivation. Moreover, any alternative motivation geared to an application in one type of evolutionary modeling, is bound to be ill-fitted in another.

In the next section, we define several notions to be used, in Section 3 we present the generalized evolutionarily stable equilibrium and show connections to equilibrium concepts in evolutionary game theory. In Section 4 we introduce the truly evolutionarily stable state and show how relations to other equilibrium concepts. Section 5 concludes. All proofs can be found in the Appendix. We stick to the usual language of mathematical biology throughout the paper for lack of an alternative.

## 2 Evolutionary dynamics and equilibria

Let  $x \in S^n$  denote a vector of population shares for a population with  $n + 1$  distinguishable, interacting subgroups. Here,  $S^n$  is the  $n$ -dimensional unit simplex, i.e., the set of all non-negative  $n + 1$ -dimensional vectors with components adding up to unity. The interaction of the subgroups has consequences on their respective abilities to reproduce, and ‘fitness’ may be seen as a measure of this ability to reproduce. As behavior of each subgroup is assumed essentially predetermined, fitness depends only on the state of the system, i.e., the composition of the population.

Let  $F : S^n \rightarrow \mathbb{R}^{n+1}$  be a **fitness function**, i.e., a continuous function attributing to every subgroup its fitness at each state  $x \in S^n$ . Then, the **relative fitness function**  $f : S^n \rightarrow \mathbb{R}^{n+1}$  is given by:

$$f_i(x) = F_i(x) - \sum_{j=1}^{n+1} x_j F_j(x), \text{ for all } i \in I^{n+1}, \text{ and } x \in S^n.$$

So, a relative fitness function attributes to each subgroup the difference between its fitness and the population share weighted average fitness taken over all subgroups.

In the sequel, we assume that there exists a given function  $h : S^n \rightarrow \mathbb{R}^{n+1}$  satisfying  $\sum_{j=1}^{n+1} h_j(x) = 0$  for all  $x \in S^n$ . Consider this system of  $n + 1$  autonomous differential equations:

$$\dot{x} = \frac{dx}{dt} = h(x) \text{ for all } x \in S^n, \quad (1)$$

where  $\frac{dx}{dt}$  denotes the continuous-time changes of the vector  $x \in S^n$ . A **trajectory** under the dynamics  $h$  is a solution,  $\{x(t)\}_{t \geq 0}$ , to  $x(0) = x_0 \in S^n$  and Equation (1) for all  $t \geq 0$ . We refrain from placing too many mathematical restrictions on  $h$  at this point, we do require existence and uniqueness of trajectories. Continuity of  $h$  implies existence, and Lipschitz

continuity or differentiability implies uniqueness. However, some interesting evolutionary dynamics are neither differentiable, nor continuous. We refer to Perko [1991] as an excellent textbook on differential equations and dynamics.

The evolution of the composition of the population is represented by system (1). To make sense in an evolutionary framework further restrictions on the system are required. The function  $h$  is therefore assumed to be connected to the relative fitness function  $f$  in one of the many ways proposed in the literature, cf., e.g., Nachbar [1990], Friedman [1991], Swinkels [1993], Joosten [1996], Ritzberger & Weibull [1995]. For so-called **sign-compatible** Darwinian dynamics, the change in population share of each subgroup with positive population share corresponds in sign with its relative fitness; for **weakly sign-compatible** Darwinian dynamics, at least one subgroup with positive relative fitness grows in population share.<sup>5</sup> An alternative class is defined by Friedman [1991], Darwinian dynamics are **weakly compatible** if  $f(x) \cdot h(x) \geq 0$  for all  $x \in S^n$ . Sign-compatible dynamics are weakly compatible, not vice versa.

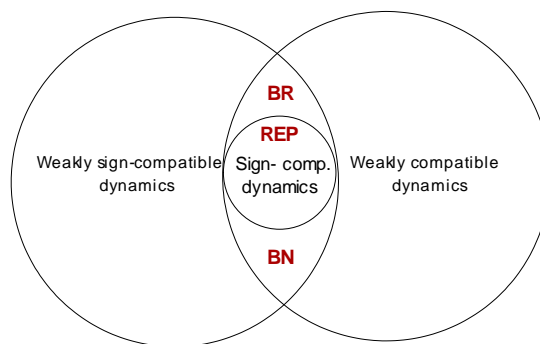


Figure 1: A Venn-diagram representing connections between different classes of evolutionary dynamics. *REP* denotes the replicator dynamics, *BR* the best-response dynamics and *BN* the dynamics of Brown & Von Neumann.

The state  $y \in S^n$  is a **saturated equilibrium** if  $f(y) \leq \mathbf{0}^{n+1}$ , a **fixed point** if  $h(y) = \mathbf{0}^{n+1}$ ; a fixed point  $y$  is **(asymptotically) stable** if, for any neighborhood  $U \subset S^n$  of  $y$ , there exists an open neighborhood  $V \subset U$  of  $y$  such that any trajectory starting in  $V$  remains in  $U$  (and converges to  $y$ ). A saturated equilibrium  $y \in S^n$  is called **strict** if  $f_j(y) = 0$  for precisely one  $j \in I^{n+1}$  in an open neighborhood  $U \subset S^n$  of  $y$ . It should be noted that strictness of a saturated equilibrium immediately implies that it is a vertex

<sup>5</sup>These classes are due to Joosten [1996]. There are more than a few connections between sign-compatible dynamics and excess payoff dynamics of Sandholm [2005].



of the unit simplex. The saturated equilibrium was introduced by Hofbauer & Sigmund [1988], the strict version is due to Joosten [1996].

At a saturated equilibrium all subgroups with below average fitness have population share equal to zero. So, rather than ‘survival of the fittest’, we have ‘extinction of the less fit’. If the fitness function is given by  $F(x) = Ax$  for some square matrix  $A$ , every (strict) saturated equilibrium coincides with a (strict) Nash equilibrium of the evolutionary bi-matrix game  $(A, A^\top)$ .

