Evolutionary Game Theory

Prepared for the Handbook on Dynamic Game Theory

by

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Abstract: Evolutionary game theory developed as a means to predict the expected distribution of individual behaviors in a biological system with a single species that evolves under natural selection. It has long since expanded beyond its biological roots and its initial emphasis on models based on symmetric games with a finite set of pure strategies where payoffs result from random one-time interactions between pairs of individuals (i.e. on matrix games). The theory has been extended in many directions (including non-random, multi-player or asymmetric interactions, and games with continuous strategy (or trait) spaces) and has become increasingly important for analyzing human and/or social behavior as well. This chapter initially summarizes features of matrix games before showing how the theory changes when the two-player game has a continuum of traits or interactions become asymmetric. It's focus is on the connection between static game-theoretic solution concepts (e.g. ESS, CSS, NIS) and stable evolutionary outcomes for deterministic evolutionary game dynamics (e.g. the replicator equation, adaptive dynamics).

Keywords: ESS, CSS, NIS, neighborhood superiority, evolutionary game dynamics, replicator equation, adaptive dynamics, Darwinian dynamics

1 Introduction

Evolutionary game theory developed as a means to predict the expected distribution of individual behaviors in a biological system with a single species that evolves under natural selection (Maynard Smith and Price, 1973; Maynard Smith, 1974). The theory's predictions of equilibrium behavior correspond to intuitive static solutions of the game formed through fitness (i.e. payoff) comparisons of different behaviors (i.e. strategies). A fundamental result is that, at a stable behavioral distribution, no individual in the population can increase its fitness by unilaterally changing strategy (see, for example, condition (1) below). That is, a stable outcome for natural selection implies individuals will exhibit Nash equilibrium (NE) behavior (Nash, 1950, 1951), a result that has come to be known as one aspect of the folk theorem of evolutionary game theory (Hofbauer and Sigmund, 1998, 2003; Cressman, 2003; Sandholm, 2010; Broom and Rychtar, 2013) given in Theorem 1 below.

However, as we will see, stability requires more than NE. The most common additional requirement, introduced already by Maynard Smith and Price (1973), is that of an *evolutionarily stable strategy* (ESS). According to John Maynard Smith (1982, page 10) in his influential book, Evolution and the Theory of Games, an ESS is "a strategy such that, if all members of the population adopt it, then no mutant strategy could invade the population under the influence of natural selection". He goes on to argue that his definition, that seems heuristically related to stability of a monomorphic resident strategy with respect to the invasion dynamics of mutants, is equivalent to the standard one (Definition 1 below) given through static payoff comparisons when the evolutionary game and invasion dynamics are modeled as in Section 2.1 by a symmetric normal form game and the replicator equation respectively.

In fact, as illustrated throughout this article, there is a complex relationship between the static stability conditions (such as the ESS) and stability with respect to game dynamics (such as the replicator equation). It is this relationship that formed the initial basis of what is now known as evolutionary game theory.

Evolutionary game theory has long since expanded beyond its biological roots and become increasingly important for analyzing human and/or social behavior. Here, changes in strategy frequencies do not result from natural selection; rather, individuals (or societies) alter their behavior based on payoff consequences. The replicator equation then emerges from, for instance, individuals making rational decisions on how to imitate observed strategies that currently receive higher payoff (Schlag, 1997). Depending on what information these decision makers have (and how they use this information), a vast array of other game dynamics are possible (Hofbauer and Sigmund, 2003; Sandholm, 2010; Sigmund, 2011). Evolutionary game theory has also become a standard method to choose among the many NE that often arise in these models of human interactions between players that can be individuals or other economic entities such as firms or even nations (e.g. Samuelson, 1997; Sandholm, 2010). Thus, the ESS can be viewed as a NE refinement or equilibrium selection technique.

It is in this latter capacity that evolutionary game theory initially gained prominence in the economic literature when applied to rational decision making in classical non-cooperative, symmetric games in either normal form or extensive form (see van Damme (1991) and Samuelson (1997) and the references therein). From this perspective, evolutionary games often consider other deterministic or stochastic evolutionary dynamics besides the replicator equation since these are thought to better represent decision making applied to economic or learning models (Weibull, 1995; Vega-Redondo, 1996; Hofbauer and Sigmund, 1998; Fudenberg and Levine, 1998; Young, 1998; Gintis, 2000; Mesterton-Gibbons, 2000; Cressman, 2003; Nowak, 2006; Sandholm, 2010).

The biological perspective of evolutionary game theory has been summarized in several survey monographs and books (e.g. Hines, 1987; Hofbauer and Sigmund, 1988, 1998; Bomze and Pötscher, 1989; Cressman, 1992; Sigmund, 1993; Mesterton-Gibbons, 2000; Vincent and Brown, 2005; Broom and Rychtar, 2013).

Evolutionary game theory and its corresponding game dynamics have also expanded well beyond their initial emphasis on single-species games with a finite set of pure strategies where payoffs result from random one-time interactions between pairs of individuals (i.e. two-player symmetric normal form games or, more simply, matrix games). In this chapter, we highlight features of matrix games in the following section before investigating in Section 3 how the theory changes when the symmetric game has a continuum of pure strategies (or traits). Section 4 then generalizes the theory developed in Sections 2 and 3 to asymmetric games. Specifically, two-player games with two roles are examined that either have finitely many pure strategies in each role (in normal or extensive form) or have a one-dimensional continuous trait space in each role.

2 Evolutionary Game Theory for Symmetric Normal Form Games

2.1 The ESS and invasion dynamics

The relationship between the ESS and stability of game dynamics is most clear when individuals in a single species can use only two possible strategies, denoted p^* and p to match notation used later in this article, and payoffs are linear. Suppose that $\pi(p, \widehat{p})$ is the payoff to a strategy p used against strategy $\widehat{p}$. In biological terms, $\pi(p, \widehat{p})$ is the fitness of an individual using strategy p in a large population exhibiting behavior $\widehat{p}$.[1] Then, an individual in a monomorphic population where everyone uses p^* cannot improve its fitness by switching to p if

$$\pi(p, p^*) \le \pi(p^*, p^*) \quad \text{NE condition.} \tag{1}$$

If p playing against p^* does equally as well as p^* playing against p^* (i.e. if $\pi(p, p^*) = \pi(p^*, p^*)$), then stability requires the extra condition that p^* must do better than p in their rare contests against p. That is,

$$\pi(p, p) < \pi(p^*, p) \text{ if } \pi(p, p^*) = \pi(p^*, p^*) \quad \text{stability condition.} \tag{2}$$

For the game with strategies p^* and p, p^* is defined to be an ESS if it satisfies conditions (1) and (2).

To see why both these conditions are necessary for dynamic stability, under the assumption of Maynard Smith (1982) that "like begets like", the per capita change in the number of individuals using strategy p is its expected payoff. This leads to the following continuous-time invasion dynamics of a resident monomorphic population p^* by a small proportion ε of mutants using p.

$$\begin{aligned}
\dot{\varepsilon} &= \varepsilon\left[\pi(p, \varepsilon p + (1-\varepsilon)p^*) - \pi(\varepsilon p + (1-\varepsilon)p^*, \varepsilon p + (1-\varepsilon)p^*)\right] \\
&= \varepsilon(1-\varepsilon)\left[\pi(p, \varepsilon p + (1-\varepsilon)p^*) - \pi(p^*, \varepsilon p + (1-\varepsilon)p^*)\right] \qquad (3) \\
&= \varepsilon(1-\varepsilon)\left[(1-\varepsilon)(\pi(p, p^*) - \pi(p^*, p^*)) + \varepsilon(\pi(p, p) - \pi(p^*, p))\right]
\end{aligned}$$

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[1] In the basic biological model for evolutionary games, individuals are assumed to engage in random pairwise interactions. Moreover, the population is assumed to be large enough that an individual's fitness (i.e. reproductive success) $\pi(p, \widehat{p})$ is the expected payoff of p if the average strategy in the population is $\widehat{p}$. In these circumstances, it is often stated that the population is effectively infinite in that there are no effects due to finite population size. Such stochastic effects are discussed briefly in the final section.

Here, we have used repeatedly that payoffs $\pi(p, \widehat{p})$ are linear in both p and $\widehat{p}$. In fact, this is the replicator equation of Section 2.2 for the matrix game with two pure strategies, p and p^*, and payoff matrix (5).

If p^* is a strict NE (i.e. the inequality in (1) is strict), then $\dot{\varepsilon} < 0$ for all positive ε that are close to 0 since $(1-\varepsilon)(\pi(p, p^*) - \pi(p^*, p^*))$ is the dominant term corresponding to the common interactions against p^*. Furthermore, if this term is 0 (i.e. if p^* is not strict), we still have $\dot{\varepsilon} < 0$ from the stability condition (2) corresponding to the less common interactions against p. Conversely, if $\dot{\varepsilon} < 0$ for all positive ε that are close to 0, then p^* satisfies (1) and (2). Thus, the resident population p^* (i.e. $\varepsilon = 0$) is locally asymptotically stable[2] under (3) (i.e. there is dynamic stability at p^* under the replicator equation) if and only if p^* satisfies (1) and (2).

In fact, dynamic stability occurs at such a p^* in these two-strategy games for any game dynamics whereby the proportion (or frequency) of users of strategy $\widehat{p}$ increases if and only if its expected payoff is higher than that of the alternative strategy. We then have the result that p^* is an ESS if and only if it satisfies (1) and (2) if and only if it is dynamically stable with respect to any such game dynamics.

These results assume that there is a resident strategy p^* and a single mutant strategy p. If there are other possible mutant strategies, an ESS p^* must be locally asymptotically stable under (3) for any such p in keeping with Maynard Smith's (1982) dictum that no mutant strategy can invade. That is, p^* is an ESS if and only if it satisfies (1) and (2) for all mutant strategies p (see also Definition 1 (b) of Section 2.2).

2.2 The ESS and the replicator equation for matrix games

In an evolutionary game with symmetric normal form, the population consists of individuals who must all use one of finitely many (say m) possible behaviors

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[2] Clearly, the unit interval $[0,1]$ is (forward) invariant under the dynamics (3) (i.e. if $\varepsilon(t)$ is the unique solution of (3) with initial value $\varepsilon(0) \in [0,1]$, then $\varepsilon(t) \in [0,1]$ for all $t \geq 0$). The rest point $\varepsilon = 0$ is (Lyapunov) *stable* if, for every neighborhood U of 0 relative to $[0,1]$, there exists a neighborhood V of 0 such that $\varepsilon(t) \in U$ for all $t \geq 0$ if $\varepsilon(0) \in V \cap [0,1]$. It is *attracting* if, for some neighborhood U of 0 relative to $[0,1]$, $\varepsilon(t)$ converges to 0 whenever $\varepsilon(0) \in U$. It is *(locally) asymptotically stable* if it is both stable and attracting. Throughout the chapter, dynamic stability is equated to local asymptotic stability.

at any particular instant in time. These strategies are denoted e_i for $i = 1, ..., m$ and called pure strategies. Moreover, $S \equiv \{e_1, ..., e_m\}$ is called the pure strategy set. An individual may also use a mixed strategy in $\Delta^m \equiv \{p = (p_1, ..., p_m) \mid \sum_{i=1}^m p_i = 1, p_i \geq 0\}$ where p_i is the proportion of the time this individual uses pure strategy e_i. If population size is large and the components of $\widehat{p} \in \Delta^m$ are the current frequencies of strategies used in the population (i.e. $\widehat{p}$ is the population state), then the payoff of an individual using p in a random pairwise interaction is given explicitly through the bilinear payoff function of the (two-player) symmetric normal form game, $\pi(p, \widehat{p}) \equiv \sum_{i,j=1}^m p_i \pi(e_i, e_j) \widehat{p}_j$, where as before $\pi(e_i, e_j)$ is the payoff to e_i against e_j.

Based on this linearity, the following notation is commonly used for these games. Let e_i be represented by the i^{th} unit column vector in R^m and $\pi(e_i, e_j)$ by entry A_{ij} in an $m \times m$ payoff matrix A. Then, with vectors in Δ^m thought of as column vectors, $\pi(p, \widehat{p})$ is the inner product $p \cdot A\widehat{p}$ of the two column vectors p and $A\widehat{p}$. For this reason, symmetric normal form games are often called matrix games with payoffs given in this latter form.

To obtain the continuous-time, pure-strategy replicator equation (4) following the original fitness approach of Taylor and Jonker (1978), individuals are assumed to use pure strategies and the per capita growth rate in the number n_i of individuals using strategy e_i at time t is taken as the expected payoff of e_i from a single interaction with a random individual in the large population. That is, $\dot{n}_i = n_i \sum_{j=1}^m \pi(e_i, e_j) p_j \equiv n_i \pi(e_i, p)$ where p is the population state in the (mixed) strategy simplex Δ^m with components $p_i = n_i / \sum_{j=1}^m n_j$ the proportion of the population using strategy e_i at time t.[3] A straightfor-

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[3] The approach of Taylor and Jonker (1978) also relies on the population being large enough (or effectively infinite) so that n_i and p_i are considered to be continuous variables.

ward calculus exercise[4] yields the replicator equation on Δ^m

$$\dot{p}_i = p_i \left(\pi(e_i, p) - \pi(p, p) \right) \quad \text{for} \quad i = 1, ..., m \tag{4}$$

where $\pi(p,p) = \sum_{j=1}^{m} p_j \pi(e_j, p)$ is the average payoff of an individual chosen at random (i.e. the population mean payoff). From the theory of dynamical systems, trajectories of (4) leave the interior of Δ^m forward invariant as well as each of its faces (Hofbauer and Sigmund, 1998).

The replicator equation can be applied to the two-strategy game (on p^* and p) of Section 2.1 by taking these as the pure strategies with corresponding payoff matrix

$$\begin{array}{cc} & \begin{array}{cc} p^* & p \end{array} \\ \begin{array}{c} p^* \\ p \end{array} & \left[\begin{array}{cc} \pi(p^*, p^*) & \pi(p^*, p) \\ \pi(p, p^*) & \pi(p, p) \end{array} \right] \end{array} . \tag{5}$$

With ε the proportion using strategy p (and $1 - \varepsilon$ using p^*), the one-dimensional replicator equation is given by (3). Then, from Section 2.1, p^* is an ESS of the matrix game on Δ^m if and only if it is locally asymptotically stable under (3) for all choices of mutant strategies $p \in \Delta^m$ with $p \neq p^*$ (see also Definition 1 (b) below).

The replicator equation (4) for matrix games is the first and most important game dynamics studied in connection with evolutionary game theory. It was defined by Taylor and Jonker (1978) (see also Hofbauer et al., 1979) and named by Schuster and Sigmund (1983). Important properties of the replicator equation are briefly summarized for this case in the Folk Theorem and

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[4] With $N \equiv \sum_{j=1}^{m} n_j$ the total population size,

$$\begin{aligned} \dot{p}_i &= \frac{\dot{n}_i N - n_i \sum_{j=1}^{m} \dot{n}_j}{N^2} \\ &= \frac{n_i \pi(e_i, p) - p_i \sum_{j=1}^{m} n_j \pi(e_j, p)}{N} \\ &= p_i \pi(e_i, p) - p_i \sum_{j=1}^{m} p_j \pi(e_j, p) \\ &= p_i \left(\pi(e_i, p) - \pi(p, p) \right) \end{aligned}$$

for $i = 1, ..., m$. This is the replicator equation (4) in the main text. Since $\dot{p}_i = 0$ when $p_i = 0$ and $\sum_{1=1}^{m} \dot{p}_i = \pi(p,p) - \pi(p,p) = 0$ when $p \in \Delta^m$, the interior of Δ^m is invariant as well as all its (sub)faces under (4). Since Δ^m is compact, there is a unique solution of (4) for all $t \geq 0$ for a given initial population state $p(0) \in \Delta^m$. That is, Δ^m is forward invariant under (4).

Theorem 2 of the following section, including the convergence to and stability of the NE and ESS. The theory has been extended to other game dynamics for symmetric games (e.g. the best response dynamics and adaptive dynamics). The replicator equation has also been extended to many other types of symmetric games (e.g. multi-player, population and games with continuous strategy spaces) as well as to corresponding types of asymmetric games.

To summarize Sections 2.1 and 2.2, we have the following definition.

Definition 1. Consider a matrix game on Δ^m.
(a) $p^* \in \Delta^m$ is a (symmetric) *NE* if it satisfies (1) for all $p \in \Delta^m$.
(b) $p^* \in \Delta^m$ is an *ESS* if it is a NE that satisfies (2) for all $p \in \Delta^m$ with $p \neq p^*$.
(c) The (pure strategy) *replicator equation* on Δ^m is

$$\dot{p}_i = p_i \left(\pi(e_i, p) - \pi(p, p)\right) \text{ for } i = 1, ..., m.$$

2.3 The Folk Theorem of Evolutionary Game Theory

Theorem 1. The replicator equation for a matrix game on Δ^m satisfies:
(a) A stable rest point is a NE.
(b) A convergent trajectory in the interior of Δ^m evolves to a NE.
(c) A strict NE is locally asymptotically stable.

Theorem 1 is the Folk Theorem of Evolutionary Game Theory (Hofbauer and Sigmund, 1998, 2003; Cressman, 2003) applied to the replicator equation. The three conclusions are true for many matrix game dynamics (in either discrete or continuous time) and serve as a benchmark to test dynamical systems methods applied to general game dynamics and to non matrix evolutionary games such as those considered in the remaining sections of this chapter.

