



Evolutionary Stability Concepts for N -species Frequency-dependent Interactions

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The classical static concept of an evolutionarily stable strategy (ESS) for a single species gives rise to two new notions when there are more than two species (called an N -species ESS and RL-stability). The paper relates these to the dynamic stability of monomorphic and polymorphic evolutionary systems. It is shown that RL-stability implies the global asymptotic stability of either system with or without mutations. However, the N -species ESS only implies stability of the monomorphic system.

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1. Introduction

The most widespread stability concept used for the frequency evolution of behavioral types (i.e. phenotypes) in a single species is that of an evolutionarily stable strategy (ESS) introduced by Maynard Smith & Price (1973). In particular, biologists expect the terminal state of phenotypic selection to be an ESS. The original ESS concept can be given either a static or dynamic interpretation, both of which are important in their own right for a heuristic understanding. For the static approach, a resident population is an ESS if the fitness of rare mutants is less than that of the residents [see Theorem 1(a)]. The dynamic approach insists that rare mutants must die out in the long run under an appropriate dynamic [i.e. the resident population must be “uninvadable” as used in Definition 1(a) and (b)].

As pointed out by Cressman (1992), these two approaches are no longer equivalent for two-species frequency-dependent evolution. Specifically, there are uninvadable two-species systems for which the mutants can temporarily have a fitness greater than the residents. The basic question of this paper is then to determine the appropriate extension of the ESS concept to models of frequency-dependent evolution among two or more species. The biologically straightforward generalization of the static approach; namely, in each species rare mutants are worse off than the residents is called a strict N -species ESS. This concept, introduced by Garay & Varga (2000), is so strong that such terminal states are unlikely to exist in interesting N -species models [see eqn (4) and the surrounding discussion]. For instance, Selten (1980) proved that no “interior” N -species ESS can exist when there are no intra-specific interactions. For these reasons, we concentrate mainly on extending the dynamic approach begun by Cressman (1992) for two-species models.

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In this paper, two possible dynamic extensions of evolutionary stability are investigated. The first (Section 2) is based on the assumption that mutation is a very rare event and selection acts much faster. This means that there is enough time between rare mutations for the fitter phenotypes to eliminate the less fit ones. In particular, only two phenotypes may coexist in each species at the same time (i.e. there is a monomorphic resident population and a small invading subpopulation that is also monomorphic but using a different phenotype in at least one species). An N -species ESS is then a phenotype that resists any such invasion. The main result here (Theorem 3) gives a complete static characterization of an “interior” N -species ESS that generalizes one of the many equivalent characterizations of an ESS when $N = 2$ [Theorem 2(b)]. A stronger concept, RL-stability, that extends another equivalent characterization is also developed (Definition 2 and Theorem 4), due partly to its importance in the polymorphic setting.

The second possible extension of evolutionary stability (Section 3) assumes that the resident population may be polymorphic (i.e. there may be individuals in the same species displaying many different phenotypes). At equilibrium, all phenotypes present for a given species must have the same fitness. This equilibrium population is stable if its average phenotype is the terminal state when the system is perturbed by any small simultaneous invasion by many mutants in each species. The emphasis here is on whether average phenotypes corresponding to the monomorphic concepts developed in Section 2 imply stability in this polymorphic model. It is shown that an N -species ESS is not necessarily stable (Example 1) and that RL-stability does imply stability (Theorem 7). Finally, Section 4 shows the importance of RL-stability when continuous mutations are added to the polymorphic setting.

2. Stability Concepts with Monomorphic Resident Populations

Maynard Smith (1982) defined a (single-species) ESS as “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 also noted that, to make

this definition precise, assumptions must be made about the evolving population. In this section, we first develop these aspects for our N -species frequency-dependent selection model that leads to the definition of an N -species ESS in Definition 1 below.

This paper departs from the following biological situation. Within each of the N -species, there is a symmetric game-theoretic conflict and between any two species, an asymmetric game is played. Specifically, assume that individuals in species n ($1 \leq n \leq N$) exhibit one of m_n phenotypes (or pure strategies) at any particular time. Let $A^{n\ell}$ be the $m_n \times m_\ell$ payoff matrix whose entries give the payoff to individuals in species n when interacting with species ℓ . We will call $\{A^{n\ell}\}_{n,\ell=1,\dots,N}$ the *interaction system of matrices* for our frequency-dependent evolution. Although this formulation of an individual strategy can clearly model a situation where an individual’s strategy cannot depend on the species its opponent belongs to,* it also allows the possibility that individual strategies can rely on the opponent’s species by increasing the strategy space appropriately.