**Example 1** *The replicator dynamics (Taylor & Jonker [1978]), given by*

$$h_i(x) = x_i f_i(x) \text{ for all } i \in I^{n+1}, x \in S^n,$$

*are sign-compatible. It can be easily confirmed that  $f(y) \leq \mathbf{0}^{n+1}$  and  $y \cdot f(y) = \mathbf{0}^{n+1}$ , imply  $y_i > 0$  and  $f_i(y) = 0$ , or  $y_i = 0$  and  $f_i(y) \leq 0$ ; therefore  $h(y) = \mathbf{0}^{n+1}$ . This means that every saturated equilibrium is a fixed point of the replicator dynamics. However, note that for  $e_i$ , i.e., the  $i$ -th vertex of the unit simplex  $S^n$ ,  $h(e_i) = \mathbf{0}^{n+1}$  as well. ■*

The fixed point  $y \in S^n$  is a **generalized evolutionarily stable state** (*GESS*, Joosten [1996]) if and only if there exists an open neighborhood  $U \subset S^n$  of  $y$  satisfying

$$(y - x) \cdot f(x) > 0 \text{ for all } x \in U \setminus \{y\}. \quad (2)$$

A geometric interpretation of (2) is that the angle between the vector pointing from  $x$  towards the equilibrium, i.e.,  $(y - x)$ , and the relative fitness vector  $f(x)$  is always acute. The *GESS* generalizes the *ESS*, the evolutionarily stable strategy, of Maynard Smith & Price [1973] in order to deal with *arbitrary* (relative) fitness functions.

Taylor & Jonker [1978] introduced the replicator dynamics into mathematical biology and gave conditions guaranteeing that each *ESS* is an asymptotically stable fixed point of these dynamics. Zeeman [1981] extended this result and pointed out that the conditions formulated by Taylor & Jonker [1978] are almost always satisfied. The most general result on asymptotic stability regarding the replicator dynamics for the *ESS* is Hofbauer *et al.* [1979] as it stipulates an equivalence of the *ESS* and existence of a Lyapunov function of which the time derivative is equal to Eq. (2).

Friedman [1991] took an elegant way of coping with evolutionary stability as he defined any asymptotically stable fixed point of given evolutionary dynamics as an evolutionary equilibrium (*EE*). Most approaches however, deal with conditions on the underlying system in order to come up with a viable evolutionary equilibrium concept, or deal with refinements of the asymptotically stable fixed point concept (e.g., Weissing [1991]).

In Joosten [1996,2006] we argued against defining an evolutionary equilibrium concept in a static manner. We also noted that early economics took

a similar path of development of concepts. Hicksian stability of an equilibrium (cf., Hicks [1939]) can be seen as a conceptual relative to the *ESS* in biology. In economics, Samuelson [1941] became the great advocate of studying dynamics directly instead of the underlying system driving them. However, the indirect approach, i.e., deriving conditions on the underlying system guaranteeing stability of equilibrium for some class of dynamics, was never completely abandoned. See Uzawa [1961] and Negishi [1962] for relevant overviews.

Joosten [1996] defined an evolutionary equilibrium concept on the dynamic system, wishing to rule out some asymptotically stable fixed points. Namely, the ones which induce trajectories starting nearby, but going far away from the equilibrium before converging to it in the end. The fixed point  $y \in S^n$  is an **evolutionarily stable equilibrium** if and only if there exists an open neighborhood  $U \subset S^n$  of  $y$  satisfying

$$(y - x) \cdot h(x) > 0 \text{ for all } x \in U \setminus \{y\}. \quad (3)$$

A geometric interpretation of (3) is that sufficiently close to the equilibrium the angle between  $(y - x)$  and the vector representing the direction of the dynamics is always acute. Note the striking similarity between Equations (2) and (3), where the relative fitness function and the function representing the dynamics take equivalent positions in the expressions. Yet, (2) does not imply (3), nor vice versa. Equivalence of (2) and (3) is guaranteed for the orthogonal projection dynamics of Lahkar & Sandholm [2008] as commented upon in Joosten & Roorda [2008]. Hofbauer & Sandholm [2009] proved that *ESS* is sufficient for monotone convergence in the Euclidean distance from all interior states for all so-called stable games under the orthogonal projection dynamics.

The evolutionarily stable equilibrium concept was inspired by the Euclidean distance approach of early contributions in economics, e.g., Arrow & Hurwicz [1958,1960a,b] and Arrow, Block & Hurwicz [1959], since under *WARP* and Samuelson's simultaneous tâtonnement process (i.e., Eq. (3) with  $h(x) = f(x)$ ) implies that the squared Euclidean distance is a (strict) Lyapunov function for  $U$ . Let namely,

$$V(x) = (y - x) \cdot (y - x),$$

then clearly  $V(y) = 0$ ; moreover,  $V(x) > 0$ , and  $\dot{V}(x) = -2(y - x) \cdot h(x) < 0$  whenever  $x \in U \setminus \{y\}$ . Note that  $h$  does not induce dynamics on the unit simplex, but on a ball with the origin as its center.

### 3 Generalized evolutionarily stable equilibria

Each evolutionarily stable equilibrium (*ESE*) is an asymptotically stable fixed point of the dynamics at hand as the Euclidean distance to the equi-

librium decreases monotonically along every trajectory sufficiently near the equilibrium. We now turn to generalizing this concept, where the generalization also depends directly on the dynamics.