The Folk Theorem means that biologists can predict the evolutionary outcome of their stable systems by examining NE behavior of the underlying game. It is as if individuals in these systems are rational decision makers when in reality it is natural selection through reproductive fitness that drives the system to its stable outcome. This has produced a paradigm shift toward strategic reasoning in population biology. The profound influence it has had on the analysis of behavioral ecology is greater than earlier game-theoretic methods applied to biology such as Fisher's (1930) argument (see also Darwin, 1871; Hamilton, 1967; Broom and Krivan, this volume) for the prevalence of the 50:50 sex ratio in diploid species and Hamilton's (1964) theory of kin selection.

The importance of strategic reasoning in population biology is further enhanced by the following result.

Theorem 2. Consider a matrix game on Δ^m.
(a) p^* is an ESS of the game if and only if $\pi(p^*, p) > \pi(p, p)$ for all $p \in \Delta^m$ sufficiently close (but not equal) to p^*.
(b) An ESS p^* is a locally asymptotically stable rest point of the replicator equation (4).
(c) An ESS p^* in the interior of Δ^m is a globally asymptotically stable rest point of the replicator equation (4).

The equivalent condition for an ESS contained in part (a) is the more useful characterization when generalizing the ESS concept to other evolutionary games.[5] It is called locally superior (Weibull, 1995), neighborhood invader strategy (Apaloo, 2006), or neighborhood superior (Cressman, 2010). One reason for different names for this concept is that there are several ways to generalize local superiority to other evolutionary games and these have different stability consequences.

From parts (b) and (c), if p^* is an ESS with full support (i.e. the support $\{i \mid p_i^* > 0\}$ of p^* is $\{1, 2, ..., m\}$), then it is the only ESS. This result easily extends to the Bishop-Cannings Theorem (Bishop and Cannings, 1976) that the support of one ESS cannot be contained in the support of another, an extremely useful property when classifying the possible ESS structure of matrix games (Broom and Rychtar, 2013). Haigh (1975) provides a procedure for finding ESSs in matrix games based on such results.

Parts (b) and (c) were an early success of evolutionary game theory since stability of the predicted evolutionary outcome under the replicator equation is assured at an ESS not only for the invasion of p^* by a subpopulation using a single mutant strategy p but also by multiple pure strategies. In fact, if individuals use mixed strategies for which some distribution have average strategy p^*, then p^* is asymptotically stable under all corresponding mixed-strategy replicator equations if and only if p^* is an ESS (see the *strong stability* concept of Cressman (1992) and Hofbauer and Sigmund (1998)).

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[5] The proof of this equivalence relies on the compactness of Δ^m and the bilinearity of the payoff function $\pi(p, q)$ as shown by Hofbauer and Sigmund (1998).

That is, stable evolutionary outcomes with respect to mixed-strategy replicator equations are equivalent to the ESS. Moreover, the converse of part (b) for the pure-strategy replicator equation (i.e. for (4)) is true when there are two pure strategies (i.e. $m = 2$). The three categories of such games (Hawk-Dove, Prisoner's Dilemma, and Coordination games) are classified and analyzed in Weibull (1995) (see also Broom and Krivan's chapter (this volume) for the Hawk-Dove and Prisoner's Dilemma games).

However, there already exist non-ESS strategies p in three-strategy symmetric normal form games (i.e. for $m = 3$) that are asymptotically stable under (4) (such strategies p must be NE by the Folk Theorem). Broom and Krivan also provide a biologically relevant illustration of this phenomenon based on a generalized Rock-Scissors-Paper (RSP) game that exhibits cyclic dominance since P strictly dominates in the two-strategy $\{R, P\}$ game, S strictly dominates in the two-strategy $\{P, S\}$ game, and R strictly dominates in the two-strategy $\{R, S\}$ game. These games always have a unique NE p^* (that must be in the interior) but conditions on payoff matrix entries for p^* to be an ESS are different than those for stability with respect to (4).

The most elegant proof (Hofbauer et al, 1979) of the stability statements in parts (b) and (c) shows that $V(p) \equiv \prod p_i^{p_i^*}$ where the product is taken over $\{i : p_i^* > 0\}$ is a strict local Lyapunov function (i.e. $V(p^*) > V(p)$ and $\dot{V}(p) = V(p)\left(\pi(p^*, p) - \pi(p, p)\right) > 0$ for all $p \in \Delta^m$ sufficiently close but not equal to an ESS p^*).[6] It is tempting to add these stability statements to the Folk Theorem since they remain valid for many matrix game dynamics through the use of other Lyapunov functions. Besides the above differences between dynamic stability and ESS noted above for the RSP example, there are other reasons to avoid this temptation.

In particular, parts (b) and (c) of Theorem 2 are not true for discrete-time matrix game dynamics. One such dynamics is the discrete-time replicator equation of Maynard Smith (1982)

$$p_i' = p_i \frac{\pi(e_i, p)}{\pi(p, p)} \tag{6}$$

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[6] Under the replicator equation, $\dot{V}(p) = \sum_{i=1}^m p_i^* p_i^{p_i^* - 1} \dot{p}_i \prod_{\{j | j \neq i, p_j^* \neq 0\}} p_j^{p_j^*} = \sum_{i=1}^m p_i^* \prod_j p_j^{p_j^*} (\pi(e_i, p) - \pi(p, p)) = V(p)(\pi(p^*, p) - \pi(p, p)) > 0$ for all $p \in \Delta^m$ sufficiently close but not equal to an ESS p^*. Since $V(p)$ is a strict local Lyapunov function, p^* is locally asymptotically stable. Global stability (i.e. in addition to local asymptotic stability, all interior trajectories of (4) converge to p^*) in part (c) follows from global superiority (i.e. $\pi(p^*, p) > \pi(p, p)$ for all $p \neq p^*$) in this case.

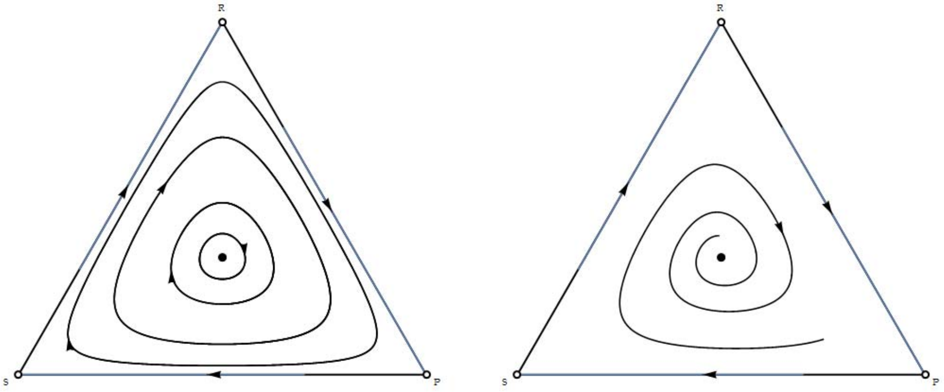
where p_i' is the frequency of strategy e_i one generation later and $\pi(e_i, p)$ is the expected nonnegative number of offspring of each e_i-individual. When applied to matrix games, each entry in the payoff matrix is typically assumed to be positive (or at least nonnegative), corresponding to the contribution of this pairwise interaction to expected offspring. It is then straightforward to verify that (6) is a forward invariant dynamic on Δ^m and on each of its faces.

To see that an ESS may not be stable under (6), fix $\mid \varepsilon \mid < 1$ and consider the generalized RSP game with payoff matrix

$$A = \begin{array}{c} \\ R \\ S \\ P \end{array} \begin{array}{c} \begin{array}{ccc} R & S & P \end{array} \\ \begin{bmatrix} -\varepsilon & 1 & -1 \\ -1 & -\varepsilon & 1 \\ 1 & -1 & -\varepsilon \end{bmatrix} \end{array} \tag{7}$$

that has a unique NE $p^* = (1/3, 1/3, 1/3)$. For $\varepsilon = 0$, this is the standard zero-sum RSP game whose trajectories with respect to the replicator equation (4) form periodic orbits around p^* (Figure 1a). For positive ε, p^* is an interior ESS and trajectories of (4) spiral inward as they cycle around p^* (Figure 1b).

It is well-known (Hofbauer and Sigmund, 1998) that adding a constant c to every entry of A does not affect either the NE/ESS structure of the game or the trajectories of the continuous-time replicator equation. The constant c is a background fitness that is common to all individuals that changes the speed of continuous-time evolution but not the trajectory. If $c \geq 1$, all entries of this new payoff matrix are nonnegative, and so the discrete-time dynamics (6) applies. Now background fitness does change the discrete-time trajectory. In fact, for the matrix $1 + A$ (i.e. if $c = 1$) where A is the RSP game (7), p^* is unstable for all $\mid \varepsilon \mid < 1$ as can be shown through the linearization of this dynamics about the rest point p^* (specifically, the relevant eigenvalues of this linearization have modulus greater than 1 (Cressman, 2003)). The intuition here is that p' is far enough along the tangent at p in Figure 1 that these points spiral outward from p^* under (6) instead of inward under (4).[7]



(a) (b)

Figure 1. Trajectories of the replicator equation (4) for the RSP game. (a) $\varepsilon = 0$. (b) $\varepsilon > 0$.

Cyclic behavior is common not only in biology (e.g. predator-prey systems) but also in human behavior (e.g. business cycles, the emergence and subsequent disappearance of fads, etc.). Thus, it is not surprising that evolutionary game dynamics include cycles as well. In fact, as the number of strategies increases, even more rich dynamical behavior such as chaotic trajectories can emerge (Hofbauer and Sigmund, 1998).

What may be more surprising is the many classes of matrix games (Sandholm, 2010) for which these complicated dynamics do not appear (e.g. potential, stable, supermodular, zero-sum, doubly symmetric games) and for these the evolutionary outcome is often predicted through rationality arguments underlying Theorems 1 and 2. Furthermore, these arguments are also relevant for other game dynamics examined in the following section.

Before doing so, it is important to mention that the replicator equation for doubly symmetric matrix games (i.e. a symmetric game whose payoff matrix is symmetric) is formally equivalent to the continuous-time model of natural selection at a single (diploid) locus with m alleles $A_1, \ldots A_m$ (Akin,

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[7] This intuition is correct for small constants c greater than 1. However, for large c, the discrete-time trajectories approach the continuous-time ones and so $p^* = (1/3, 1/3, 1/3)$ will be asymptotically stable under (6) when $\varepsilon > 0$.

1982; Hines 1987; Cressman, 1992; Hofbauer and Sigmund, 1998). Specifically, if a_{ij} is the fitness of genotype A_iA_j and p_i is the frequency of allele A_i in the population, then (4) is the continuous-time selection equation of population genetics (Fisher, 1930). It can then be shown that population mean fitness $\pi(p,p)$ is increasing (c.f. one part of the fundamental theorem of natural selection). Furthermore, the locally asymptotically stable rest points of (4) correspond precisely to the ESSs of the symmetric payoff matrix $A = (a_{ij})_{i.j=1}^m$ and all trajectories in the interior of Δ^m converge to a NE of A (Cressman 1992, 2003). Analogous results hold for the classical discrete-time viability selection model with non overlapping generations and corresponding dynamics (6) (Nagylaki, 1992).

2.4 Other Game Dynamics

A monotone selection dynamics (Samuelson and Zhang, 1992) is of the form $\dot{p}_i = p_i g_i(p)$ where $g_i(p) > g_j(p)$ if and only if $\pi(e_i,p) > \pi(e_j,p)$ for $i,j = 1,...,m$ and Δ^m is forward invariant (i.e. $\sum_{j=1}^m p_j g_j(p) = 0$). The replicator equation is the special case where $g_i(p) \equiv \pi(e_i,p) - \sum_{j=1}^m p_j \pi(e_j,p) = \pi(e_i,p) - \pi(p,p)$. For strategies e_i and e_j that are currently in use, monotone selection dynamics increase the relative frequency (p_i/p_j) of e_i compared to e_j if and only if e_i has higher expected payoff than e_j. For the RSP game (7) with $0 < \varepsilon < 1$ fixed, the $g_i(p)$ can be chosen as continuously differentiable functions for which the interior ESS $p^* = (1/3, 1/3, 1/3)$ is not globally asymptotically stable under the corresponding monotone selection dynamic (c.f. Theorem 2(c)). In particular, Cressman (2003) shows there may be trajectories that spiral outward from initial points near p^* to a stable limit cycle in the interior of Δ^3 for these games.[8]

The best response dynamics (8) for matrix games was introduced by Gilboa and Matsui (1991) (see also Matsui,1992) as the continuous-time version of the fictitious play process, the first game dynamics introduced well before the advent of evolutionary game theory by Brown (1951) and Robinson (1951).

$$\dot{p} = BR(p) - p \tag{8}$$

In general, $BR(p)$ is the set of best responses to p and so may not be a single

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[8] On the other hand, an ESS remains locally asymptotically stable for all selection dynamics that are uniformly monotone according to Cressman (2003) (see also Sandholm, 2010).

strategy. That is, (8) is a differential inclusion (Aubin and Cellina, 1984). The stability properties of this game dynamics were analyzed by Hofbauer (1995) (see also Hofbauer and Sigmund, 2003) who first showed that there is a solution for all $t \geq 0$ given any initial condition.[9]

The best response dynamics (8) is a special case of a general dynamics of the form

$$\dot{p} = I(p)p - p \tag{9}$$

where $I_{ij}(p)$ is the probability an individual switches from strategy j to strategy i per unit time if the current state is p. Then the corresponding continuous-time game dynamics in vector form is then given by (9) where $I(p)$ is the $m \times m$ matrix with entries $I_{ij}(p)$. The transition matrix $I(p)$ can also be developed using the revision protocol approach promoted by Sandholm (2010).

The best response dynamics (8) results by always switching to the best strategy when a revision opportunity arises in that $I_{ij}(p)$ is given by

$$I_{ij}(p) = \begin{cases} 1 & \text{if } e_i = \arg\max \pi(e_j, p) \\ 0 & \text{otherwise} \end{cases} . \tag{10}$$

The Folk Theorem is valid when the best response dynamics replaces the replicator equation (Hofbauer and Sigmund, 2003) as are parts (b) and (c) of Theorem 2. In contrast to the replicator equation, convergence to the NE may occur in finite time (compare Figure 2, panels (a) and (c)) .

The replicator equation (4) can also be expressed in the form (9) using the proportional imitation rule (Schlag, 1997) given by

$$I_{ij}(p) = \begin{cases} kp_i(\pi(e_i, p) - \pi(e_j, p)) & \text{if } \pi(e_i, p) \geq \pi(e_j, p) \\ 0 & \text{if } \pi(e_i, p) < \pi(e_j, p) \end{cases}$$

for $i \neq j$. Here k is a positive proportionality constant for which $\sum_{i \neq j} I_{ij}(p) \leq 1$ for all $1 \leq j \leq m$ and $p \in \Delta^m$. Then, since $I(p)$ is a transition matrix, $I_{jj}(p) = 1 - \sum_{i \neq j} I_{ij}(p)$. This models the situation where information is

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[9] Since the best response dynamics is a differential inclusion, it is sometimes written as $\dot{p} \in BR(p) - p$ and there may be more than one solution to an initial value problem (Hofbauer and Sigmund, 2003). Due to this, it is difficult to provide an explicit formula for the vector field corresponding to a particular solution of (8) when $BR(p)$ is multi-valued. Since such complications are beyond the scope of this chapter, the vector field is only given when $BR(p)$ is a single point for the examples in this section (see, for example, the formula in (10)).

gained by sampling a random individual and then switching to the sampled individual's strategy with probability proportional to the payoff difference only if the sampled individual has higher fitness.

An interesting application of these dynamics is to the following single-species habitat selection game.

Example 1 (Habitat Selection Game and IFD). The foundation of the habitat selection game for a single species was laid by Fretwell and Lucas (1969) before evolutionary game theory appeared. They were interested in predicting how a species (specifically, a bird species) of fixed population size should distribute itself among several resource patches if individuals would move to patches with higher fitness. They argued the outcome will be an ideal free distribution (IFD) defined as a patch distribution whereby the fitness of all individuals in any occupied patch would be the same and at least as high as what would be their fitness in any unoccupied patch (otherwise some individuals would move to a different patch). If there are H patches (or habitats) and an individual's pure strategy e_i corresponds to being in patch i (for $i = 1, 2, ..., H$), we have a population game by equating the payoff of e_i to the fitness in this patch. The verbal description of an IFD in this "habitat selection game" is then none other than that of a NE. Although Fretwell and Lucas (1969) did not attach any dynamics to their model, movement among patches is discussed implicitly.