**Definition 2** *Given relative fitness function  $f : S^n \rightarrow \mathbb{R}^{n+1}$  and evolutionary dynamics  $h : S^n \rightarrow \mathbb{R}^{n+1}$ , let  $d : \mathbb{R}^{n+1} \times \mathbb{R}^{n+1} \rightarrow \mathbb{R}$  be a distance function,  $\xi : \mathbb{R}_+ \cup \{0\} \rightarrow \mathbb{R}$  be differentiable, and monotonically strictly either decreasing or increasing, with  $\xi(0) = \xi_0$ . Let furthermore,  $V : \mathbb{R}^{n+1} \times \mathbb{R}^{n+1} \rightarrow \mathbb{R}$  be given by*

$$V(x, y) = \xi(d(x, y)) \text{ for all } x, y \in \mathbb{R}^{n+1}.$$

*Then,  $y \in S^n$  is a **generalized evolutionarily stable equilibrium** if and only if an open neighborhood  $U \subseteq S^n$  containing  $y$ , exists such that for all  $x \in U \setminus \{y\}$  it holds that  $[V(x, y) - \xi_0] \cdot \dot{V}(x, y) < 0$ , where  $\dot{V}(x, y) = \sum_{i=1}^{n+1} \frac{\partial V}{\partial x_i} h_i(x)$ .*

In words, the function  $V$  above is a monotone transformation of a distance function. Under the dynamics the function increases (decreases) in time close to a local maximum (minimum).

We show now that each generalized evolutionarily stable equilibrium (*GESE*) is an asymptotically stable fixed point of the dynamics attracting all trajectories nearby monotonically for at least one metric.

**Theorem 3** *Each generalized evolutionarily stable equilibrium is an asymptotically stable fixed point for the dynamics at hand, and along any trajectory sufficiently nearby the distance to the equilibrium decreases monotonically in time for at least one metric.*

The name generalized evolutionarily stable equilibrium is motivated by the circumstance that replacing the function  $V$  above by the squared Euclidean distance, yields the definition of an *ESE*. Namely, take  $\xi(x) = x^2$  for all  $x \in \mathbb{R}$  and  $d(x, y) = d_2(x, y)$  where  $d_2(x, y)$  is the Euclidean distance, then it follows that an *ESE* is a special case of a *GESE*.

**Corollary 4** *Each evolutionarily stable equilibrium is a generalized evolutionarily stable equilibrium.*

Essentially, Definition 2 implies that along any trajectory of the dynamics sufficiently near the *GESE* converges to it with at least one distance (not necessarily the Euclidean) decreasing monotonically in time. So, for this distance function at least, the convergence towards the equilibrium is very well-behaved and it is excluded that any trajectory sufficiently close by moves away from it before finally converging to it.

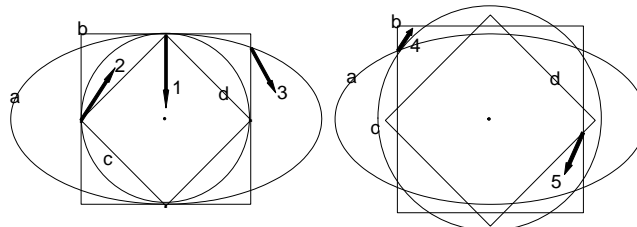


Figure 2: Monotonic convergence in one metric need not imply the same in another. Here,  $a, b, c$  and  $d$  denote level curves with respect to the equilibrium  $y$  of four different types of distance functions. Left: for dynamics 1 all distances decrease; dynamics 2 approach  $y$  in type  $c$  but not in type  $d$  metric; for 3 the distance decreases for type  $a$  but not for type  $b$ . Right: dynamics 4 move closer to  $y$  for  $b$ , not for  $c$ , 5 move closer to  $y$  for  $b$ , not for  $d$ . Four types induce 24 similar discrepancies.

By now, the reader may have understood that unlike for many results in topology and geometry where distance functions are essentially equivalent, for monotonic convergence as meant above, distance functions are not. Figure 2 may serve to illustrate this point.

Although Definition 2 implies the existence of a Lyapunov function as shown in the proof of the result following it, it is not true that asymptotic ‘Lyapunov’ stability implies evolutionary stability in the sense described. Even if only evolutionary dynamics are considered (as the definition demands) not every Lyapunov stable fixed point of the dynamics is a generalized evolutionarily stable equilibrium. For instance, the level curves of the Lyapunov functions implied by Definition 2 can not take any form as the triangular inequality must hold. The latter implies that the sets of points enclosed by those level curves are convex. So, ‘Lyapunov stability’ is a less stringent requirement than evolutionary stability as formulated in Definition 2, but a more stringent requirement than asymptotic stability.

### 3.1 Relations to other equilibrium concepts

Recently, Hofbauer & Sandholm [2009] introduced an interesting class of games, called strictly stable games. A game is strictly stable iff

$$(y - x) \cdot (F(y) - F(x)) < 0 \text{ for all } x, y \in S^n, x \neq y$$

which straightforwardly translates into our notations as

$$(y - x) \cdot (f(y) - f(x)) < 0 \text{ for all } x, y \in S^n, x \neq y.$$

If an equilibrium  $y \in S^n$  is located in the interior of the unit simplex, it follows furthermore that

$$(y - x) \cdot f(x) > 0 \text{ for all } x \in S^n \setminus \{y\}.$$

Since every interior equilibrium of a stable game satisfies (2) for the entire state space, the following is immediate.

**Corollary 5** *Every interior equilibrium of a strictly stable game is a GESS.*

It is well established that every *ESS* is an asymptotically stable fixed point of the replicator dynamics (cf., e.g., Taylor & Jonker [1978], Zeeman [1981], Hofbauer *et al.* [1979]). An analogous result was proven in Joosten [1996] with respect to the generalized evolutionarily stable state. However, an interior equilibrium of a strictly stable game, can be shown an asymptotically stable fixed point of many types of evolutionary dynamics<sup>6</sup>, cf., Joosten [2006], Joosten & Roorda [2008], Hofbauer [2000], Hopkins [1999].

To show connections between the *GESS* and *GESE*, we need to introduce two rather new evolutionary dynamics.