If patch fitness is decreasing in patch density (i.e. in the population size in the patch), Fretwell and Lucas proved that there is a unique IFD at each fixed total population size.[10] Moreover, the IFD is an ESS that is globally asymptotically stable under the replicator equation (Cressman et al., 2004; Cressman and Krivan, 2006; Krivan et al., 2008). To see this, let $p \in \Delta^H$ be a distribution among the patches and $\pi(e_i, p)$ be the fitness in patch i. Then $\pi(e_i, p)$ depends only on the proportion p_i in this patch (i.e. has the form $\pi(e_i, p_i)$). To apply matrix game techniques, assume this is a linearly decreasing function of p_i.[11] Then, since the vector field

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[10] Broom and Krivan (this volume) give more details of this result and use it to produce analytic expressions for the IFD in several important biological models. They also generalize the IFD concept when the assumptions underlying the analysis of Fretwell and Lucas (1969) are altered. Here, we concentrate on the dynamic stability properties of the IFD in its original setting.

[11] The results summarized in this example do not depend on linearity as shown in Krivan et al. (2008) (see also Cressman and Tao, 2014).

$(\pi(e_1,p_1),...,\pi(e_H,p_H))$ is the gradient of a real-valued function $F(p)$ defined on Δ^H, we have a potential game. Following Sandholm (2010), it is a strictly stable game and so has a unique ESS p^* which is globally asymptotically stable under the replicator equation. In fact, it is globally asymptotically stable under many other game dynamics as well that satisfy the intuitive conditions in the following Theorem.[12]

Theorem 3. Suppose patch fitness is a decreasing function of patch density in a single-species habitat selection game. Then any migration dynamics (9) that satisfies the following two conditions evolves to the unique IFD.
(a) Individuals never move to a patch with lower fitness.
(b) If there is a patch with higher fitness than some occupied patch, some individuals move to a patch with highest fitness.

We illustrate Theorem 3 when there are three patches. Suppose that at p, patch fitnesses are ordered $\pi(e_1,p) > \pi(e_2,p) > \pi(e_3,p)$ and consider the two migration matrices

$$I^1(p) \equiv \begin{bmatrix} 1 & 1 & 1 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{bmatrix} \qquad I^2(p) \equiv \begin{bmatrix} 1 & 1/3 & 1/3 \\ 0 & 2/3 & 1/3 \\ 0 & 0 & 1/3 \end{bmatrix}.$$

$I^1(p)$ corresponds to a situation where individuals who move go to patch 1 since they know it has highest fitness and so is associated with the best response dynamics (8).

On the other hand, $I^2(p)$ models individuals who only gain fitness information by sampling one patch at random, moving to this patch if it has higher fitness than its current patch (e.g. an individual in patch 2 moves if it samples patch 1 and otherwise stays in its own patch (with probabilities

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[12] To see that the habitat selection game is a potential game, take $F(p) \equiv \sum_{i=1}^{H} \int_0^{p_i} \pi(e_i,u_i)du_i$. Then $\frac{\partial F(p)}{\partial p_i} = \pi(e_i,p_i)$. If patch payoff decreases as a function of patch density, the habitat selection game is a strictly stable game (i.e. $\sum (p_i - q_i)(\pi(e_i,p) - \pi(e_i,q)) < 0$ for all $p \neq q$ in Δ^H). This follows from the fact that $F(p)$ is strictly concave since $\frac{\partial^2 F(p)}{\partial p_i \partial p_j} = \begin{cases} \frac{\partial \pi(e_i,p_i)}{\partial p_i} & \text{if } i = j \\ 0 & \text{if } i \neq j \end{cases}$ and $\frac{\partial \pi(e_i,p_i)}{\partial p_i} < 0$. Global asymptotic stability of p^* for any dynamics (9) that satisfies the conditions of Theorem 3 follows from the fact that $W(p) \equiv \max_{1 \leq i \leq H} \pi(e_i,p)$ is a (decreasing) Lyapunov function (Krivan et al., 2008).

1/3 and 2/3 respectively)). Trajectories for each of these two migration dynamics with the same initial conditions are illustrated in Figure 2 (a) and (b) respectively. As can be seen, both converge to the IFD (as they must by Theorem 3) in finite time, even though their paths to this rational outcome are quite different. For comparison sake, Figure 2 (c) provides the trajectory for the replicator equation.

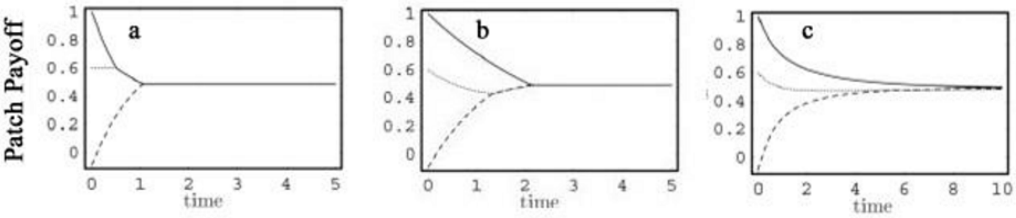

Figure 2. Trajectories for payoffs of the habitat selection game when initially almost all individuals are in patch 2 and patch payoff functions are $\pi(e_1, p) = 1 - p_1, \pi(e_2, p) = 0.8(1 - \frac{10p_2}{9})$ and $\pi(e_3, p) = 0.6(1 - \frac{10p_3}{8})$. (a) best response dynamics with migration matrices of the form $I^1(p)$; (b) dynamics for non-ideal animals with migration matrices of the form $I^2(p)$; and (c) the replicator equation. In all panels, the top curve is the payoff in patch 1, the middle curve in patch 3 and the bottom curve in patch 2. The IFD (which is approximately $(p_1, p_2, p_3) = (0.51, 0.35, 0.14)$ with payoff 0.49) is reached at the smallest t where all three curves are the same (this takes infinite time in panel c).

Fretwell and Lucas (1969) briefly consider their IFD concept when patch fitness increases with patch density when density is low (the so-called Allee effect). Although Theorem 3 no longer applies, these habitat selection games are still potential games (but not strictly stable). Thus, each interior trajectory under many game dynamics (including the replicator equation and best response dynamics) converge to a NE (Sandholm, 2010). Several NE are already possible for a given two-patch model (Morris, 2002), some of which are locally asymptotically stable and some not (Krivan, 2014; Cressman and Tran, 2015). From these references, it is clear that there is a difference of opinion whether to define IFD as any of these NE or restrict the concept to only those that are locally superior and/or asymptotically stable.

Habitat selection games also provide a natural setting for the effect of evolving population sizes, a topic of obvious importance in population biology that has so far received little attention in models of social behavior.

A "population-migration" dynamics emerges if population size N evolves through fitness taken literally as reproductive success (Cressman and Krivan, 2013; Broom and Krivan's chapter, this volume). As discussed there, if patch fitness is positive when unoccupied, decreases with patch density and eventually becomes negative, then the system evolves to carrying capacity whenever the migration matrix $I(p;N)$ satisfies the two conditions in Theorem 3 for each population size N. In particular, the evolutionary outcome is independent of the time scale of migration compared to that of changing population size, a notable result since it is often not true when two dynamical processes are combined (Cressman and Krivan, 2013).

3 Symmetric Games with a Continuous Trait Space

It was recognized early on that the relationship between evolutionary outcomes and the ESS concept is more complex when an individual's pure strategy (or trait) is taken from a continuum. As stated by Maynard Smith (1982, Appendix D), "Eshel (1983) and A. Grafen (personal communication) have independently noticed a criterion for the stability of an ESS which is different in kind ... when the strategy set is a continuous one." Although Eshel and Grafen (see also Eshel and Motro, 1981) both came to this realization by analyzing examples of evolutionary outcomes for games from biology (e.g. stable sex ratios; investment in a competitive trait) or economics (e.g. adaptation of prices to demand), the issues that arise can already be illustrated by the following elementary mathematical example.

Consider the symmetric game whose pure strategy set S is parameterized by real number v in an interval that contains 0 in its interior. Suppose the payoff $\pi(v,u)$ of strategy v against strategy u has the form

$$\pi(v,u) = av^2 + buv \tag{11}$$

where a and b are fixed parameters (which are real numbers). It is straightforward to check that 0 is a strict NE if and only if $a < 0$.[13] Then, with the assumption that $a < 0$, $u^* = 0$ is an ESS according to Definition 1 (a) and (b) and so cannot be invaded.[14]

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[13] Specifically, $\pi(v,0) = av^2 < 0 = \pi(0,0)$ for all $v \neq 0$ if and only if $a < 0$.

[14] Much of the literature on evolutionary games for continuous trait space uses the term

On the other hand, a strategy v against a monomorphic population using strategy u satisfies

$$\pi(v,u) > \pi(u,u) \text{ if and only if } (v-u)[a(v+u)+bu] > 0. \tag{12}$$

For v close to $u \neq 0$, $a(v+u)+bu \cong (2a+b)u$. Thus, if $2a+b>0$, then strategy v close to $u \neq 0$ can invade if v is farther from $u^* = 0$ than u (since $\pi(v,u) > \pi(u,u)$) but cannot invade if it is closer to u^* than u. Thus, if the system is slightly perturbed from $u^* = 0$ to $u \neq 0$, the monomorphic population will evolve away from u^*. That is, although the strict NE $u^* = 0$ when $a < 0$ cannot be invaded, it is not attainable as an outcome of evolution when $2a + b > 0$.

This result led Eshel (1983) to propose the continuously stable strategy (CSS) concept that requires more than u^* being a strict NE and others to develop (the canonical equation of) adaptive dynamics (see Definition 2 below and the literature cited there). Furthermore, although a strict NE is automatically locally superior for matrix games (as in Theorem 2(a)), this is no longer true for games with continuous trait space. This discrepancy leads to the concept of a neighborhood invader strategy (NIS) in Section 3.2 below that is closely related to stability with respect to the replicator equation (see Theorem 4 there).

3.1 The CSS and adaptive dynamics

To avoid mathematical technicalities that arise in threshold cases, the following definition assumes that, if u^* is a pure strategy NE in the interior of an interval S that is the pure-strategy set of the evolutionary game, then u^* is a strict NE.

Definition 2. (a) A strict NE u^* in the interior of a one-dimensional continuous strategy set is a CSS if, for some $\varepsilon > 0$ and any u with $| u - u^* | < \varepsilon$, there is a $\delta > 0$ such that, for $| v - u | < \delta$, $\pi(v,u) > \pi(u,u)$ if and only if $| v - u^* | < | u - u^* |$.[15]

ESS to denote a strategy that is uninvadable in this sense. However, this usage is not universal. Since ESS has in fact several possible connotations for games with continuous trait space (Apaloo et al., 2009), we prefer to use the more neutral game-theoretic term of strict NE in these circumstances when the game has a continuous trait space.

[15] Typically, $\delta > 0$ depends on u (e.g. $\delta < | u - u^* |$). Sometimes the assumption that u^* is a strict NE is relaxed to the condition of being a neighborhood (or local) strict NE (i.e. for some $\varepsilon > 0$, $\pi(v,u) < \pi(u,u)$ for all $0 < | v - u | < \varepsilon$).

(b) Up to a change in time scale, the canonical equation of adaptive dynamics is

$$\dot{u} = \frac{\partial \pi(v,u)}{\partial v} \mid_{v=u} \equiv \pi_1(u,u). \tag{13}$$

(c) An interior u^* is called convergence stable if it is locally asymptotically stable under (13).

To paraphrase Eshel (1983), the intuition behind Definition 2(a) is that, if a large majority of a population chooses a strategy close enough to a CSS, then only those mutant strategies which are even closer to the CSS will be selectively advantageous.

The canonical equation of adaptive dynamics (13) is the most elementary dynamics to model evolution in a one-dimensional continuous strategy set. It assumes that the population is always monomorphic at some $u \in S$ and that u evolves through trait substitution in the direction v of nearby mutants that can invade due to their higher payoff than u when playing against this monomorphism. Adaptive dynamics (13) was introduced by Hofbauer and Sigmund (1990) assuming monomorphic populations. It was given a more solid interpretation when populations are only approximately monomorphic by Dieckmann and Law (1996) (see also Vincent and Brown, 2005; Dercole and Rinaldi, 2008) where $\dot{u} = k(u)\pi_1(u,u)$ and $k(u)$ is a positive function that scales the rate of evolutionary change. Typically, adaptive dynamics is restricted to models for which $\pi(v,u)$ has continuous partial derivatives up to (at least) second order.[16] Since invading strategies are assumed to be close to the current monomorphism, their success can then be determined through a local analysis.

Historically, convergence stability was introduced earlier than the canonical equation as a u^* that satisfies the second part of Definition 2 (a).[17] In

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[16] In particular, adaptive dynamics is not applied to examples such as the War of Attrition, the original example of a symmetris evolutionary game with a continuous trait space (Maynard Smith, 1974, 1982; Broom and Krivan, this volume), which have discontinuous payoff functions. In fact, by allowing invading strategies to be far away or individuals to play mixed strategies, it is shown in these references that the evolutionary outcome for the War of Attrition is a continuous distribution over the interval S. Distributions also play a central role in the following section. Note that, in Section 3, subscripts on π denote partial derivatives. For instance, the derivative of π with respect to the first argument is denoted by π_1 in (13). For the asymmetric games of Section 4, π_1 and π_2 denote the payoffs to player one and to player two respectively.

[17] This concept was first called m-stability by Taylor (1989) and then convergence sta-

particular, a convergence stable u^* may or may not be a strict NE. Furthermore, u^* is a CSS if and only if it is a convergence stable strict NE. These subtleties can be seen by applying Definition 2 to the game with quadratic payoff function (11) whose corresponding canonical equation is $\dot{u} = (2a+b)u$. The rest point (often called a singular point in the adaptive dynamics literature) $u^* = 0$ of (13) is a strict NE if and only if $a < 0$ and convergence stable if and only if $2a + b < 0$. From (12), it is clear that u^* is a CSS if and only if it is convergence stable and a strict NE.

That the characterization[18] of a CSS as a convergence stable strict NE extends to general $\pi(v, u)$ can be seen from the Taylor expansion of $\pi(u, v)$ about (u^*, u^*) up to second order; namely,

$$\begin{aligned}\pi(u,v) &= \pi(u^*,u^*) + \pi_1(u^*,u^*)(u-u^*) + \pi_2(u^*,u^*)(v-u^*) \\ &\quad + \frac{1}{2}\pi_{11}(u^*,u^*)(u-u^*)^2 + \pi_{12}(u^*,u^*)(u-u^*)(v-u^*) \qquad (14) \\ &\quad + \frac{1}{2}\pi_{22}(u^*,u^*)(v-u^*)^2 + \text{ higher order terms.}\end{aligned}$$

That is, u^* is convergence stable if and only if $\pi_1(u^*, u^*) = 0$ and $\pi_{11}(u^*, u^*) + \pi_{12}(u^*, u^*) < 0$ since $\frac{d}{du}\left[\frac{\partial \pi(v,u)}{\partial v}\mid_{v=u}\right]\mid_{u=u^*} = \pi_{11}(u^*, u^*) + \pi_{12}(u^*, u^*)$. It is a CSS if and only if it is a neighborhood strict NE (i.e. $\pi_1(u^*, u^*) = 0$ and $\pi_{11}(u^*, u^*) < 0$) that is convergence stable. From now on, assume all partial derivatives are evaluated at (u^*, u^*) (e.g. $\pi_{11} = \pi_{11}(u^*, u^*)$).

Since conditions for convergence stability are independent of those for strict NE, there is a diverse classification of singular points. Circumstances where a rest point u^* of (13) is convergence stable but not a strict NE (or vice versa) have received considerable attention in the literature. In particular, u^* can be a convergence stable rest point without being a neighborhood strict NE (i.e. $\pi_1 = 0$, $\pi_{11} + \pi_{12} < 0$ and $\pi_{11} > 0$). These have been called evolutionarily stable minima (Abrams et al., 1993)[19] and bifurcation points (Brown and Pavlovic, 1992) that produce evolutionary branching (Geritz et al., 1998) via adaptive speciation (Cohen et al, 1999; Doebeli and Dieckmann,

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bility by Christiansen (1991), the latter becoming standard usage. It is straightforward to show that the original definition is equivalent to Definition 2 (c).

[18] This general characterization of a CSS ignores threshold cases where $\pi_{11}(u^*, u^*) = 0$ or $\pi_{11}(u^*, u^*) + \pi_{12}(u^*, u^*) = 0$. We assume throughout Section 3 that these degenerate situations do not arise for our payoff functions $\pi(v, u)$.

[19] We particularly object to this phrase since it causes great confusion with the ESS concept. We prefer calling these evolutionary branching points.

2003; Ripa et al., 2009). For (11), the evolutionary outcome is then a stable dimorphism supported on the endpoints of the interval S when (the canonical equation of) adaptive dynamics is generalized beyond the monomorphic model to either the replicator equation (see Remark 2 in Section 3.2) or to the Darwinian dynamics of Section 3.3.

Conversely, u^* can be a neighborhood strict NE without being a convergence stable rest point (i.e. $\pi_1 = 0$, $\pi_{11} + \pi_{12} > 0$ and $\pi_{11} < 0$). We now have bistability under (13) with the monomorphism evolving to one of the endpoints of the interval S.