**Definition 6** (Joosten & Roorda [2008]) *The ray-projection dynamics are for the interior of the unit simplex given by*

$$h_i^r(x) = f_i(x) - x_i \sum_{k \in I^{n+1}} f_k(x). \quad (4)$$

**Definition 7** (Lahkar & Sandholm [2008]) *The orthogonal-projection dynamics for the interior of the unit simplex are given by*

$$h_i^o(x) = f_i(x) - \frac{1}{n+1} \sum_{k \in I^{n+1}} f_k(x). \quad (5)$$

These dynamics can be regarded as projections of the vector  $f(x)$  at  $x \in S^n$  unto the unit simplex. As the names suggest, in one variant a projection along a ray is chosen and in the other an orthogonal projection (see Joosten & Roorda [2008] for more detailed descriptions).

Now, we are ready to present the following results connecting (*G*)*ESS* stability to real, i.e., dynamic, evolutionary stability.

<sup>6</sup>The property defining a (strictly) stable game is called (strong) monotonicity in economics (see Joosten [2006]). Many results link monotonicity to stability, e.g., Nikaidô [1959] who was in turn inspired by Brown & Von Neumann [1950].

**Proposition 8** *Let  $y \in \text{int } S^n$ . For the orthogonal-projection dynamics*

- *$y$  is a GESS implies  $y$  is a GESE,*
- *$y$  is an ESE implies that  $y$  is a GESS.*

Joosten & Roorda [2008] prove that every interior evolutionarily stable state is an asymptotically stable fixed point of the ray-projection dynamics. We now prove a slightly more precise statement.

**Proposition 9** *Every interior GESS is a GESE for the ray-projection dynamics.*

The converse statement of the proposition does not hold. However, every interior ESE for the ray-projection dynamics is a GESS (cf., Joosten & Roorda [2008]).

Joosten & Roorda [2008] formulated two generalized projections of the price-adjustment dynamics of Nikaidô & Uzawa [1960]. The latter dynamics are defined component-wise and for strictly positive  $\rho$  by

$$g_i^\rho(x) = \max\{0, \rho f_i(x) + x_i\} - x_i \text{ for all } i \in I^{n+1}. \quad (6)$$

Here,  $x \in S^n$  is a vector of relative prices normalized to add up to unity, and  $f(x)$  is a generalized excess demand function, i.e., a function characterized by continuity and Walras' law, i.e.,  $x \cdot f(x) = 0$  for all  $x \in S^n$ . In Joosten [1996, 2006] many formal correspondences were shown between concepts in mathematical biology and mathematical economics. To be interesting for application in an evolutionary framework in game theory, it should hold that the dynamics are defined on the unit simplex and stay there. It is obvious, however, that these price-adjustment dynamics do not induce trajectories on the unit simplex. Using the approach introduced in Joosten & Roorda [2008], we project the dynamics of Nikaidô & Uzawa [1960] on the unit simplex and obtain as evolutionary dynamics:

$$h_i^r(x) = \max\{0, \rho f_i(x) + x_i\} - x_i \sum_{j=1}^{n+1} \max\{0, \rho f_j(x) + x_j\}, \quad (7a)$$

$$h_i^o(x) = \max\{0, \rho f_i(x) + x_i\} - x_i + \frac{1}{n+1} - \frac{1}{n+1} \sum_{j=1}^{n+1} \max\{0, \rho f_j(x) + x_j\}, \quad (7b)$$

where  $x \in S^n$ , and superscripts  $r$  and  $o$  denote ray projection respectively orthogonal projection. By continuity of the relative fitness function  $f$ , it

holds for every interior saturated equilibrium that a neighborhood  $U$  containing  $y$  exists such that  $\rho f_i(x) + x_i > 0$  for all  $i \in I^{n+1}$ ,  $x \in U$ . Then, this implies that for all  $i \in I^{n+1}$ ,  $x \in U$  :

$$\begin{aligned} h_i^r(x) &= \rho f_i(x) + x_i - x_i \sum_{j=1}^{n+1} (\rho f_j(x) + x_j) \\ &= \rho f_i(x) + x_i - x_i - x_i \sum_{j=1}^{n+1} \rho f_j(x) = \rho \left[ f_i(x) - x_i \sum_{j=1}^{n+1} f_j(x) \right]. \end{aligned}$$

Similarly, we obtain for all  $i \in I^{n+1}$ ,  $x \in U$  :

$$h_i^o(x) = \rho \left[ f_i(x) - \frac{1}{n+1} \sum_{j=1}^{n+1} f_j(x) \right].$$

Since both generalized projection dynamics are a multiple of the corresponding projection dynamics, the results of this section apply. Hence, the validity of the following is immediate.

**Corollary 10** *Let  $y$  be an interior GESS. Then,  $y$  is a GESE for (7a), moreover  $y$  is a GESE for (7b).*

We now recall a result from Joosten [1996] where it was shown that every strict saturated equilibrium (SSAT) is an asymptotically stable fixed point for all weakly sign-compatible evolutionary dynamics. In the proof of this result it was shown that

$$V(x) = 1 - x_i$$

is a strict Lyapunov function near the strict saturated equilibrium  $e(i)$ , where  $e(i) \in S^n$  is the vertex determined by  $e(i)_i = 1$ . Observing that this function can be rewritten as

$$V(x) = d_\infty(e(i), x) = \lim_{p \rightarrow +\infty} \left( \sum_{j=1}^{n+1} |e(i)_j - x_j|^p \right)^{1/p},$$

we may immediately draw the following conclusion.

**Corollary 11** *Every SSAT is a GESE for all weakly sign-compatible evolutionary dynamics.*

This result means that such a strict saturated equilibrium is an asymptotically stable fixed point for a very large collection of dynamics plausible for modeling evolutionary processes. Moreover, the distance measured in the

so-called maximum norm decreases monotonically in time for each trajectory started sufficiently close to the equilibrium.

We now give an overview of the results presented in this section. The abbreviations *ASFP*, *SFP*, *FP*, *SSAT* and *SAT* mean the sets of asymptotically stable fixed points, stable fixed points, fixed points, strict saturated equilibria, and saturated equilibria respectively. Here, we abuse notations introduced somewhat by using them for the corresponding sets as well.

**Summary** We have the following relations with respect to the generalized evolutionarily stable equilibrium.

- For arbitrary evolutionary dynamics  $GESE \subseteq ASFP \subseteq SFP \subseteq FP$ .
- For weakly sign-compatible dynamics  $SSAT \subseteq GESE \subseteq ASFP \subseteq SFP \subseteq FP$ .
- For sign-compatible dynamics  $SSAT \subseteq GESE \subseteq ASFP \subseteq SFP \subseteq SAT \subseteq FP$ .
- For orthogonal- and ray-projection dynamics  $SSAT \subseteq GESS \subseteq GESE$ .
- For the generalized orthogonal- and ray-projections of the dynamics of Nikaidô & Uzawa [1960]  $GESS \subseteq GESE$ .

## 4 Truly evolutionarily stable states

The generalization of the *ESS* to be presented here, is inspired by this concept, but avoids the traditional mistake of defining a static evolutionary equilibrium concept.

**Definition 12** *Let relative fitness function  $f : S^n \rightarrow \mathbb{R}^{n+1}$  and evolutionary dynamics  $h : S^n \rightarrow \mathbb{R}^{n+1}$  be given. Let furthermore  $C(z) = \{i \in I^{n+1} \mid z_i > 0\}$  for all  $z \in S^n$  and let  $S^n(S) = \{x \in S^n \mid x_i > 0 \text{ for all } i \in S \subset I^{n+1}\}$ . Then, the state  $y \in S^n$  is a **truly evolutionarily stable state** iff*

- a.  $h(y) = 0^{n+1}$ ;
- b. a nonempty open neighborhood  $U \subset S^n(C(y))$  containing  $y$  exists such that

$$\sum_{i \in C(y)} (y_i - x_i) \frac{h_i(x)}{x_i} - \sum_{i \notin C(y)} h_i(x) > 0.$$

Condition (a) guarantees that the truly evolutionarily stable state (*TESS*) is indeed a fixed point of the evolutionary dynamics. Condition (b) guarantees the stability of the equilibrium as we are about to prove. The latter condition applied to interior fixed points is closely related to the so-called



Shahshahani-gradient, introduced by Shahshahani [1979] and employed to prove asymptotic stability of *ESS* for the replicator dynamics by e.g., Sigmond [1985].

Our major source of inspiration for the *TESS* was Weissing [1991], who deals with discrepancies between the *ESS* and the *EE*. Weissing analyzes generalized Rock-Scissor-Paper (*RSP*) games with the replicator dynamics. In the standard *RSP* game all trajectories cycle around a unique interior fixed point of the replicator dynamics. This Nash equilibrium is therefore neither unstable, nor asymptotically stable, but merely stable. Changing the structure of the *RSP* game slightly, as the class of generalized *RSP* games allows, turns the Nash equilibrium into an asymptotically stable fixed point of the replicator dynamics, or into a repeller, a point from which all trajectories nearby move away. Weissing stops short of presenting a concept generalizing the *ESS*. He demonstrates that some *EE*, while not being *ESS*'s, can be turned into an *ESS* by applying a so-called barycentric transformation. This approach seems hardly generalizable to our framework as relative fitness functions are characterized by continuity and complementarity, but it inspired us to introduce the above.

To show asymptotic stability of a *TESS*, we use a variant of the second method of Lyapunov introduced by Uzawa [1961]. For this method it suffices to show that a function bounded from above exists having a time derivative which is strictly positive in an open neighborhood of a fixed point (cf., e.g., Perko [1991]).

**Theorem 13** *Every TESS is an asymptotically stable fixed point of the dynamics at hand.*

#### 4.1 Relations to other equilibrium concepts

The following extends results from Joosten [1996] to the present generalization of the *ESS* concept. The validity of the statement follows from the fact that every *TESS* is asymptotically stable, whereas a result in Joosten [1996] states that all asymptotically stable fixed point of weakly sign-compatible dynamics belong to the set of saturated equilibria.

**Corollary 14** *Every TESS of weakly sign-compatible dynamics is a saturated equilibrium.*

The converse statement does not hold, as unstable interior fixed points of weakly-sign compatible dynamics are saturated equilibria, which would yield a contradiction with the previous result.

The following minor result is not implied by any previous one known to us, but its proof is certainly inspired by a similar one in Joosten [1996].

**Lemma 15** *Every strict saturated equilibrium is a TESS for all weakly sign-compatible dynamics.*

This means that a strict saturated equilibrium combines a large number of properties desirable in evolutionary modeling. Not only is every strict saturated equilibrium a *TESS* for a large family of evolutionary dynamics, it is a (*G*)*ESS* regardless of the dynamics and it is a *GESE* for weakly sign-compatible dynamics.

One may wonder what the relation of the *TESS* to the *GESS* is. The following result sheds some light on this question.

**Proposition 16** *For the replicator dynamics,  $y$  is a *TESS* if and only if  $y$  is a *GESS*.*

So, we may regard the *TESS* as a generalization of the *GESS* concept with respect to the dynamic stability properties holding for a set of evolutionary dynamics of which the replicator dynamics are a special example.

**Summary** We have the following relations with respect to the truly evolutionarily stable state.

- For arbitrary evolutionary dynamics  $TESS \subseteq ASFP \subseteq SFP \subseteq FP$ .
- For weakly sign-compatible dynamics  $SSAT \subseteq TESS \subseteq ASFP \subseteq SFP \subseteq FP$ .
- For sign-compatible dynamics  $SSAT \subseteq TESS \subseteq ASFP \subseteq SFP \subseteq SAT \subseteq FP$ .
- For weakly compatible dynamics  $TESS \subseteq ASFP \subseteq SFP \subseteq SAT \subseteq FP$ .
- For the replicator dynamics  $TESS = GESS$ .