3.2 The NIS and the replicator equation

The replicator equation (4) of Section 2 has been generalized to symmetric games with continuous trait space S by Bomze and Pötscher (1989) (see also Bomze, 1991; Oechssler and Riedel, 2001). When payoffs result from pairwise interactions between individuals and $\pi(v,u)$ is interpreted as the payoff to v against u, then the expected payoff to v in a random interaction is $\pi(v,P) \equiv \int_S \pi(v,u)P(du)$ where P is the probability measure on S corresponding to the current distribution of the population's strategies. With $\pi(P,P) \equiv \int_S \pi(v,P)P(dv)$ the mean payoff of the population and B a Borel subset of S, the replicator equation given by

$$\frac{dP_t}{dt}(B) = \int_B \left(\pi(u,P_t) - \pi(P_t,P_t)\right) P_t(du) \tag{15}$$

is well-defined on the set of Borel probability measures $P \in \Delta(S)$ if the payoff function is continuous (Oechssler and Riedel, 2001). The replicator equation describes how the population strategy distribution $P \in \Delta(S)$ evolves over time. From this perspective, the canonical equation (13) becomes a heuristic tool that approximates the evolution of the population mean by ignoring effects due to the diversity of strategies in the population (Cressman and Tao, 2014).

For instance, if B is a subinterval of S, (15) describes how the proportion $P_t(B)$ of the population with strategy in this set evolves over time. In general, B can be any Borel subset of S (i.e. any element of the smallest $\sigma-$algebra that contains all subintervals of S). In particular, if B is the finite set $\{u_1, ..., u_m\}$ and $P_0(B) = 1$ (i.e. the population initially consists of m strategy-types), then $P_t(B) = 1$ for all $t \geq 1$ and (15) becomes the replicator equation (4) for the matrix game with $m \times m$ payoff matrix whose entries are $A_{ij} = \pi(u_i, u_j)$.

Unlike adaptive dynamics, a CSS may no longer be stable for the replicator equation (15). To see this, a topology on $\Delta(S)$ is needed. In the weak topology, $Q \in \Delta(S)$ is close to a $P \in \Delta(S)$ with finite support $\{u_1, ..., u_m\}$ if the $Q-$measure of a small neighborhood of each u_i is close to $P(\{u_i\})$ for all $i = 1, ..., m$. In particular, if the population P is monomorphic at a CSS u^* (i.e. P is the Dirac delta distribution δ_{u^*} with all of its weight on u^*), then any neighborhood of P will include all populations whose support is close enough to u^*. Thus, stability of (15) with respect to the weak topology requires that P_t evolves to δ_{u^*} whenever P_0 has support $\{u, u^*\}$ where u is near enough to u^*. That is, u^* must be globally asymptotically stable for the replicator equation (4) of Section 2 applied to the two-strategy matrix game with payoff matrix (c.f. (5))

$$\begin{array}{cc} & \begin{array}{cc} u^* & u \end{array} \\ \begin{array}{c} u^* \\ u \end{array} & \left[\begin{array}{cc} \pi(u^*, u^*) & \pi(u^*, u) \\ \pi(u, u^*) & \pi(u, u) \end{array} \right] \end{array} .$$

Ignoring threshold circumstances again, u^* must strictly dominate u in this game (i.e. $\pi(u^*, u^*) > \pi(u, u^*)$ and $\pi(u^*, u) > \pi(u, u)$).

When this dominance condition is applied to the game with payoff function (11), $u^* = 0$ satisfies $\pi(u^*, u^*) > \pi(u, u^*)$ (respectively, $\pi(u^*, u) > \pi(u, u)$) if and only if $a < 0$ (respectively $a + b < 0$). Thus, if u^* is a strict NE (i.e. $a < 0$) and $2a + b < 0 < a + b$, then u^* is a CSS that is an unstable rest point of (15) with respect to the weak topology.

For general payoff functions, a monomorphic population δ_{u^*} is a stable rest point of (15) with respect to the weak topology if and only if $\pi(u^*, u^*) > \pi(u, u^*)$ and $\pi(u^*, u) > \pi(u, u)$ for all u sufficiently close but not equal to u^*.[20] This justifies the first part of the following definition.

Definition 3. Consider a symmetric game with continuous trait space S.

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[20] Here, stability means that δ_{u^*} is neighborhood attracting (i.e. for any initial distribution P_0 with support sufficiently close to u^* and with $P_0(u^*) > 0$, P_t converges to δ_{u^*} in the weak topology). As explained in Cressman (2011) (see also Cressman et al., 2006), one cannot assert that δ_{u^*} is locally asymptotically stable under the replicator equation with respect to the weak topology or consider initial distributions with $P_0(u^*) = 0$. The support of P is the closed set given by $\{u \in S \mid P(\{y : \mid y - u \mid < \varepsilon\}) > 0 \text{ for all } \varepsilon > 0\}$.

(a) $u^* \in S$ is a neighborhood invader strategy (NIS) if $\pi(u^*, u) > \pi(u, u)$ for all u sufficiently close but not equal to u^*. It is a neighborhood strict NE if $\pi(u^*, u^*) > \pi(u, u^*)$ for all u sufficiently close but not equal to u^*.
(b) Suppose $0 \leq p^* < 1$ is fixed. Strategy $u^* \in S$ is *neighborhood* p^**-superior* if $\pi(u^*, P) > \pi(P, P)$ for all $P \in \Delta(S)$ with $1 > P(\{u^*\}) \geq p^*$ and the support of P sufficiently close to u^*. It is *neighborhood superior* (respectively, *neighborhood half-superior*) if $p^* = 0$ (respectively, $p^* = \frac{1}{2}$). Strategy $u^* \in S$ is *globally* p^**-superior* if $\pi(u^*, P) > \pi(P, P)$ for all $P \in \Delta(S)$ with $1 > P(\{u^*\}) \geq p^*$.

The NIS concept was introduced by Apaloo (1997) (see also McKelvey and Apaloo (1995), the "good invader" strategy of Kisdi and Meszéna (1995), and the "invading when rare" strategy of Courteau and Lessard (2000)). Cressman and Hofbauer (2005) developed the neighborhood superiority concept (they called it local superiority), showing its essential equivalence to stability under the replicator equation (15). It is neighborhood p^*-superiority that unifies the concepts of strict NE, CSS, and NIS as well as stability with respect to adaptive dynamics and with respect to the replicator equation for games with a continuous trait space. These results are summarized in the following theorem.

Theorem 4. Suppose that S is one dimensional and $u^* \in \text{int}(S)$ is a rest point of adaptive dynamics (13) (i.e. $\pi_1(u^*, u^*) = 0$).
(a) u^* is a NIS and a neighborhood strict NE if and only if it is neighborhood superior.
(b) u^* is neighborhood attracting with respect to the replicator equation (15) if and only if it is neighborhood superior.
(c) u^* is a neighborhood strict NE if and only if it is neighborhood p^*-superior for some $0 \leq p^* < 1$.
(d) u^* is a CSS if and only if it is neighborhood half-superior if and only if it is a neighborhood strict NE that is locally asymptotically stable with respect to adaptive dynamics (13).

The proof of Theorem 4 relies on results based on the Taylor expansion (14). For instance, along with the characterizations of a strict NE as $\pi_{11} < 0$ and convergence stability as $\pi_{11} + \pi_{12} < 0$ from Section 3.1, u^* is a NIS if and only if $\frac{1}{2}\pi_{11} + \pi_{12} < 0$. Thus, strict NE, CSS and NIS are clearly distinct concepts for a game with a continuous trait space. On the other hand, it is also clear that a strict NE that is a NIS is automatically CSS.[21]

Remark 1. When Definition 3 (b) is applied to matrix games with the standard topology on the mixed strategy space Δ^m, the bilinearity of the payoff function implies that p is neighborhood p^*-superior for some $0 \leq p^* < 1$ if and only if $\pi(p, p') > \pi(p', p')$ for all p' sufficiently close but not equal to p (i.e. if and only if p is an ESS by Theorem 2 (a)). That is, neighborhood p^*-superiority is independent of the value of p^* for $0 \leq p^* < 1$. Consequently, the ESS, NIS, and CSS are identical for matrix games or, to rephrase, NIS and CSS of Section 3 are different generalizations of the matrix game ESS to games with continuous trait space.

Remark 2. It was shown above that a CSS u^* which is not a NIS is unstable with respect to the replicator equation by restricting the continuous trait space to finitely many nearby strategies. However, if the replicator equation (15) is only applied to distributions with interval support, Cressman and Hofbauer (2005) have shown, using an argument based on the iterated elimination of strictly dominated strategies, that a CSS u^* attracts all initial distributions whose support is a small interval containing u^*. This gives a measure-theoretic interpretation of Eshel's (1983) original idea that a population would move toward a CSS by successive invasion and trait substitution. The proof in Cressman and Hofbauer (2005) is most clear for the game with quadratic payoff function (11).

In fact, for these games, Cressman and Hofbauer (2005) give a complete analysis of the evolutionary outcome under the replicator equation for initial distributions with interval support $[\alpha, \beta]$ containing $u^* = 0$. Of particular interest is the outcome when u^* is an evolutionary branching point (i.e. it is convergence stable ($2a + b < 0$) but not a strict NE ($a > 0$)). It can then be shown that a dimorphism P^* supported on the endpoints of the interval attracts all such initial distributions except the unstable δ_{u^*}.[22]

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[21] This result is often stated as ESS + NIS implies CSS (e.g. Apaloo, 1997; Apaloo et al., 2009). Furthermore, an ESS + NIS is often denoted ESNIS in this literature.

[22] In fact, $P^* = -\frac{(a+b)\alpha + a\beta}{b(\beta-\alpha)}\delta_\beta + \frac{(a+b)\beta + a\alpha}{b(\beta-\alpha)}\delta_\alpha$ since this dimorphism satisfies $\pi(P^*, Q) > \pi(Q, Q)$ for all distributions Q not equal to P^* (i.e. P^* is globally superior by the natural extension of Definition 3 (b) to non monomorphic P^* as developed by Cressman and Hofbauer (2005)).

3.3 Darwinian Dynamics and the Maximum Principle

The processes of biological evolution are inherently dynamic. Of fundamental importance is the size of the population(s) and how this evolves in the ecological system. Thus any theory of evolutionary games is incomplete without methods to address both population dynamics and strategy evolution. Sections 3.1 and 3.2 discuss two dynamics for strategy evolution when the trait space is continuous; namely, adaptive dynamics and the replicator equation respectively. Here we present the so called Darwinian Dynamics (Vincent et al. 1993, Vincent and Brown 2005) that also considers changing population size.[23] The development of this evolutionary and ecological dynamics is informed by Darwin's postulates. The key component of the method is the fitness generating function (or, for short, G-function) which is given as follows.

Suppose the incumbent population currently has individuals using traits $u_1, ..., u_r$ taken from a continuous valued trait v in an interval S. Let $n_i > 0$ be the number of individuals using trait u_i. Then the population state is given by $(\mathbf{u}, \mathbf{n})$ where $\mathbf{u} = (u_1, ..., u_r)$ and $\mathbf{n} = (n_1, ..., n_r)$. The fitness generating function, $G(v, \mathbf{u}, \mathbf{n})$, gives the expected per capita growth rate of a focal individual using strategy $v \in S$ when the population is in state $(\mathbf{u}, \mathbf{n})$. Interpreting this rate as reproductive success (or fitness), n_i evolves according to the population (or ecological) dynamics, $\frac{dn_i}{dt} = n_i G\left(v, \mathbf{u}, \mathbf{n}\right) \mid_{v=u_i} = n_i G\left(u_i, \mathbf{u}, \mathbf{n}\right)$. Strategy evolution follows the adaptive dynamics approach; namely, $\frac{du_i}{dt} = k_i \frac{\partial G(v,\mathbf{u},\mathbf{n})}{\partial v} \mid_{v=u_i}$for $i = 1, \cdots, r$, where k_i is positive and represents some measure of additive genetic variance. However we will assume for simplicity that the k_i's are all the same and have common value denoted by k. Darwinian dynamics is then modeled by combining these two processes to produce the following system of differential equations:

$$\frac{dn_i}{dt} = n_i G\left(u_i, \mathbf{u}, \mathbf{n}\right) \text{ for } i = 1, ..., r \qquad \textbf{(ecological dynamics)} \tag{16}$$

and

$$\frac{du_i}{dt} = k \frac{\partial G(v, \mathbf{u}, \mathbf{n})}{\partial v} \mid_{v=u_i} \text{ for } i = 1, ..., r \ \textbf{(evolutionary dynamics)} \tag{17}$$

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[23] Although Darwinian dynamics can also be based solely on changing strategy frequency with population size fixed (Vincent and Brown, 2005), the theory developed here considers changing population size combined with strategy evolution.

The rest points $(\mathbf{u}^*, \mathbf{n}^*)$ of this resident system with all components of $\mathbf{u}^*$ different and with all components of $\mathbf{n}^*$ positive that are locally (globally) asymptotically stable are expected to be the outcomes in a corresponding local (or global) sense for this r strategy resident system.

As an elementary example, the payoff function (11) can be extended to include population size:

$$\begin{aligned} G(v, \mathbf{u}, \mathbf{n}) &= \pi\left(v, \tfrac{u_1 n_1 + u_2 n_2 + \ldots + u_r n_r}{n_1 + n_2 + \ldots + n_r}\right) + 1 - (n_1 + n_2 + \ldots + n_r) \\ &= av^2 + b\left(\tfrac{u_1 n_1 + u_2 n_2 + \ldots + u_r n_r}{n_1 + n_2 + \ldots + n_r}\right) v + 1 - (n_1 + n_2 + \ldots + n_r)\,. \end{aligned} \tag{18}$$

The story behind this mathematical example is that v plays one random contest per unit time and receives an expected payoff $\pi\left(v, \frac{u_1 n_1 + u_2 n_2 + \ldots + u_r n_r}{n_1 + n_2 + \ldots + n_r}\right)$ since the average strategy in the population is $\frac{u_1 n_1 + u_2 n_2 + \ldots + u_r n_r}{n_1 + n_2 + \ldots + n_r}$. The term $1 - (n_1 + n_2 + \ldots + n_r)$ is a strategy-independent background fitness so that fitness decreases with total population size.

For $r = 1$, $G(v, u; n) = av^2 + buv + 1 - n$. From this, the Darwinian dynamics is

$$\begin{aligned} \tfrac{dn}{dt} &= nG(v, u; n) \mid_{v=u} = n\left((a+b)u^2 + 1 - n\right) \\ \tfrac{du}{dt} &= k\tfrac{\partial G(v,u;n)}{\partial v} \mid_{v=u} = k(2a + b)u. \end{aligned} \tag{19}$$

The rest point of the evolutionary dynamics (i.e. $\frac{du}{dt} = 0$) is $u = 0$. With $u = 0$, the relevant rest point of the ecological dynamics (i.e. $\frac{dn}{dt} = 0$) is $n = 1$. The rest point $(u^*, n^*) = (0, 1)$ of (19) is globally asymptotically stable for this resident system if and only if u^* is convergence stable for adaptive dynamics (i.e. $2a + b < 0$) when population size is fixed at $n^* = 1$.

However, to be a stable evolutionary outcome, $(u^*, n^*) = (0, 1)$ must resist invasion by any mutant strategy using strategy $v \neq u^* = 0$. Since the invasion fitness is $G(v, u^*, n^*) = av^2$, this requires that u^* is a strict NE (i.e. $a < 0$) when population size is fixed at n^*. That is, $(u^*, n^*) = (0, 1)$ is a stable evolutionary outcome for Darwinian dynamics with respect to the G-function (18) if and only if u^* is a CSS.[24]

Now suppose that $u^* = 0$ is convergence stable but not a strict NE (i.e. $a > 0$ and $2a + b < 0$) and so can be invaded by $v \neq 0$ since $G(v, u^*, n^*) > 0$. We then look for a dimorphism $(\mathbf{u}^*, \mathbf{n}^*) = (u_1^*, u_2^*, n_1^*, n_2^*)$ of the resident

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[24] As in Section 3.1, we ignore threshold cases. Here, we assume that a and $2a + b$ are both non-zero.

system (i.e. $r = 2$) for Darwinian dynamics with respect to the G-function (18). That is, we consider the four-dimensional dynamical system

$$\begin{aligned}
\frac{dn_1}{dt} &= n_1 G(v, u_1, u_2; n_1, n_2) \mid_{v=u_1} = n_1 \left(a u_1^2 + b u_1 \frac{u_1 n_1 + u_2 n_2}{n_1 + n_2} + 1 - (n_1 + n_2) \right) \\
\frac{dn_2}{dt} &= n_2 G(v, u_1, u_2; n_1, n_2) \mid_{v=u_2} = n_2 \left(a u_2^2 + b u_2 \frac{u_1 n_1 + u_2 n_2}{n_1 + n_2} + 1 - (n_1 + n_2) \right) \\
\frac{du_1}{dt} &= \frac{\partial G(v, u_1, u_2; n_1, n_2)}{\partial v} \mid_{v=u_1} = k \left(2 a u_1 + b \frac{u_1 n_1 + u_2 n_2}{n_1 + n_2} \right) \\
\frac{du_2}{dt} &= \frac{\partial G(v, u_1, u_2; n_1, n_2)}{\partial v} \mid_{v=u_2} = k \left(2 a u_2 + b \frac{u_1 n_1 + u_2 n_2}{n_1 + n_2} \right).
\end{aligned}$$

From the evolutionary dynamics, a rest point must satisfy $2au_1 = 2au_2$ and so $u_1 = u_2$ (since we assume that $a \neq 0$). That is, this two-strategy resident system has no relevant stable rest points since this requires $u_1^* \neq u_2^*$. However, it also follows from this dynamics that $\frac{d(u_1 - u_2)}{dt} = 2ka\,(u_1 - u_2)$, suggesting that the dimorphic strategies are evolving as far as possible from each other since $ka > 0$. Thus, if the strategy space S is restricted to the bounded interval $[-\beta, \beta]$, we might expect that u_1 and u_2 evolve to the endpoints β and $-\beta$, respectively. With $(u_1^*, u_2^*) = (\beta, -\beta)$, a positive equilibrium (n_1^*, n_2^*) of the ecological dynamics must satisfy $u_1 n_1 + u_2 n_2 = 0$, and so $n_1^* = n_2^* = \frac{1+a\beta^2}{2}$. That is, the rest point is $(u_1^*, u_2^*, n_1^*, n_2^*) = \left(\beta, -\beta; \frac{1+a\beta^2}{2}, \frac{1+a\beta^2}{2}\right)$ and it is locally asymptotically stable.[25] Furthermore, it resists invasion by mutant

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[25] Technically, at this rest point, $\frac{du_1}{dt} = 2ka\beta > 0$ and $\frac{du_2}{dt} = -2ka\beta < 0$ are not 0. However, their sign (positive and negative, respectively) means that the dimorphism strategies would evolve past the endpoints of S, which is impossible given the constraint on the strategy space.

These signs mean that local asymptotic stability follows from the linearization of the ecological dynamics at the rest point. It is straightforward to confirm this 2×2 Jacobian matrix has negative trace and positive determinant (since $a > 0$ and $b < 0$), implying both eigenvalues have negative real part.

The method can be generalized to show that, if $S = [\alpha, \beta]$ with $\alpha < 0 < \beta$, the stable evolutionary outcome predicted by Darwinian dynamics is now $u_1^* = \beta, u_2^* = \alpha$ with $n_1^* = (a\alpha\beta - 1)\frac{(a+b)\alpha + a\beta}{b(\beta - \alpha)}, n_2^* = (1 - a\alpha\beta)\frac{(a+b)\beta + a\alpha}{b(\beta - \alpha)}$ both positive under our assumption that $a > 0$ and $2a+b < 0$. In fact, this is the same stable dimorphism (up to the population size factor $1 - a\alpha\beta$) given by the replicator equation of Section 3.2 (see Remark 2).

strategies since

$$\begin{aligned} G(v, u_1^*, u_2^*, n_1^*, n_2^*) &= av^2 + bv\frac{u_1^* n_1^* + u_2^* n_2^*}{n_1^* + n_2^*} + 1 - (n_1^* + n_2^*) \\ &= a\left(v^2 - \beta^2\right) < 0 \end{aligned}$$

for all $v \in S$ different from u_1^* and u_2^*.

To summarize the above discussion of Darwinian dynamics applied to G-function (18) on the interval $[\beta, -\beta]$, $(u^*, n^*) = (0, 1)$ is a stable evolutionary outcome if and only if u^* is a CSS (i.e. $a < 0$ and $2a + b < 0$). On the other hand, if $a > 0$ and $2a + b < 0$, then there is evolutionary branching and the dimorphism $(\mathbf{u}^*, \mathbf{n}^*) = \left(\beta, -\beta; \frac{1+a\beta^2}{2}, \frac{1+a\beta^2}{2}\right)$ becomes a stable evolutionary outcome. These two results are shown in Figure 3 (see regions II and III there respectively) along with the stable evolutionary outcomes in other regions of parameter space a and b. For instance, although we do not have a complete analysis of Darwinian dynamics with r traits initially present, our simulations suggest that, in region I which contains the first quadrant, a bistable situation arises whereby almost all trajectories converge to one of the monomorphisms supported at one end of the interval. Similarly, in the fourth quadrant (which comprises the evolutionary branching region III as well as region IV), we expect all trajectories to converge to the dimorphism.

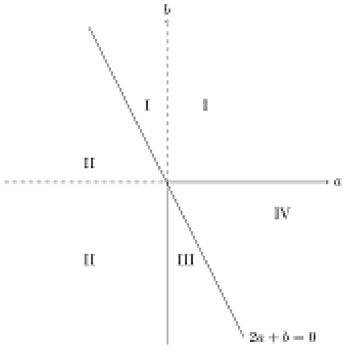


Figure 3. Stable evolutionary outcomes for G-function (18) on the interval $[\beta, -\beta]$. From the theoretical analysis, there are four regions of parameter space (given by a and b) of interest. In region I, there are two stable evolutionary outcomes that are monomorphisms (u^*, n^*) given by $(\beta, 1 + (a + b)\beta^2)$ and $(-\beta, 1 + (a + b)\beta^2)$. In region II, the only stable evolutionary outcome is the CSS $(u^*, n^*) = (0, 1)$. In region III (evolutionary

branching) and IV, the only stable evolutionary outcome is the dimorphism $(\mathbf{u}^*, \mathbf{n}^*) = \left(\beta, -\beta; \frac{1+a\beta^2}{2}, \frac{1+a\beta^2}{2}\right)$.

In fact, the use of Darwinian dynamics to confirm the results of Figure 3 can be generalized to find stable evolutionary outcomes when their analysis become theoretically intractable. That is, if

(i) the Darwinian dynamics for an r strategy system converges to a locally asymptotically stable equilibrium with all strategies present and
(ii) this r strategy equilibrium remains stable when the system is increased to $r+1$ strategies by introducing a new strategy (i.e. one strategy dies out),
then we expect this equilibrium to be a stable evolutionary outcome.

On the other hand, the following Maximum Principle can often be used to find these stable evolutionary outcomes without the dynamics (or, conversely, to check that an equilibrium outcome found by Darwinian dynamics may in fact be a stable evolutionary outcome).

Theorem 5 (Maximum Principle). Suppose that $(\mathbf{u}^*, \mathbf{n}^*)$ is an asymptotically stable rest point for Darwinian dynamics (16) and (17) applied to a resident system. If $(\mathbf{u}^*, \mathbf{n}^*)$ is a stable evolutionary outcome, then

$$\max_{v \in S} G\left(v, \mathbf{u}^*, \mathbf{n}^*\right) = G\left(v, \mathbf{u}^*, \mathbf{n}^*\right)|_{v=u_i^*} = 0. \tag{20}$$

This fundamental result promoted by Vincent and Brown (see, for instance, their 2005 book) gives biologists the candidate solutions they should consider when looking for stable evolutionary outcomes to their biological systems. That is, by plotting the G-function as a function of v for a fixed candidate $(\mathbf{u}^*, \mathbf{n}^*)$, the maximum fitness must never be above 0 (otherwise, such a v could invade) and, furthermore, the fitness at each component strategy u_i^* in the $r-$strategy resident system $\mathbf{u}^*$ must be 0 (otherwise, u_i^* is not at a rest point of the ecological system). For many cases, $\max_{v \in S} G\left(v, \mathbf{u}^*, \mathbf{n}^*\right)$ occurs only at the component strategies u_i^* in $\mathbf{u}^*$. In these circumstances, $\mathbf{u}^*$ is known as a quasi-strict NE in the game-theoretic literature (i.e. $G\left(v, \mathbf{u}^*, \mathbf{n}^*\right) \leq G\left(u_i, \mathbf{u}^*, \mathbf{n}^*\right)$ for all $i = 1, ..., r$ with equality if and only if $v = u_i^*$ for some i). If $r = 1$, $\mathbf{u}^*$ is a strict NE as remarked in Section 3.1.

When applied to the above example with G-function (18), $(u^*, n^*) = (0, 1)$ satisfies the Maximum Principle if and only if $a < 0$. Thus, an application of this Principle is entirely consistent with the two cases examined above when $2a + b < 0$. However, one must be cautious in assuming there is an equivalence between $(\mathbf{u}^*, \mathbf{n}^*)$ being a stable evolutionary outcome and it satisfying the Maximum Principle. For instance, if $a < 0$ and $2a + b > 0$, then $(u^*, n^*) = (0, 1)$ satisfies the Maximum Principle but it is not a stable evolutionary outcome. This was realized early on by Vincent and Brown who called a $(\mathbf{u}^*, \mathbf{n}^*)$ that satisfies the Maximum Principle a "candidate ESS" (e.g. Vincent and Brown, 2005) which we would prefer to label as a "candidate stable evolutionary outcome".

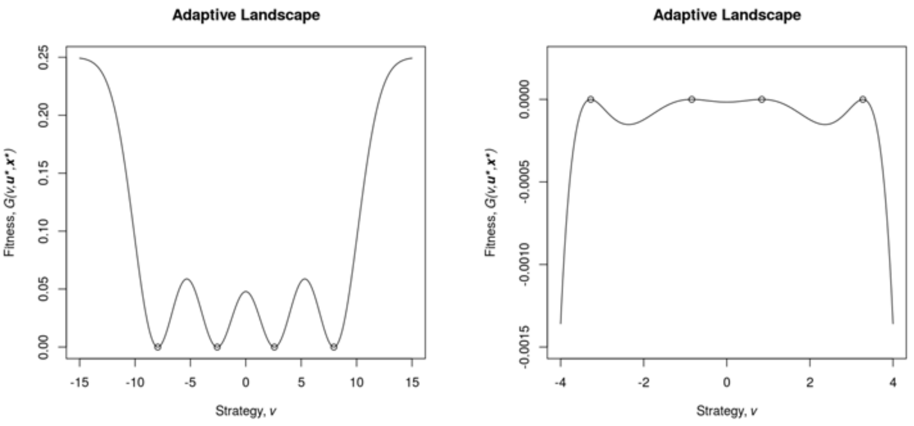
As stated at the beginning of Section 3, the payoff function (11) (and its offshoot (18)) are used for mathematical convenience to illustrate the complex issues that arise for a game with continuous trait space. A more biologically relevant example is the so-called Lotka-Volterra (LV) competition model, whose basic $G-$function is of the form

$$G(v, \mathbf{u}, \mathbf{n}) = \frac{k}{K(v)} \left[K(v) - \sum_{j=1}^{r} a(v, u_j) n_j \right] \tag{21}$$

where $a(v, u_j)$ (the competition coefficient) and $K(v)$ (the carrying capacity) are given by

$$a(v, u_i) = \exp\left[-\frac{(v - u_i)^2}{2\sigma_a^2} \right] \quad \text{and} \quad K(v) = K_m \exp\left[-\frac{v^2}{2\sigma_k^2} \right] \tag{22}$$

respectively with trait space $\mathbf{R}$.



(a) (b)

Figure 4. The $G-$function $G(v, \mathbf{u}^*, \mathbf{n}^*)$ at a stable resident system $(\mathbf{u}^*, \mathbf{n}^*)$ with four traits where u_i^* for $i = 1, 2, 3, 4$ are the $v-$intercepts of the $G-$function (21) on the horizontal axis. (a) For (22), $(\mathbf{u}^*, \mathbf{n}^*)$ does not satisfy the Maximum Principle since $G(v, \mathbf{u}^*, \mathbf{n}^*)$ is at a minimum when $v = u_i^*$. (b) With carrying capacity adjusted so that it is only positive in the interval $(-\beta, \beta)$, $(\mathbf{u}^*, \mathbf{n}^*)$ does satisfy the Maximum Principle. Parameters: $\sigma_a^2 = 4, \sigma_k^2 = 200, K_m = 100, k = 0.1$ and for (b) $\beta = 6.17$.

This particular $G-$function was already examined by Roughgarden (1979) from a non game-theoretic approach,[26] who showed that the expected outcome of evolution for this model is a Gaussian distribution $P^*(u)$ of traits when the width of the niche axis, σ_k, and of the competition coefficient, σ_a, satisfy $\sigma_a < \sigma_k$.[27] Recently, Cressman et al. (2016) have re-examined the basic model as an evolutionary game, using the Darwinian dynamics approach of this section. They show that, for each resident system with r traits, there is a stable equilibrium $(\mathbf{u}^*, \mathbf{n}^*)$ for Darwinian dynamics (16) and (17). However, $(\mathbf{u}^*, \mathbf{n}^*)$ does not satisfy the Maximum Principle (in fact, the components of $\mathbf{u}^*$ are minima of the G-function since $G(v, \mathbf{u}^*, \mathbf{n}^*)\mid_{v=u_i} = 0 < G(v, \mathbf{u}^*, \mathbf{n}^*)$ for all $v \neq u_i^*$ as in Figure 4a). The resultant evolutionary branching leads eventually to $P^*(u)$ as the stable evolutionary outcome. Moreover, they also examined what happens when the trait space is effectively restricted to the compact interval $[-\beta, \beta]$ in place of $\mathbf{R}$ by adjusting the carrying capacity so that it is only positive between $-\beta$ and β. Now, the stable evolutionary outcome is supported on four strategies (Figure 4b), satisfying the Maximum Principle (20).[28]

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[26] Many others (e.g. Bulmer 1974; Sasaki and Ellner 1995; Sasaki 1997; Gyllenberg and Meszéna 2005; Meszéna et al. 2006; Szabó and Meszéna 2006; Barabás and Meszéna 2009; Parvinen and Meszéna 2009; Barabás et al. 2012; Barabás et al. 2013; D'Andrea et al. 2013) have examined the general LV competition model.

[27] Specifically, the Gaussian distribution is given by
$P^*(u) = \frac{K_m \sigma_k}{\sigma_a \sqrt{2\pi(\sigma_k^2 - \sigma_a^2)}} \exp(-u^2/(2(\sigma_k^2 - \sigma_a^2)))$.

[28] Cressman et al. (2016) also examined what happens when there is a baseline competition between all individuals no matter how distant their trait values are. This leads to a stable evolutionary outcome supported on finitely many strategies as well. That is, modifications of the basic LV competition model tend to break up its game-theoretic solution $P^*(u)$ with full support to a stable evolutionary outcome supported on finitely many traits, a result consistent with the general theory developed by Barabás et al. (2012) (see also Gyllenberg and Meszéna, 2005).

3.4 Symmetric games with a multi-dimensional continuous trait space

The replicator equation (15), neighborhood strict NE, NIS and neighborhood p^*-superiority developed in Section 3.2 have straightforward generalizations to multi-dimensional continuous trait spaces. In fact, the definitions there do not assume that S is a subset of $\mathbf{R}$ and Theorem 4(b) on stability of $\mathbf{u}^*$ under the replicator equation remains valid for general subsets S of $\mathbf{R}^n$ (see Theorem 5 (b) below). On the other hand, the CSS and canonical equation of adaptive dynamics (Definition 2) from Section 3.1 do depend on S being a subinterval of $\mathbf{R}$.

For this reason, our treatment of multi-dimensional continuous trait spaces will initially focus on generalizations of the CSS to multi-dimensional continuous trait spaces. Since these generalizations depend on the direction(s) in which mutants are more likely to appear, we assume that S is a compact convex subset of $\mathbf{R}^n$ with $u^* \in S$ in its interior. Following the static approach of Lessard (1990) (see also Meszéna et al., 2001), u^* is a neighborhood CSS if it is a neighborhood strict NE that satisfies Definition 2 (a) along each line through u^*. Furthermore, adaptive dynamics for the multi-dimensional trait spaces S has the form (Cressman, 2009; Leimar, 2009)

$$\frac{du}{dt} = C_1(u)\nabla_1 \pi(v,u) \mid_{v=u} \tag{23}$$

generalizing (13). Here $C_1(u)$ is an $n \times n$ covariance matrix modeling the mutation process (by scaling the rate of evolutionary change) in different directions (Leimar, 2009).[29] We will assume that $C_1(u)$ for $u \in \mathrm{int}(S)$ depends continuously on u. System (23) is called the canonical equation of adaptive dynamics (when S is multi-dimensional). u^* in the interior of S is called convergence stable with respect to $C_1(u)$ if it is a locally asymptotically stable rest point (also called a singular point) of (23).

The statement of the following theorem (and the proof of its various parts given in Cressman (2009) or Leimar (2009)) relies on the Taylor expansion

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[29] Covariance matrices C_1 are assumed to be positive-definite (i.e., for all nonzero $u \in \mathbf{R}^n$, $u \cdot C_1 u > 0$) and symmetric. Similarly, a matrix A is negative-definite if, for all nonzero $u \in \mathbf{R}^n$, $u \cdot Au < 0$.

about (u^*, u^*) of the payoff function; namely,

$$\begin{aligned}\pi(u,v) &= \pi(u^*,u^*) + \nabla_1\pi(u^*,u^*)(u-u^*) + \nabla_2\pi(u^*,u^*)(v-u^*) \\ &\quad + \frac{1}{2}\left[(u-u^*)\cdot A(u-u^*) + 2(u-u^*)\cdot B(v-u^*) + (v-u^*)\cdot C(v-u^*)\right] \\ &\quad + \text{higher order terms.}\end{aligned}$$

Here, ∇_1 and ∇_2 are gradient vectors with respect to u and v respectively (e.g. the i^{th} component of $\nabla_1\pi(u^*,u^*)$ is $\frac{\partial\pi(u',u^*)}{\partial u'_i}\,|_{u'=u^*}$) and A, B, C are the $n \times n$ matrices with ij^{th} entries (all partial derivatives are evaluated at u^*)

$$A_{ij} \equiv \left[\frac{\partial^2}{\partial u'_j \partial u'_i}\pi(u',u^*)\right];\, B_{ij} \equiv \left[\frac{\partial}{\partial u'_i}\frac{\partial}{\partial u_j}\pi(u',u)\right];\, C_{ij} \equiv \left[\frac{\partial}{\partial u'_j}\frac{\partial}{\partial u'_i}\pi(u^*,u')\right].$$

Theorem 6. Suppose $u^* \in \text{int}(S)$ is a rest point of (23) (i.e. $\nabla_1\pi(u^*,u^*) = 0$).
(a) u^* is a neighborhood strict NE if and only if A is negative definite. It is convergence stable for all choices of $C_1(u)$ if and only if $A + B$ is negative definite. It is a CSS if and only if it is neighborhood half-superior if and only if it is a neighborhood strict NE that is convergence stable for all choices of $C_1(u)$.
(b) u^* is a NIS if and only if $\frac{1}{2}A + B$ is negative definite. It is neighborhood superior if and only if it is neighborhood attracting under the replicator equation (15) if and only if it is a NIS that is a neighborhood strict NE.