Figure 3 visualizes connections between concepts introduced in this paper.

## 5 Conclusion

We presented two equilibrium concepts for evolutionary modeling in the social sciences, the generalized evolutionarily stable equilibrium (*GESE*) and the truly evolutionarily stable strategy (*TESS*). Each *GESE* attracts all trajectories nearby such that the distance to the equilibrium decreases monotonically over time. An *ESE* (Joosten [1996]) is a special example in the class, as the concept implies monotonic convergence it with respect to the Euclidean distance.

The *TESS* is a generalization of the generalized evolutionarily stable state (*GESS*, Joosten [1996]) which is in itself a generalization of the evolutionarily stable strategy of Maynard Smith & Price [1973]. The *GESS* allows

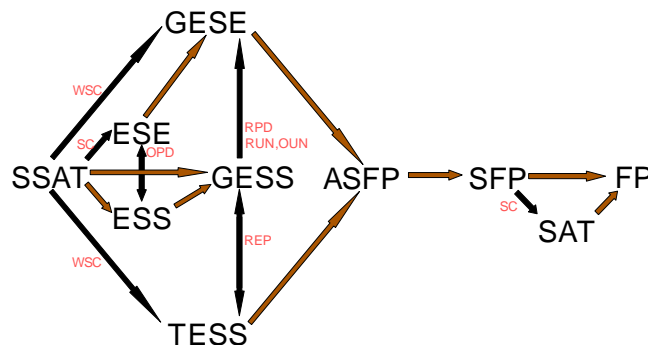


Figure 3: An overview of equilibrium concepts under evolutionary dynamics. Arrows indicate inclusions; brown arrows are inclusions holding in general; otherwise the notation implies the inclusion for special (classes of) dynamics.  $(W)SC$  denotes (weakly) sign-compatible dynamics;  $RPD$ ,  $OPD$ ,  $REP$  denote ray-projection, orthogonal-projection respectively replicator dynamics.  $RUN$  ( $OUN$ ) are the generalized ray (orthogonal) projections of the dynamics of Nikaidô & Uzawa [1960].

essentially all continuous fitness functions, where the original approach and definitions of Maynard Smith & Price [1973] only allow bi-linear continuous ones. So, in many models the  $GESE$  and  $ESS$  concepts coincide. Moreover, the  $GESE$  concept implies asymptotic stability of the replicator dynamics of Taylor & Jonker [1978].  $TESS$  implies asymptotic stability of the dynamics under consideration and in the special case that the replicator dynamics are examined the  $TESS$  and  $GESE$  coincide. Hence, in the original model of Maynard Smith & Price [1973] examined under the assumption that the population evolves according to the replicator dynamics, the  $TESS$  and  $ESS$  coincide.

With this contribution we in fact open a discussion and a critical evaluation of equilibrium concepts in evolutionary modeling.<sup>7</sup> We defined two new equilibrium notions being ‘refinements’ of the well-known asymptotic stability concept for deterministic dynamics. However, anyone could come up with alternative ideas for refinements, and there is hardly any one way to decide which concept should be preferred to another. To structure a discus-

<sup>7</sup>The discussion will be very short if a vast majority of the field is satisfied with the approach taken by Friedman [1991], where all asymptotically stable fixed points of evolutionary dynamics are defined as evolutionary equilibria, suffices. Certainly, these equilibria will withstand Samuelson’s critique, but on the one hand, refinements might be required for meaningful evolutionary equilibrium concepts, on the other this critique might not be the only possible one.

sion on appropriate properties regarding evolutionary equilibrium concepts the field may turn to axiomatics, i.e., formulating a set of desirable properties that a ‘good’ concept should have and then select among the total of imaginable ones a subset or ideally a singleton fulfilling them.

Axiomatic approaches are not alien to game theory as these have been applied to solution concepts in cooperative game theory (see e.g., Peleg & Sudhölter [2003]). Neither are they alien to the social sciences as demonstrated for instance in consumer theory in economics, cf., e.g., Varian [1992] for an excellent textbook on the matter. Somewhat closer to the framework of this paper is the work of Sandholm where axioms (called desiderata) are formulated in order to motivate or reject certain evolutionary dynamics (see e.g., Sandholm [2005,2007]). Future research should aid in devising criteria to select among equilibrium concepts in evolutionary theorizing in the social sciences, i.e., beyond the framework of mathematical biology.

## 6 Appendix

**Proof of Theorem 3.** Let relative fitness function  $f : S^n \rightarrow \mathbb{R}^{n+1}$  and evolutionary dynamics  $h : S^n \rightarrow \mathbb{R}^{n+1}$  be given. Let  $y$  be a *GESS*. So, the following items exist.

- A distance function  $\tilde{d} : \mathbb{R}^{n+1} \times \mathbb{R}^{n+1} \rightarrow \mathbb{R}$ ;
- A differentiable function  $\tilde{\xi} : \mathbb{R}_+ \cup \{0\} \rightarrow \mathbb{R}$  which is monotonically strictly either decreasing or increasing, with  $\tilde{\xi}(0) = \tilde{\xi}_0$ ;
- A function  $\tilde{V} : \mathbb{R}^{n+1} \times \mathbb{R}^{n+1} \rightarrow \mathbb{R}$  given by

$$\tilde{V}(x, y) = \tilde{\xi}(\tilde{d}(x, y)) \text{ for all } x, y \in \mathbb{R}^{n+1};$$

- An open neighborhood  $U \subseteq S^n$  containing  $y$  such that for all  $x \in U \setminus \{y\}$  it holds that  $[\tilde{V}(x, y) - \tilde{\xi}_0] \cdot \dot{\tilde{V}}(x, y) < 0$ , where  $\dot{\tilde{V}}(x, y) = \sum_{i=1}^{n+1} \frac{\partial \tilde{V}}{\partial x_i} h_i(x)$ .

Define  $W : S^n \rightarrow \mathbb{R}$  for all  $x \in U$  by

$$W(x) = \begin{cases} \tilde{V}(x, y) - \tilde{\xi}_0 & \text{if } \tilde{V}(x, y) - \tilde{\xi}_0 \geq 0, \\ -(\tilde{V}(x, y) - \tilde{\xi}_0) & \text{otherwise.} \end{cases}$$

Hence,  $W(y) = 0$  and  $W(x) > 0$  for all  $x \in U \setminus \{y\}$ . Furthermore, for all  $x \in U \setminus \{y\}$ :

$$\begin{aligned} \dot{W}(x) &= \sum_{i=1}^{n+1} \frac{\partial W}{\partial x_i} h_i(x) \\ &= \begin{cases} \dot{\tilde{V}}(x, y) = \sum_{i=1}^{n+1} \frac{\partial \tilde{V}}{\partial x_i} h_i(x) < 0 & \text{if } \tilde{V}(x, y) - \tilde{\xi}_0 > 0, \\ -\dot{\tilde{V}}(x, y) = -\sum_{i=1}^{n+1} \frac{\partial \tilde{V}}{\partial x_i} h_i(x) > 0 & \text{if } \tilde{V}(x, y) - \tilde{\xi}_0 < 0. \end{cases} \end{aligned}$$

This implies that  $W$  is a strict Lyapunov function on  $U$  and by Lyapunov's second method this in turn implies that  $y$  is an asymptotically stable fixed point of  $h$  (cf., e.g., Perko [1991]). Observe that  $W$  is a monotone transformation of  $d$ , positively valued outside  $y$  and always decreasing in  $U \setminus \{y\}$ . Given the monotonicity of the transformation, it follows immediately that there is a one-to-one relationship between  $W$  and  $\tilde{d}$  decreasing monotonically over time. ■

**Proof of Proposition 8.** Let  $y$  be an interior *GESS*, i.e., Eq. (2) holds for some open neighborhood  $U$  containing  $y$ . Let  $x \in U \setminus \{y\}$ , then

$$\begin{aligned} (y - x) \cdot f(x) > 0 &\Leftrightarrow \\ (y - x) \cdot f(x) - \left( \frac{1}{n+1} \sum_{h \in I^{n+1}} f_h(x) \right) \sum_{i \in I^{n+1}} (y_i - x_i) > 0 &\Leftrightarrow \\ \sum_{i \in I^{n+1}} (y_i - x_i) \cdot \left[ f_i(x) - \frac{1}{n+1} \sum_{h \in I^{n+1}} f_h(x) \right] > 0. \end{aligned}$$

The first equivalence holds because  $\sum_{i \in I^{n+1}} (y_i - x_i) = 0$ . This means that there exists a neighborhood  $U$  of  $y$  containing  $y$  such that (3) holds for the dynamics given by (5). Hence,  $y$  is a *GESE*. To show the other implication, note that if  $y$  is an *ESE* of the orthogonal-projection dynamics given by (5), there exists a neighborhood  $U'$  such that (3) holds, i.e., the final inequality in the above. Going backward in the equivalences, we obtain that (2) must hold for  $U'$  as well. This means that  $y$  is a *GESS*. ■

**Proof of Proposition 9.** Let  $y \in \text{int } S^n$  be a *GESS*, then an open neighborhood  $U$  exists such that  $y \in U$  and  $(y - x) \cdot f(x) > 0$  for all  $x \in U \setminus \{y\}$ . Let  $U' = \{x \in \mathbb{R}_+^{n+1} \setminus \{0\} \mid \lambda_x^{-1} x \in U \text{ and } \|x\|_2 = 1\}$ . Define distance function  $d : S^n \times S^n \rightarrow \mathbb{R}_+^{n+1} \cup \{0\}$  by

$$d(x, y) \equiv d_2 \left( \frac{x}{\sqrt{\sum_{i=1}^{n+1} x_i^2}}, \frac{y}{\sqrt{\sum_{i=1}^{n+1} y_i^2}} \right) \text{ for every } x, y \in S^n. \quad (9)$$

Since  $U$  is open and  $y$  is in the interior, we can find a nonempty open ball  $B \subseteq U' \cap \text{int } \mathbb{R}_+^{n+1} \setminus \{0\}$ . Given relative fitness function  $f : S^n \rightarrow \mathbb{R}^{n+1}$ , define function  $f : \mathbb{R}_+^{n+1} \setminus \{0\} \rightarrow \mathbb{R}^{n+1}$  by

$$f(x) = f(\lambda_x^{-1}x) \text{ for } x \in \mathbb{R}_+^{n+1} \setminus \{0\}.$$

Let trajectory  $\{x(t)\}_{t \geq 0}$  be determined by

$$\begin{aligned} x(0) &= x_0 \in B \setminus \{y\}, \\ \frac{dx}{dt} &= f(x) \text{ for all } \text{int } x \in \mathbb{R}_+^{n+1} \setminus \{0\}. \end{aligned}$$

Since,  $x \cdot f(x) = x \cdot f(\lambda_x^{-1}x) = \lambda_x (\lambda_x^{-1}x) \cdot f(\lambda_x^{-1}x) = \lambda_x 0$  for all  $x \in \mathbb{R}_+^{n+1} \setminus \{0\}$ ,

$$\frac{d\|x\|_2^2}{dt} = \frac{d(x \cdot x)}{dt} = 2x \cdot \frac{dx}{dt} = 2x \cdot f(x) = 0.$$

Hence,  $\|z\|_2 = 1$  for  $z \in \{x(t)\}_{t \geq 0}$ .