Clearly, Theorem 6 generalizes the results on strict NE, CSS and NIS given in Theorem 4 of Section 3.2 to games with a multi-dimensional continuous trait space. As we have done throughout Section 3, these statements assume threshold cases (e.g. A or $A+B$ negative semi-definite) do not arise. Based on Theorem 6 (a), Leimar (2009) defines the concept of strong convergence stability as a u^* that is convergence stable for all choices of $C_1(u)$.[30] He goes on to show (see also Leimar, 2001) that, in a more general canonical equation where $C_1(u)$ need not be symmetric but only positive definite, u^* is

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[30] A similar covariance approach was applied by Hines (1980) (see also Cressman and Hines, 1984) for matrix games to show that $p^* \in \text{int}(\Delta^m)$ is an ESS if and only if it is locally asymptotically stable with respect to the replicator equation (4) adjusted to include an arbitrary mutation process.

convergence stable for all such choices (called absolute convergence stability) if and only if $A+B$ is negative definite and symmetric.

In general, if there is no u^* that is a CSS (respectively, neighborhood superior), the evolutionary outcome under adaptive dynamics (respectively, the replicator equation) can be quite complex for a multi-dimensional trait space. This is already clear for multi-variable quadratic payoff functions that generalize (11) as seen by the subtleties that arise for the two dimensional trait space example analyzed by Cressman et al. (2006). These complications are beyond the scope of this chapter.

4 Asymmetric Games

Sections 2 and 3 introduced evolutionary game theory for two fundamental classes of symmetric games (normal form games and games with continuous trait space, respectively). Evolutionary theory also applies to non-symmetric games. An asymmetric game is a multi-player game where the players are assigned one of N roles with a certain probability and, to each role, there is a set of strategies. If it is a two-player game and there is only one role (i.e. $N=1$), we then have a symmetric game as in the previous sections.

This section concentrates on two-player, two-role asymmetric games. These are also called two-species games (roles correspond to species) with intraspecific (respectively, interspecific) interactions among players in the same role (respectively, different roles). Sections 4.1 and 4.2 consider games when the players have finite pure strategy sets $S=\{e_1,e_2,...,e_m\}$ and $T=\{f_1,f_2,...,f_n\}$ in roles one and two, respectively, whereas Section 4.3 has continuous trait spaces in each role.

4.1 Asymmetric Normal Form Games (Two-Player, Two-Role)

Following Selten (1980) (see also van Damme, 1991; Cressman, 2003; Cressman, 2011; Cressman and Tao, 2014), in a two-player asymmetric game with two roles (i.e. $N=2$), the players interact in pairwise contests after they are assigned a pair of roles, k and ℓ, with probability $\rho_{\{k,\ell\}}$. In the two-role asymmetric normal form games, it is assumed that the expected payoffs $\pi_1(e_i;p,q)$ and $\pi_2(f_j;p,q)$ to e_i in role one (or species 1) and to f_j in role two (or species 2) are linear in the components of the population states $p\in\Delta^m$

and $q \in \Delta^n$. One interpretation of linearity is that each player engages in one intraspecific and one interspecific random pairwise interaction per unit time.

A particularly important special class, called truly asymmetric games (Selten, 1980), has $\rho_{\{1,2\}} = \rho_{\{2,1\}} = \frac{1}{2}$ and $\rho_{\{1,1\}} = \rho_{\{2,2\}} = 0$. The only interactions in these games are between players in different roles (or equivalently, $\pi_1(e_i; p, q)$ and $\pi_2(f_j; p, q)$ are independent of p and q, respectively). Then, up to a possible factor of $\frac{1}{2}$ that is irrelevant in our analysis,

$$\pi_1(e_i; p, q) = \sum_{j=1}^{n} A_{ij} q_j = e_i \cdot Aq \text{ and } \pi_2(f_j; p, q) = \sum_{i=1}^{m} B_{ji} p_i = f_j \cdot Bp$$

where A and B are $m \times n$ and $n \times m$ (interspecific) payoff matrices. For this reason, these games are also called bimatrix games.

Evolutionary models based on bimatrix games have been developed to investigate such biological phenomena as male-female contribution to care of offspring in the Battle of the Sexes game of Dawkins (1976) and territorial control in the Owner-Intruder Game (Maynard Smith, 1982).[31] Unlike the biological interpretation of asymmetric games in most of Section 4 that identifies roles with separate species, the two players in both these examples are from the same species but in different roles. In general, asymmetric games can be used to model behavior when the same individual is in each role with a certain probability or when these probabilities depends on the players' strategy choices. These generalizations, which are beyond the scope of this chapter, can affect the expected evolutionary outcome (see, for example, Broom and Rychtar (2013)).

To extend the ESS definition developed in Sections 2.1 and 2.2 to asymmetric games, the invasion dynamics of the resident monomorphic population $(p^*, q^*) \in \Delta^m \times \Delta^n$ by (p, q) generalizes (3) to become

$$\begin{aligned} \dot{\varepsilon}_1 &= \varepsilon_1(1-\varepsilon_1)(\pi_1(p; \varepsilon_1 p + (1-\varepsilon_1)p^*, \varepsilon_2 q + (1-\varepsilon_2)q^*) \\ &\quad -\pi_1(p^*; \varepsilon_1 p + (1-\varepsilon_1)p^*, \varepsilon_2 q + (1-\varepsilon_2)q^*)) \\ \dot{\varepsilon}_2 &= \varepsilon_2(1-\varepsilon_2)(\pi_2(q; \varepsilon_1 p + (1-\varepsilon_1)p^*, \varepsilon_2 q + (1-\varepsilon_2)q_1^*) \\ &\quad -\pi_2(q^*; \varepsilon_1 p + (1-\varepsilon_1)p^*, \varepsilon_2 q + (1-\varepsilon_2)q^*)) \end{aligned} \tag{24}$$

where $\pi_1(p; \varepsilon_1 p + (1-\varepsilon_1)p^*, \varepsilon_2 q + (1-\varepsilon_2)q^*)$ is the payoff to p when the current state of the population in roles one and two are $\varepsilon_1 p + (1-\varepsilon_1)p^*$ and

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[31] These two games are described more fully in Broom and Krivan's chapter, this volume.

$\varepsilon_2 q + (1-\varepsilon_2)q^*$ respectively, etc. Here ε_1 (respectively, ε_2) is the frequency of the mutant strategy p in species 1 (respectively, q in species 2).

By Cressman (1992), (p^*, q^*) exhibits evolutionary stability under (24) (i.e. $(\varepsilon_1, \varepsilon_2) = (0,0)$ is locally asymptotically stable under the above dynamics for all choices $p \neq p^*$ and $q \neq q^*$) if and only if

$$\text{either} \quad \pi_1(p;p,q) < \pi_1(p^*;p,q) \quad \text{or} \quad \pi_2(q;p,q) < \pi_2(q^*;p,q) \tag{25}$$

for all strategy pairs sufficiently close (but not equal) to (p^*, q^*). Condition (25) is the two role analogue of local superiority for matrix games (see Theorem 2 (a)). If (25) holds for all $(p,q) \in \Delta^m \times \Delta^n$ sufficiently close (but not equal) to (p^*, q^*), then (p^*, q^*) is called a two-species ESS (Cressman, 2003) or neighborhood superior (Cressman, 2010).

The two-species ESS (p^*, q^*) enjoys similar evolutionary stability properties to the ESS of symmetric normal form games. It is locally asymptotically stable with respect to the replicator equation for asymmetric games given by

$$\begin{array}{l} \dot{p}_i = p_i\left[\pi_1(e_i;p,q) - \pi_1(p;p,q)\right] \text{ for } i = 1,...,m \\ \dot{q}_j = q_j\left[\pi_2(f_j;p,q) - \pi_2(q;p,q)\right] \text{ for } j = 1,...,n \end{array} \tag{26}$$

and for all its mixed strategy counterparts (i.e. (p^*, q^*) is strongly stable). Furthermore, if (p^*, q^*) is in the interior of $\Delta^m \times \Delta^n$, then it is globally asymptotically stable with respect to (26) and with respect to the best response dynamics that generalizes (8) to asymmetric games (Cressman, 2003). Moreover, the Folk Theorem (Theorem 1) is valid for the replicator equation (26) where a NE is a strategy pair (p^*, q^*) such that $\pi_1(p;p^*,q^*) \leq \pi_1(p^*;p^*,q^*)$ for all $p \neq p^*$ and $\pi_2(q;p^*,q^*) \leq \pi_2(q^*;p^*,q^*)$ for all $q \neq q^*$ (it is a strict NE if both inequalities are strict).

For bimatrix games, (p^*, q^*) is a two-species ESS if and only if it is a strict NE (i.e. $p \cdot Aq^* < p^* \cdot Aq^*$ for all $p \neq p^*$ and $q \cdot Bp^* < q^* \cdot Bp^*$ for all $q \neq q^*$).[32] Furthermore, for these games, (p^*, q^*) is locally asymptotically stable with respect to (26) if and only if it is a two-species ESS (i.e. a strict NE). Thus, in contrast to symmetric games, we have an equivalence between the static two-species ESS concept (25) and stable evolutionary outcomes. However, this is an unsatisfactory result in the sense that strict NE must be

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[32] To see this result first proven by Selten (1980), take $(p,q) = (p, q^*)$. Then (25) implies $p \cdot Aq^* < p^* \cdot Aq^*$ or $q^* \cdot Bp^* < q^* \cdot Bp^*$ for all $p \neq p^*$. Thus, $p \cdot Aq^* < p^* \cdot Aq^*$ for all $p \neq p^*$. The same method can now be applied to $(p,q) = (p^*, q)$.

pure-strategy pairs and so the two-species ESS is a very restrictive concept for bimatrix games.

At the other extreme from bimatrix games, suppose that there are no interspecific interactions (e.g. $\rho_{\{1,2\}} = \rho_{\{2,1\}} = 0$ and $\rho_{\{1,1\}} = \rho_{\{2,2\}} = \frac{1}{2}$). These are also called completely symmetric two-role asymmetric games. Then, (p^*, q^*) is a two-species ESS if and only if p^* is a single-species ESS for species one and q^* is a single-species ESS for species two. For example, when $q = q^*$, we need $p^* \cdot Ap > p \cdot Ap$ for all p that are sufficiently close (but not equal) to p^*. From Theorem 2 (a), this last inequality characterizes the single-species ESS (of species one). From this result, there can be two-species ESSs that are not strict NE (see also Example 2 below). In particular, there can be completely mixed ESSs.

From these two extremes, we see that the concept of a two-species ESS combines and generalizes the concepts of single-species ESS of matrix games and the strict NE of bimatrix games.

A more biologically relevant example of two-species interactions analyzed by evolutionary game theory (where there are both interspecific and intraspecific interactions) is the following two-habitat selection model of Cressman et al. (2004). Specifically, this model is a Lotka-Volterra competitive two-species system in each patch where it is assumed that each species' migration is always toward the patch with the highest payoff for this species (see Example 1). An ESS always exists in this model and, depending on parameters, the ESS is mixed (i.e. both species coexist in each patch) in some cases while, in others, one of the species resides only in one patch at the ESS.

Example 2. (Two-species habitat selection game) Suppose that there are two species competing in two different habitats (or patches) and that the overall population size (i.e. density) of each species is fixed. Also assume that the fitness of an individual depends only on its species, the patch it is in and the density of both species in this patch. Then strategies of species one and two can be parameterized by the proportions p_1 and q_1 respectively of these species that are in patch one. If individual fitness (i.e. payoff) is positive when a patch is unoccupied and linearly decreasing in patch densities, then payoff functions have the form

$$\begin{aligned} \pi_1(e_i; p, q) &= r_i \left(1 - \frac{p_i M}{K_i} - \frac{\alpha_i q_i N}{K_i}\right) \\ \pi_2(f_i; p, q) &= s_i \left(1 - \frac{q_i N}{L_i} - \frac{\beta_i p_i M}{L_i}\right). \end{aligned}$$

Here, $\pi_1(e_i; p, q)$ (respectively, $\pi_2(f_j; p, q)$) is the fitness of a species one individual (respectively, species two individual) in patch i, $p_2 = 1 - p_1$ and $q_2 = 1 - q_1$. All other parameters are fixed and positive.[33]

By linearity, these payoffs can be represented by a two-species asymmetric game with payoff matrices

$$A = \begin{bmatrix} r_1 - \frac{r_1 M}{K_1} & r_1 \\ r_2 & r_2 - \frac{r_2 M}{K_2} \end{bmatrix} \qquad B = \begin{bmatrix} -\frac{\alpha_1 r_1 N}{K_1} & 0 \\ 0 & -\frac{\alpha_2 r_2 N}{K_2} \end{bmatrix}$$

$$C = \begin{bmatrix} -\frac{\beta_1 s_1 M}{L_1} & 0 \\ 0 & -\frac{\beta_2 s_2 M}{L_2} \end{bmatrix} \qquad D = \begin{bmatrix} s_1 - \frac{s_1 N}{L_1} & s_1 \\ s_2 & s_2 - \frac{s_2 N}{L_2} \end{bmatrix}.$$

For example, $\pi_1(e_i; p, q) = e_i \cdot (Ap + Bq)$. At a rest point (p, q) of the replicator equation (26), all individuals present in species one must have the same fitness as do all individuals present in species two.

Suppose that both patches are occupied by each species at the rest point (p, q). Then (p, q) is a NE and (p_1, q_1) is a point in the interior of the unit square that satisfies

$$\begin{aligned} r_1\left(1 - \frac{p_1 M}{K_1} - \frac{\alpha_1 q_1 N}{K_1}\right) &= r_2\left(1 - \frac{(1-p_1)M}{K_2} - \frac{\alpha_2 (1-q_1) N}{K_2}\right) \\ s_1\left(1 - \frac{q_1 N}{L_1} - \frac{\beta_1 p_1 M}{L_1}\right) &= s_2\left(1 - \frac{(1-q_1)N}{L_2} - \frac{\beta_2 (1-p_1) M}{L_2}\right). \end{aligned}$$

That is, these two "equal fitness" lines (which have negative slopes) intersect at (p_1, q_1) as in Figure 5.

The interior NE (p, q) is a two-species ESS if and only if the equal fitness line of species one is steeper than that of species two. That is, (p, q) is an interior two-species ESS in Figure 5 (a) but not in Figure 5 (b). The interior two-species ESS in Figure 5 (a) is globally asymptotically stable under the replicator equation.

Figure 5 (b) has two two-species ESSs, both on the boundary of the unit square. One is a pure strategy pair strict NE with species one and two occupying separate patches ($p_1 = 1, q_1 = 0$) whereas the other has species two in

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[33] This game is also considered briefly by Broom and Krivan (this volume). There the model parameters are given biological interpretations (e.g. M is the fixed total population size of species one and K_1 is its carrying capacity in patch one, etc.). Linearity then corresponds to Lotka-Volterra type interactions. As in Example 1 of Section 2.4, our analysis again concentrates on the dynamic stability of the evolutionary outcomes.

patch one and species one split between the two patches ($0 < p_1 < 1, q_1 = 1$). Both are locally asymptotically stable under the replicator equation with basins of attraction whose interior boundaries form a common invariant separatrix. Only for initial conditions on this separatrix that joins the two vertices corresponding to both species in the same patch, do trajectories evolve to the interior NE.

If the equal fitness lines do not intersect in the interior of the unit square, then there is exactly one two-species ESS. This is on the boundary (either a vertex or on an edge) and is globally asymptotically stable under the replicator equation (Krivan et al., 2008).

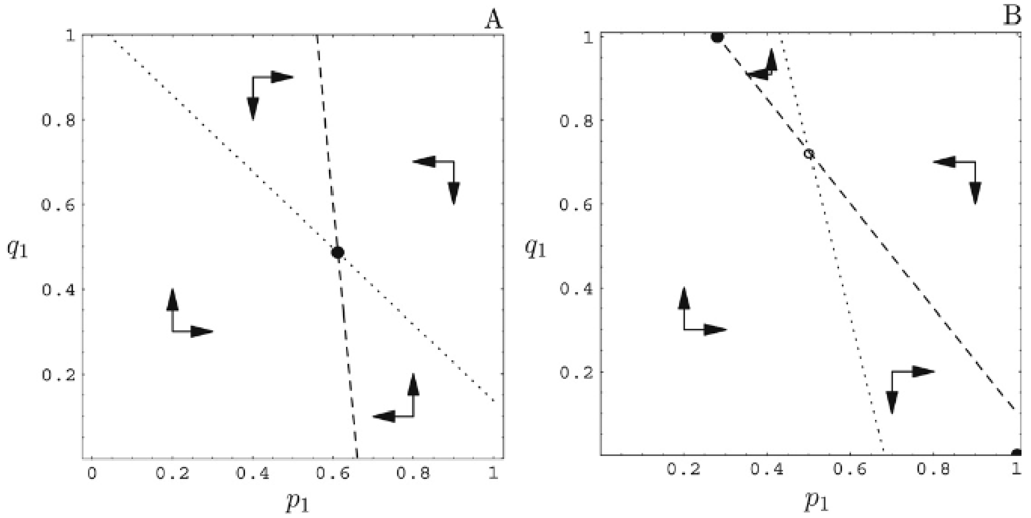

Figure 5. The ESS structure of the two-species habitat selection game. The arrows indicate the direction of best response. The equal fitness lines of species one (dashed line) and species two (dotted line) intersect in the unit square. Solid dots are two-species ESSs. (A) A unique ESS in the interior. (B) Two ESSs on the boundary.

For these two species models, some authors consider an interior NE to be a (two-species) IFD (see Example 1 for the intuition of a single-species IFD). Example 2 shows such NE may be unstable (Figure 5 (b)) and so justifies the perspective of others who restrict the IFD concept to two-species ESSs (Krivan et al., 2008).

Remark 3. The generalization of the two-species ESS concept (25) to three (or more) species is a difficult problem (Cressman et al., 2001). It is shown there that it is possible to characterize a monomorphic three-species ESS as one where, at all nearby strategy distributions, at least one species does better using its ESS strategy. However, such an ESS concept does not always imply stability of the three-species replicator equation that is based on the entire set of pure strategies for each species.

4.2 Perfect Information Games

Two-player extensive form games whose decision trees describe finite series of interactions between the same two players (with the set of actions available at later interactions possibly depending on what choices were made previously) were introduced alongside normal form games by von Neumann and Morgenstern (1944). Although (finite, two-player) extensive form games are most helpful when used to represent a game with long (but finite) series of interactions between the same two players, differences with normal form intuition already emerge for short games (Cressman, 2003; Cressman and Tao, 2014). In fact, from an evolutionary game perspective, these differences with normal form intuition are apparent for games of perfect information with short decision trees as illustrated in the remainder of this section that follows the approach of Cressman (2011).

A (finite, two-player) *perfect information game* is given by a rooted game tree Γ where each non-terminal node is a decision point of one of the players or of nature. In this latter case, the probabilities of following each of the edges that start at the decision point and lead away from the root are fixed (by nature). A path to a node x is a sequence of edges and nodes connecting the root to x. The edges leading away from the root at each player decision node are this player's choices (or actions) at this node. There must be at least two choices at each player decision node. A pure (behavior) strategy for a player specifies a choice at all of his decision nodes. A mixed behavior strategy for a player specifies a probability distribution over the set of actions at each of his decision nodes. Payoffs to both players are specified at each terminal node $z \in Z$. A probability distribution over Z is called an outcome.

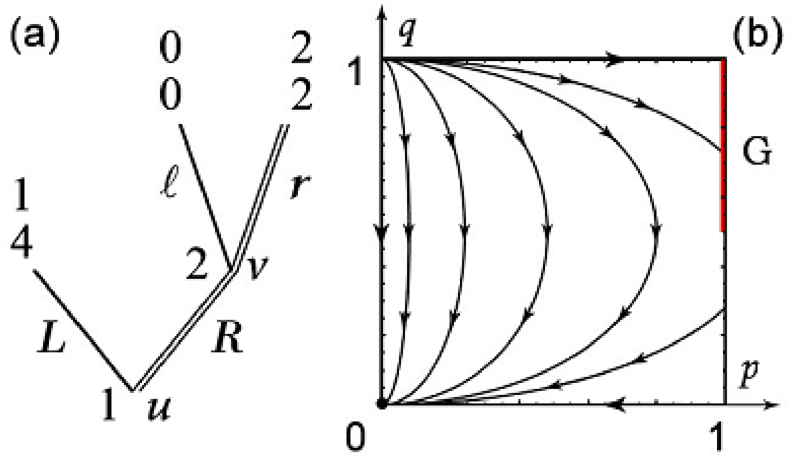

Figure 6: The Chain Store game. (a) The extensive form. (b) Trajectories of the replicator equation with respect to the game's normal form and the NE structure given by the NE component G (shown as a red line segment) and the solid dot at the origin corresponding to the SPNE.

Example 3. (Chain Store game) Figure 6 (a) is an elementary perfect information game with no moves by nature. At each terminal node, payoffs to both players are indicated with the payoff of player 1 above that of player 2. Player 1 has one decision node u where he chooses between the actions L and R. If he takes action L, player 1 gets payoff 1 and player 2 gets 4. If he takes action R, then we reach the decision point v of player 2 who then chooses between ℓ and r leading to both players receiving payoff 0 or both payoff 2, respectively.

What are the Nash equilibria (NE) for this example? If players 1 and 2 choose R and r respectively with payoff 2 for both, then
1. player 2 does worse through unilaterally changing his strategy by playing r with probability $1-q$ less than 1 (since $0q + 2(1-q) < 2$) and
2. player 1 does worse through unilaterally changing his strategy by playing L with positive probability p (since $1p + 2(1-p) < 2$).
Thus, the strategy pair (R, r) is a strict NE corresponding to the outcome $(2, 2)$.[34]

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[34] When the outcome is a single node, this is understood by saying the outcome is the payoff pair at this node.

In fact, if player 1 plays R with positive probability at a NE, then player 2 must play r. From this it follows that player 1 must play R with certainty (i.e. $p = 0$) (since his payoff of 2 is better than 1 obtained by switching to L). Thus any NE with $p < 1$ must be (R, r). On the other hand, if $p = 1$ (i.e. player 1 chooses L), then player 2 is indifferent to what strategy he uses since his payoff is 4 for any (mixed) behavior. Furthermore, player 1 is no better off by playing R with positive probability if and only if player 2 plays ℓ at least half the time (i.e. $\frac{1}{2} \leq q \leq 1$). Thus

$$G \equiv \{(L, q\ell + (1-q)r \mid \frac{1}{2} \leq q \leq 1\}$$

is a set of NE, all corresponding to the outcome $(1, 4)$. G is called a NE component since it is a connected set of NE that is not contained in any larger connected set of NE.

The NE structure of Example 3 consists of the single strategy pair $G^* = \{(R, r)\}$ which is a strict NE and the set G. These are indicated as a solid point and line segment, respectively, in Figure 6 (b) where $G^* = \{(p, q) \mid p = 0, q = 0\} = \{(0, 0)\}$.

Remark 4. Example 3 is a famous game known as the Entry Deterrence Game or the Chain Store Game introduced by the Nobel laureate Reinhard Selten (Selten, 1978; see also van Damme (1991) and Weibull (1995)). Player 2 is a monopolist who wants to keep the potential entrant (player 1) from entering the market that has a total value of 4. He does this by threatening to ruin the market (play ℓ giving payoff 0 to both players) if player 1 enters (plays R), rather than accepting the entrant (play r and split the total value of 4 to yield payoff 2 for each player). However, this is often viewed as an incredible (or unbelievable) threat since the monopolist should accept the entrant if his decision point is reached (i.e. if player 1 enters) since this gives the higher payoff to him (i.e. $2 > 0$).

Some game theorists argue that a generic perfect information game (see Remark 6 below for the definition of generic) has only one rational NE equilibrium outcome and this can be found by backward induction. This procedure starts at a final player decision point (i.e. a player decision point that has no player decision points following it) and decides which unique action this player chooses there to maximize his payoff in the subgame with this as its root. The original game tree is then truncated at this node by creating a terminal node there with payoffs to the two players given by this action. The process is continued until the game tree has no player decision nodes left and yields the subgame perfect NE (SPNE). That is, the strategy constructed by backward induction produces a NE in each subgame Γ_u corresponding to the subtree with root at the decision node u (Kuhn, 1953). For generic perfect information games (see Remark 6), the SPNE is a unique pure strategy pair and is indicated by the double lines in the game tree of Figure 6 (a). The SPNE of Example 3 is G^*. If a NE is not subgame perfect, then this perspective argues that there is at least one player decision node where an incredible threat would be used.

Example 3. (Continued) Can evolutionary dynamics be used to select one of the two NE outcomes of the Chain Store Game? Suppose players 1 and 2 use mixed strategies p and q respectively. The payoffs of pure strategies L and R for player 1 (denoted $\pi_1(L,q)$ and $\pi_1(R,q)$ respectively) are 1 and $0q + 2(1-q)$ respectively. Similarly, the payoffs of pure strategies ℓ and r for player 2 are $\pi_2(p,\ell) = 4p + (1-p)0$ and $\pi_2(p,r) = 4p + (1-p)2$ respectively. Thus, the expected payoffs are $\pi_1(p,q) = p + (1-p)2(1-q)$ and $\pi_2(p,q) = q4p + (1-q)(4p + (1-p)2)$ for players 1 and 2 respectively. Under the replicator equation, the probability of using a pure strategy increases if its payoff is higher than these expected payoffs. For this example, the replicator equation is (Weibull, 1995; see also Remark 5 below)

$$\begin{aligned} \dot{p} &= p(1-(p+(1-p)2(1-q))) = p(1-p)(2q-1) \\ \dot{q} &= q(4p - [q4p + (1-q)(4p + (1-p)2)]) = -2q(1-q)(1-p). \end{aligned} \tag{27}$$

The rest points are the two vertices $\{(0,0),(0,1)\}$ and the edge $\{(1,q) \mid 0 \leq q \leq 1\}$ joining the other two vertices. Notice that, for any interior trajectory, q is strictly decreasing and that p is strictly increasing (decreasing) if and only $q > \frac{1}{2}$ $(q < \frac{1}{2})$.

Trajectories of (27) are shown in Figure 6 (b). The SPNE of the Chain Store Game G^* is the only asymptotically stable NE.[35] That is, asymptotic stability of the evolutionary dynamics selects a unique outcome for this example whereby player 1 enters the market and the monopolist is forced to accept this.

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[35] This is clear for the replicator equation (27). For this example with two strategies for each player, it continues to hold for all other game dynamics that satisfy the basic assumption that the frequency of one strategy increases if and only if its payoff is higher than that of the player's other strategy.

Remark 5. Extensive form games can always be represented in normal form. The bimatrix normal form of Example 3 is

$$\begin{array}{r} \\ \text{Not Enter } (L) \\ \text{Enter } (R) \end{array} \begin{array}{c} \begin{array}{cc} \text{Ruin } (\ell) & \text{Accept } (r) \end{array} \\ \left[\begin{array}{cc} 1,4 & 1,4 \\ 0,0 & 2,2 \end{array}\right] \end{array}.$$

By convention, player 1 is the row player and player 2 the column player. Each bimatrix entry specifies payoffs received (with player 1's given first) when the two players use their corresponding pure strategy pair. That is, the bimatrix normal form, also denoted $\left[A, B^T\right]$, is given by

$$A = \begin{bmatrix} 1 & 1 \\ 0 & 2 \end{bmatrix} \text{ and } B = \begin{bmatrix} 4 & 4 \\ 0 & 2 \end{bmatrix}^T = \begin{bmatrix} 4 & 0 \\ 4 & 2 \end{bmatrix}$$

where A and B are the payoff matrices for player 1 and 2 respectively. With these payoff matrices, the replicator equation (26) becomes (27).

This elementary example already shows a common feature of the normal form approach for such games; namely, that some payoff entries are repeated in the bimatrix. As a normal form, this means the game is non-generic (in the sense that at least two payoff entries in A (or in B) are the same) even though it arose from a generic perfect information game. For this reason, most normal form games cannot be represented as perfect information games.

To generalize the evolutionary analysis of Example 3 to other perfect information games, the following results for Example 3 are straightforward to prove. By Theorem 7 below, these results continue to hold for most perfect information games.

1. Every NE outcome is a single terminal node.[36]
2. Every NE component G includes a pure strategy pair.
3. The outcomes of all elements of G are the same.
4. Every interior trajectory of the replicator equation converges to a NE.
5. Every pure strategy NE is stable but not necessarily asymptotically stable.
6. Every NE that has a neighborhood whose only rest points are NE is stable.
7. If a NE component is interior attracting, it includes the SPNE.
8. Suppose (p, q) is a NE. It is asymptotically stable if and only if it is strict. Furthermore, (p, q) is asymptotically stable if and only if playing this strategy

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[36] For Example 1, this is either $(2, 2)$ or $(1, 4)$.

pair reaches every player decision point with positive probability (i.e. (p, q) is pervasive).

Theorem 7. (Cressman, 2003) Results 2 to 8 are true for all generic perfect information games. Result 1 holds for generic perfect information games without moves by nature.

Remark 6. By definition, an extensive form game Γ is *generic* if no two pure strategy pairs that yield different outcomes have the same payoff for one of the players. For a perfect information game Γ with no moves by nature, Γ is generic if and only if no two terminal nodes have the same payoff for one of the players. If Γ is not generic, the SPNE outcome may not be unique since several choices may arise at some player decision point in the backward induction process when there are payoff ties. Some of the results of Theorem 7 are true for general perfect information games and some are not. For instance, Result 1 is not true for some non-generic games or for generic games with moves by nature. Result 4, which provides the basis to connect dynamics with NE in Results 5 to 8, remains an open problem for non-generic perfect information games. On the other hand, Result 4 has recently been extended to other game dynamics. Specifically, every trajectory of the best response dynamics[37] converges to a NE component for all generic perfect information games (Xu, 2016).

Theorem 7 applies to all generic perfect information games such as that given in Figure 7. Since no pure strategy pair in Figure 7 can reach both the left-side subgame and the right-side subgame, none are pervasive. Thus, no NE can be asymptotically stable by Theorem 7 (Results 1 and 8), and so no single strategy pair can be selected on dynamic grounds by the replicator equation.

However, it is still possible that a NE outcome is selected on the basis of its NE component being locally asymptotically stable as a set. By Result 7, the NE component containing the SPNE is the only one that can be selected in this manner. In this regard, Figure 7 is probably the easiest example (Cressman, 2003) of a perfect information game where the NE component G^* of the SPNE outcome $(2, 3)$ is not interior attracting (i.e. there are interior initial points arbitrarily close to G^* whose interior trajectory under

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[37] This is the obvious extension to bimatrix games of the best response dynamics (8) for symmetric (matrix) games.

the replicator equation does not converge to this NE component). That is, Figure 7 illustrates that the converse of Result 7 (Theorem 7) is not true and so the SPNE outcome is not always selected on dynamic grounds.

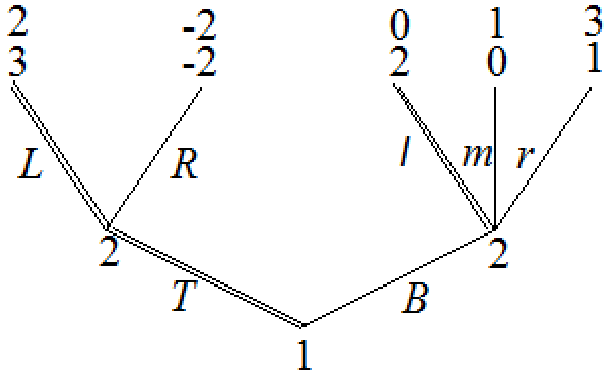

Figure 7. The extensive form of a perfect information game with unstable SPNE component.

To see this, some notation is needed. The (mixed) strategy space of player 1 is the one-dimensional strategy simplex $\Delta(\{T,B\}) = \{(p_T,p_B) \mid p_T+p_B = 1, 0 \le p_T,p_B \le 1\}$. This is also denoted $\Delta^2 \equiv \{(p_1,p_2) \mid p_1+p_2 = 1, 0 \le p_i \le 1\}$. Similarly, the strategy simplex for player 2 is the five-dimensional set $\Delta(\{L\ell, Lm, Lr, R\ell, Rm, Rr\}) = \{(q_{L\ell}, q_{Lm}, q_{Lr}, q_{R\ell}, q_{Rm}, q_{Rr}) \in \Delta^6\}$. The replicator equation is then a dynamics on the 6 dimensional space $\Delta(\{T,B\}) \times \Delta(\{L\ell, Lm, Lr, R\ell, Rm, Rr\})$. The SPNE component (i.e. the NE component containing the SPNE $(T, L\ell)$) is

$$G^* = \{(T,q) \mid q_{L\ell}+q_{Lm}+q_{Lr} = 1, q_{Lm}+3q_{Lr} \le 2\}$$

corresponding to the set of strategy pairs with outcome $(2,3)$ where neither player can improve his payoff by unilaterally changing his strategy (Cressman, 2003). For example, if player 1 switches to B, his payoff of 2 changes to $0q_{L\ell}+1q_{Lm}+3q_{Lr} \le 2$. The only other pure strategy NE is $\{B, R\ell\}$ with outcome $(0,2)$ and corresponding NE component $G = \{(B,q) \mid q_{L\ell}+q_{R\ell} = 1, \frac{1}{2} \le q_{R\ell} \le 1\}$. In particular, $(T, \frac{1}{2}q_{Lm} + \frac{1}{2}q_{Lr}) \in G^*$ and $(B, R\ell) \in G$.