Furthermore, for  $\tilde{y} = \frac{1}{\sqrt{\sum_{i=1}^{n+1} y_i^2}} y$  and  $\tilde{x} \in U'_1$ , we have

$$\begin{aligned} \frac{d(d_2(\tilde{y}, \tilde{x}))^2}{dt} &= \frac{d(\tilde{y} - \tilde{x}) \cdot (\tilde{y} - \tilde{x})}{dt} = -2(\tilde{y} - \tilde{x}) \frac{dx}{dt} = -2(\tilde{y} - \tilde{x}) \cdot f(\tilde{x}) \\ &= -2(\lambda_{\tilde{y}} y - \lambda_{\tilde{x}} \lambda_{\tilde{x}}^{-1} \tilde{x}) \cdot f(\lambda_{\tilde{x}}^{-1} \tilde{x}) \\ &= -2\lambda_{\tilde{y}} (y - \lambda_{\tilde{x}}^{-1} \tilde{x}) \cdot f(\lambda_{\tilde{x}}^{-1} \tilde{x}) + 2(\lambda_{\tilde{y}} - \lambda_{\tilde{x}}) (\lambda_{\tilde{x}}^{-1} \tilde{x}) \cdot f(\lambda_{\tilde{x}}^{-1} \tilde{x}) \\ &= -2\lambda_{\tilde{y}} (y - \lambda_{\tilde{x}}^{-1} \tilde{x}) \cdot f(\lambda_{\tilde{x}}^{-1} \tilde{x}) < 0. \end{aligned}$$

So,  $\{x(t)\}_{t \geq 0}$  converges monotonically to  $\tilde{y}$  in  $d_2$ , hence  $\{\lambda_{x(t)}^{-1} x(t)\}_{t \geq 0}$  converges monotonically to  $y$  in  $d$ . It was established in Joosten & Roorda [2008] that the dynamics on the unit simplex connected to  $\{\lambda_{x(t)}^{-1} x(t)\}_{t \geq 0}$  are precisely the ray-projection dynamics:

$$h_i(x) = \sqrt{\sum_{i=1}^{n+1} x_i^2} \left[ f_i(x) - x_i \left( \sum_{k \in I^{n+1}} f_k(x) \right) \right]. \blacksquare$$

**Proof of Theorem 13.** Let  $y \in S^n$  be a *TESS*. Let

$$V(x) = \sum_{i=1}^{n+1} (y_i \ln x_i - x_i) \text{ for all } x \in U.$$

Then clearly,  $V(x) \leq -1$  for all  $x \in U$ , and for  $x \neq y$  :

$$\begin{aligned} \dot{V}(x) &= \frac{dV(x)}{dt} = \sum_{i=1}^{n+1} \left( \frac{y_i}{x_i} - 1 \right) h_i(x) \\ &= \sum_{i \in C(y)} (y_i - x_i) \frac{h_i(x)}{x_i} - \sum_{i \notin C(y)} h_i(x) > 0, \end{aligned}$$

This implies that  $V$  is a strict generalized Lyapunov function in the terminology of Uzawa [1961], hence  $y$  is an asymptotically stable fixed point of the dynamics (cf., Uzawa [1961]). ■

**Proof of Lemma 15.** Let  $y$  be a strict saturated equilibrium, then  $y$  is a vertex of the unit simplex. Without loss of generality we may assume that this vertex is  $e_1 = (1, 0, \dots, 0) \in S^n$ . For all  $j = 2, \dots, n + 1$  we have  $f_j(e_1) < 0$ , hence there exists a neighborhood  $U$  containing  $e_1$  such that

$$f_1(x) \geq 0 > \max_{j=2, \dots, n+1} f_j(x) \text{ for all } x \in U.$$

Complementarity of  $f$  implies that the weak inequality on the left hand side is an equality only for  $e_1$ . Hence,  $h(y) = 0^{n+1}$  for weakly sign-compatible dynamics and Condition (a) is fulfilled. Furthermore,

$$h_1(x) \geq 0 \text{ for all } x \in U,$$

with strict inequality if  $x \neq e_1$ . Observe that for  $x \in U \setminus \{y\}$  :

$$\begin{aligned} \sum_{i \in C(y)} (y_i - x_i) \frac{h_i(x)}{x_i} - \sum_{i \notin C(y)} h_i(x) &= (1 - x_1) \frac{h_1(x)}{x_1} - \sum_{i \neq 1} h_i(x) = \\ \frac{h_1(x)}{x_1} - \sum_{i=1}^{n+1} h_i(x) &= \frac{h_1(x)}{x_1} > 0. \end{aligned}$$

Hence Condition (b) is fulfilled. ■

**Proof of Proposition 16.** Let  $h_i(x) = x_i f_i(x)$  for all  $i \in I^{n+1}$  and all  $x \in S^n$ . Observe that

$$\begin{aligned} (y - x) \cdot f(x) &= \sum_{i=1}^{n+1} (y_i - x_i) f_i(x) \\ &= \sum_{i \in C(y)} (y_i - x_i) \frac{x_i f_i(x)}{x_i} + \sum_{i \notin C(y)} (y_i - x_i) f_i(x) \\ &= \sum_{i \in C(y)} (y_i - x_i) \frac{h_i(x)}{x_i} - \sum_{i \notin C(y)} x_i f_i(x) \\ &= \sum_{i \in C(y)} (y_i - x_i) \frac{h_i(x)}{x_i} - \sum_{i \notin C(y)} h_i(x). \end{aligned}$$

So,  $\sum_{i \in C(y)} (y_i - x_i) \frac{h_i(x)}{x_i} - \sum_{i \notin C(y)} h_i(x) > 0$  is equivalent to  $(y - x) \cdot f(x) > 0$ . Hence, for these replicator dynamics *TESS* and *GESS* concur. ■

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