Using the fact that the face $\Delta(\{T,B\}) \times \Delta(\{Lm, Lr\})$ has the same structure as the Chain Store Game of Example 1 (where p corresponds to the probability player 1 uses T and q the probability player 2 uses Lr), points in the interior of this face with $q_{Lr} > \frac{1}{2}$ that start close to $(T, \frac{1}{2}q_{Lm} + \frac{1}{2}q_{Lr})$ converge to (B, Lr). From this, Cressman (2011) shows that there are trajectories in the interior of the full game that start arbitrarily close to G^* that converge to a point in the NE component G. In particular, G^* is not interior attracting.

Remark 7. The partial dynamic analysis of Figure 7 given in the preceding two paragraphs illustrates nicely how the extensive form structure (i.e. the game tree for this perfect information game) helps with properties of NE and the replicator equation. Similar considerations become even more important for extensive form games that are not of perfect information. For instance, all matrix games can be represented in extensive form (c.f. Remark 5) but these never have perfect information.[38] Thus, for these symmetric extensive form games (Selten, 1983), the eight Results of Theorem 7 are no longer true, as we know from Section 2. However, the backward induction procedure can be generalized to the subgame structure of a symmetric extensive form game Γ to produce a SPNE (Selten, 1983). When the process is applied to NE of the (symmetric) subgames that are locally asymptotically stable under the replicator equation (4), a locally asymptotically stable SPNE p^* of Γ emerges (Cressman, 2003) when (p^*, p^*) is pervasive (c.f. Result 8, Theorem 7). As Selten (1988) showed, this result is no longer true when local asymptotic stability is replaced by the ESS structure of the subgames. A description of the issues that arise in these games is beyond the scope of this chapter. The interested reader is directed to van Damme (1991) and Cressman (2003) as well as Selten (1983, 1988) for further details.

4.3 Asymmetric games with one-dimensional continuous trait spaces

In this section, we will assume that the trait spaces S and T for the two roles are both one-dimensional compact intervals and that payoff functions have continuous partial derivatives up to second order so that we avoid technical

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[38] An extensive form game that is not of perfect information has at least one player “information set” containing more than one decision point of this player. This player must take the same action at all these decision points. Matrix games then correspond to symmetric extensive form games (Selton, 1983) where there is a bijection from the information sets of player 1 to those of player 2. Bimatrix games can also be represented in extensive form.

and/or notational complications. For $(u,v) \in S \times T$, let $\pi_1(u';u,v)$ (respectively, $\pi_2(v';u,v)$) be the payoff to a player in role 1 (respectively, in role 2) using strategy $u' \in S$ (respectively $v' \in T$) when the population is monomorphic at (u,v). Note that π_1 has a different meaning here than in Section 3 where it was used to denote a partial derivative (e.g. equation (13)). Here, we extend the concepts of Section 3 (CSS, adaptive dynamics, NIS, replicator equation, neighborhood superior, Darwinian dynamics) to asymmetric games.

To start, the canonical equation of adaptive dynamics (c.f. (13)) becomes

$$\begin{aligned} \dot{u} &= k_1(u,v)\tfrac{\partial}{\partial u'}\pi_1(u';u,v) \mid_{u'=u} \\ \dot{v} &= k_2(u,v)\tfrac{\partial}{\partial v'}\pi_2(v';u,v) \mid_{v'=v} \end{aligned} \tag{28}$$

where $k_i(u,v)$ for $i=1,2$ are positive continuous functions of (u,v). At an interior rest point (u^*,v^*) of (28),

$$\frac{\partial \pi_1}{\partial u'} = \frac{\partial \pi_2}{\partial v'} = 0.$$

Following Cressman (2009), (u^*,v^*) is called convergence stable if it is locally asymptotically stable under (28) for any choice of k_1 and k_2. Furthermore, (u^*,v^*) is a neighborhood strict NE if $\pi_1(u';u^*,v^*) < \pi_1(u^*;u^*,v^*)$ and $\pi_2(v';u^*,v^*) < \pi_2(v^*;u^*,v^*)$ for all u' and v' sufficiently close but not equal to u^* and v^* respectively. Clearly, a neighborhood strict NE (u^*,v^*) in the interior of $S \times T$ is a rest point of (28).

The characterizations of convergence stability and strict NE in the following theorem are given in terms of the linearization of (28) about (u^*,v^*); namely,

$$\begin{bmatrix} \dot{u} \\ \dot{v} \end{bmatrix} = \begin{bmatrix} k_1(u^*,v^*) & 0 \\ 0 & k_2(u^*,v^*) \end{bmatrix} \begin{bmatrix} A+B & C \\ D & E+F \end{bmatrix} \begin{bmatrix} u-u^* \\ v-v^* \end{bmatrix} \tag{29}$$

where

$$\begin{aligned} A &\equiv \frac{\partial^2}{\partial u' \partial u'}\pi_1(u';u^*,v^*); B \equiv \frac{\partial}{\partial u'}\frac{\partial}{\partial u}\pi_1(u';u,v^*); C \equiv \frac{\partial}{\partial u'}\frac{\partial}{\partial v}\pi_1(u';u^*,v) \\ D &\equiv \frac{\partial}{\partial v'}\frac{\partial}{\partial u}\pi_2(v';u,v^*); E \equiv \frac{\partial}{\partial v'}\frac{\partial}{\partial v}\pi_2(v';u^*,v); F \equiv \frac{\partial^2}{\partial v' \partial v'}\pi_2(v';u^*,v^*) \end{aligned}$$

and all partial derivatives are evaluated at the equilibrium. If threshold values involving these six second order partial derivatives are ignored throughout this section, the following result is proved by Cressman (2010, 2011) using the Taylor series expansions of $\pi_1(u'; u, v)$ and $\pi_2(v'; u, v)$ about (u^*, v^*) that generalize (14) to three variable functions.

Theorem 8. Suppose (u^*, v^*) is a rest point of (28) in the interior of $S \times T$.
(a) (u^*, v^*) is a neighborhood strict NE if and only if A and F are negative.
(b) (u^*, v^*) is convergence stable if and only if, for all non-zero $(u, v) \in \mathbf{R}^2$, either $u((A + B)\, u + Cv) < 0$ or $v\,(Du + (E + F)\, v) < 0$ if and only if $A + B < 0, E + F < 0$ and $(A + B)\,(E + F) > CD$.[39]

In Sections 3.1 and 3.4, it was shown that a CSS for symmetric games is a neighborhood strict NE that is convergence stable under all adaptive dynamics (e.g. Theorem 6 (a)). For asymmetric games, we define a CSS as a neighborhood strict NE that is convergence stable. That is, (u^*, v^*) is a CSS if it satisfies both parts of Theorem 8. Although the inequalities in the latter part of (b) are the easiest to use to confirm convergence stability in practical examples, it is the first set of inequalities that is most directly tied to the theory of CSS, NIS and neighborhood p^*-superiority (as well as stability under evolutionary dynamics), especially as the trait spaces become multi-dimensional. It is again neighborhood superiority according to the following definition that unifies this theory (see Theorem 9 below).

Definition 4. Suppose (u^*, v^*) is in the interior of $S \times T$.
(a) Fix $0 \le p^* < 1$. Strategy pair (u^*, v^*) is *neighborhood* p^*-*superior* if

$$\text{either } \pi_1(u^*; P, Q) > \pi_1(P; P, Q) \ \text{ or } \pi_2(v^*; P, Q) > \pi_2(Q; P, Q) \qquad (30)$$

for all $(P, Q) \in \Delta(S) \times \Delta(T)$ with $1 \ge P(\{u^*\}) \ge p^*$, $1 \ge Q(\{v^*\}) \ge p^*$ and the support of (P, Q) sufficiently close (but not equal) to (u^*, v^*). (u^*, v^*) is *neighborhood half-superior* if $p^* = \frac{1}{2}$.[40] (u^*, v^*) is *neighborhood superior* if $p^* = 0$. (u^*, v^*) is *(globally)* p^*-*superior* if the support of (P, Q) in (30) is an arbitrary subset of $S \times T$ (other than $\{(u^*, v^*)\}$).

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[39] These equivalences are also shown by Leimar (2009) who called the concept strong convergence stability.

[40] In (30), we assume payoff linearity in the distributions P and Q. For example, the expected payoff to u' in a random interaction is $\pi(u'; P, Q) \equiv \int_S \int_T \pi_1(u'; u, v) Q(dv) P(du)$ where P (Q) is the probability measure on S (T) corresponding to the current distribution of the population one's (two's) strategies. Furthermore, $\pi(P; P, Q) \equiv \int_S \pi(u'; P, Q) P(du')$, etc.

(b) Strategy pair (u^*, v^*) is a *neighborhood invader strategy (NIS)* if, for all (u, v) sufficiently close (but not equal) to (u^*, v^*), either $\pi_1(u^*; u, v) > \pi_1(u; u, v)$ or $\pi_2(v^*; u, v) > \pi_2(v; u, v)$.

Definition 4 from Cressman (2010, 2011) is the generalization to asymmetric games of Definition 3 in Section 3.2. It is also clear that the concept of neighborhood p^*-superior in (30) is close to that of two-species ESS given in (25). In fact, for asymmetric normal form games (i.e. with S and T finite strategy spaces and payoff linearity), a strategy pair is a two-species ESS if and only if it is neighborhood p^*-superior according to Definition 4 for some $0 \leq p^* < 1$ (c.f. Remark 1 in Section 3.2). The following result then generalizes Theorem 4 in Section 3.2 (see also Theorem 6 in Section 3.4) to asymmetric games (Cressman, 2010, 2011).

Theorem 9. Suppose that (u^*, v^*) is in the interior of $S \times T$.
(a) (u^*, v^*) is a neighborhood CSS if and only if it is neighborhood half-superior.
(b) (u^*, v^*) is a NIS if and only if, for all non-zero $(u, v) \in \mathbf{R}^2$, either $u((A + 2B)\, u + 2Cv) < 0$ or $v\,(2Du + (2E + F)\, v) < 0$.
(c) (u^*, v^*) is a neighborhood strict NE and NIS if and only if it is neighborhood superior.
(d) Consider evolution under the replicator equation (31) that generalizes (15) to asymmetric games. (u^*, v^*) is neighborhood attracting if and only if it is neighborhood superior.[41]

The replicator equation for an asymmetric game with continuous trait spaces is given by

$$\begin{array}{l} \frac{dP_t}{dt}(U) = \int_U \left(\pi_1(u'; P_t, Q_t) - \pi_1(P_t; P_t, Q_t)\right) P_t(du') \\ \frac{d,Q_t}{dt}(V) = \int_V \left(\pi_2(v'; P_t, Q_t) - \pi_2(Q_t; P_t, Q_t)\right) Q_t(dv') \end{array} \tag{31}$$

where U and V are Borel subsets of S and T, respectively.

Remark 8. The above theory for asymmetric games with one-dimensional continuous trait spaces has been extended to multi-dimensional trait spaces

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[41] Note that (u^*, v^*) is neighborhood attracting if (P_t, Q_t) converges to $(\delta_{u^*}, \delta_{v^*})$ in the weak topology whenever the support of (P_0, Q_0) is sufficiently close to (u^*, v^*) and $(P_0, Q_0) \in \Delta(S) \times \Delta(T)$ satisfies $P_0(\{u^*\})Q_0(\{v^*\}) > 0$.

(Cressman, 2009, 2010). Essentially, the results from Section 3.4 for symmetric games with multi-dimensional trait space carry over with the understanding that CSS, NIS and neighborhood p^*-superiority are now given in terms of Definition 4 and Theorem 9.

Darwinian dynamics for asymmetric games have also been studied (Brown and Vincent 1987, 1992; Marrow et al., 1992; Abrams and Matsuda, 1997; Pintor et al., 2011). For instance, in predator-prey systems, the G-function for predators will most likely be different from that of the prey (Brown and Vincent, 1987, 1992). Darwinian dynamics, which combines ecological and evolutionary dynamics (c.f. Section 3.3), will now model strategy and population size evolution in both species. The advantage to this approach to evolutionary games is that, as in Section 3.3, stable evolutionary outcomes can be found that do not correspond to monomorphic populations (Brown and Vincent, 1992; Pintor et al., 2011).

5 Conclusion

This chapter has summarized evolutionary game theory for two-player symmetric and asymmetric games based on random pairwise interactions. In particular, it has focused on the connection between static game-theoretic solution concepts (e.g. ESS, CSS, NIS) and stable evolutionary outcomes for deterministic evolutionary game dynamics (e.g. the replicator equation, adaptive dynamics).[42] As we have seen, the unifying principle of local superiority (or neighborhood p^*-superiority) has emerged in the process. These game-theoretic solutions then provide a definition of stability that does not rely on an explicit dynamical model of behavioral evolution. When such a solution corresponds to a stable evolutionary outcome, the detailed analysis of the underlying dynamical system can be ignored. Instead, it is the heuristic static conditions of evolutionary stability that become central to understanding behavioral evolution when complications such as genetic, spatial and population size effects are added to the evolutionary dynamics.

In fact, stable evolutionary outcomes are of much current interest for other, often non-deterministic, game-dynamic models that incorporate stochas-

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[42] These deterministic dynamics all rely on the assumption that the population size is large enough (sometimes stated as "effectively infinite") so that changes in strategy frequency can be given through the payoff function (i.e. through the strategy's expected payoff in a random interaction).

tic effects due to finite populations or models with assortative (i.e. non-random) interactions (e.g. games on graphs). These additional features, summarized ably by Nowak (2006), are beyond the scope of this chapter. So too are models investigating the evolution of human cooperation whose underlying games are either the two-player Prisoner's Dilemma Game or the multi-player Public Goods Game (Binmore, 2007). This is another area where there is a great deal of interest, both theoretically and through game experiments.

As the evolutionary theory behind these models is a rapidly expanding area of current research, it is impossible to know in what guise the conditions for stable evolutionary outcomes will emerge in future applications. On the other hand, it is certain that Maynard Smith's original idea underlying evolutionary game theory will continue to play a central role.

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Figure Captions

Figure 1. Trajectories of the replicator equation (4) for the RSP game.
(a) $\varepsilon = 0$. (b) $\varepsilon > 0$.

Figure 2. Trajectories for payoffs of the habitat selection game when initially almost all individuals are in patch 2 and patch payoff functions are $\pi(e_1, p) = 1 - p_1, \pi(e_2, p) = 0.8(1 - \frac{10p_2}{9})$ and $\pi(e_3, p) = 0.6(1 - \frac{10p_3}{8})$. (a) best response dynamics with migration matrices of the form $I^1(p)$; (b) dynamics for non-ideal animals with migration matrices of the form $I^2(p)$; and (c) the replicator equation. In all panels, the top curve is the payoff in patch 1, the middle curve in patch 3 and the bottom curve in patch 2. The IFD (which is approximately $(p_1, p_2, p_3) = (0.51, 0.35, 0.14)$ with payoff 0.49) is reached at the smallest t where all three curves are the same (this takes infinite time in panel c).

Figure 3. Stable evolutionary outcomes for G-function (18) on the interval $[\beta, -\beta]$. From the theoretical analysis, there are four regions of parameter space (given by a and b) of interest. In region I, there are two stable evolutionary outcomes that are monomorphisms (u^*, n^*) given by $(\beta, 1 + (a + b)\beta^2)$ and $(-\beta, 1 + (a + b)\beta^2)$. In region II, the only stable evolutionary outcome is the CSS $(u^*, n^*) = (0, 1)$. In region III (evolutionary branching) and IV, the only stable evolutionary outcome is the dimorphism $(\mathbf{u}^*, \mathbf{n}^*) = \left(\beta, -\beta; \frac{1+a\beta^2}{2}, \frac{1+a\beta^2}{2}\right)$.

Figure 4. The $G-$function $G(v, \mathbf{u}^*, \mathbf{n}^*)$ at a stable resident system $(\mathbf{u}^*, \mathbf{n}^*)$ with four traits where u_i^* for $i = 1, 2, 3, 4$ are the $v-$intercepts of the $G-$function (21) on the horizontal axis. (a) For (22), $(\mathbf{u}^*, \mathbf{n}^*)$ does not satisfy the Maximum Principle since $G(v, \mathbf{u}^*, \mathbf{n}^*)$ is at a minimum when $v = u_i^*$. (b) With carrying capacity adjusted so that it is only positive in the interval $(-\beta, \beta)$, $(\mathbf{u}^*, \mathbf{n}^*)$ does satisfy the Maximum Principle. Parameters: $\sigma_a^2 = 4, \sigma_k^2 = 200, K_m = 100, k = 0.1$ and for (b) $\beta = 6.17$.

Figure 5. The ESS structure of the two-species habitat selection game. The arrows indicate the direction of best response. The equal fitness lines of species one (dashed line) and species two (dotted line) intersect in the unit square. Solid dots are two-species ESSs. (A) A unique ESS in the interior. (B) Two ESSs on the boundary.

Figure 6: The Chain Store game. (a) The extensive form. (b) Trajectories of the replicator equation with respect to the game's normal form and the NE structure given by the NE component G (shown as a red line segment) and the solid dot at the origin corresponding to the SPNE.

Figure 7. The extensive form of a perfect information game with unstable SPNE component.

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