In fact, for the monomorphic resident and invading populations considered in this section, we assume individuals in species n may be using a mixed strategy $p^n \in \Delta^n \equiv \{p^n = (p^n_1, \dots, p^n_{m_n}) | p^n_i \geq 0, \sum_{i=1}^{m_n} p^n_i = 1\}$ where p^n_i represents the probability that this individual exhibits the i th phenotype at a given instant in time. Assume that, for each n , all individuals in species n of the resident population adopt the same (mixed) strategy $p^{*n} \in \Delta^n$. That is, when population size is ignored, the resident N -species system is given by $p^* = (p^{*1}, \dots, p^{*N}) \in \Delta \equiv \times_{n=1}^N \Delta^n$.

Suppose this system is perturbed by the introduction of a small subsystem given by a different $p \in \Delta$ (i.e. all individuals in species n of this subsystem use strategy p^n). In this perturbed subsystem, let $0 \leq \varepsilon_n \leq 1$ be the frequency of individuals in the n th species who use the mutant strategy p^n (so $1 - \varepsilon_n$ is the frequency of those using the resident strategy p^{*n}). The dynamic

$$\dot{\varepsilon}_n = \varepsilon_n(p^n - x^n) \sum_{\ell=1}^N A^{n\ell} x^\ell, \quad (1)$$

*This could mean that each individual displays a fixed behavior for all opponents, perhaps because individuals do not know their actual opponent’s species.

where $x^n \equiv \varepsilon_n p^n + (1 - \varepsilon_n) p^{*n}$ models frequency-dependent evolution for the interaction system of matrices $\{A^{n\ell}\}_{n,\ell=1,\dots,N}$. This assumes that each individual interacts once per unit time with one random individual in each species (and so all species have the same number of individuals[†]). The N payoffs each individual receives are additively superimposed and this total payoff then translates directly into reproductive fitness (i.e. the relative frequency of the mutant changes at a rate equal to the difference between its expected fitness $p^n \sum_{\ell=1}^N A^{n\ell} x^\ell$ and the species' mean fitness $x^n \sum_{\ell=1}^N A^{n\ell} x^\ell$).

Biologically, eqn (1) is the replicator dynamic (Hofbauer & Sigmund, 1998) for an N -species system where each individual plays one of the two possible (mixed) phenotypes. Such replicator dynamics model a situation where offspring inherit the identical strategy of their genetic parent (e.g. reproduction is asexual or each species is haploid). Mathematically, this dynamic is on the hypercube $\times_{n=1}^N [0, 1]$ and leaves the interior of this hypercube as well as each of its lower dimensional faces forward invariant.[‡] We say p^* is locally asymptotically stable (l.a.s.) for the dynamic (1) if it is stable [i.e. all trajectories of eqn (1) that start initially sufficiently close to the origin of the hypercube stay close] and all trajectories in some neighborhood of the origin converge to the origin. With these assumptions and notations, the ESS concept for N -species is given in the following definition.

Definition 1. (a) $p^* \in \Delta$ is *uninvadable* by the mutant strategy $p \in \Delta \setminus \{p^*\}$ for the N -species frequency-dependent interaction matrices $\{A^{n\ell}\}_{n,\ell=1,\dots,N}$ if p^* is locally asymptotically stable for the dynamic (1).

[†]The model is easily adaptable to systems where only the relative population sizes of different species remains constant by including suitable factors in the interaction matrices $A^{n\ell}$. On the other hand, if the relative population sizes of different species do not remain constant, the frequency-dependent evolution modelled in eqn (1) would require some mechanism to force each individual to have the same rate of interactions with each species. In this situation, it may be more realistic to consider a density dynamic in place of eqn (1), a topic that is not pursued further in this paper.

[‡]If $p^n = p^{*n}$ for some n , then $x^n = p^{*n}$ and so $\dot{\varepsilon}_n = 0$. In this case, we restrict attention to the invariant face that has $\varepsilon_n = 0$. To avoid degenerate situations, we assume throughout that $m_n \geq 2$ for all $1 \leq n \leq N$.

(b) $p^* \in \Delta$ is an N -species ESS for the N -species frequency-dependent interaction matrices $\{A^{n\ell}\}_{n,\ell=1,\dots,N}$ if it is uninvadable by any mutant strategy $p \in \Delta \setminus \{p^*\}$.[§]

The power and general acceptance of the ESS concept in Definition 1 relies to a great extent on the equivalence of the dynamic conditions given then to the static conditions involving payoff comparisons. For instance, it is well known (Maynard Smith, 1982) that p^* is a single-species ESS with respect to payoff matrix A if and only if the ESS is at least as fit as the mutant against the resident population (i.e. $pAp^* \leq p^*Ap^*$ for all $p^* \in \Delta^1$) and, when the mutant has the same fitness, the ESS is more fit than the mutant in its rare interactions with the mutant (i.e. $pAp < p^*Ap$ when $pAp^* = p^*Ap^*$).

The following two theorems summarize other equivalent static conditions for one and two species ESSs. These results can be found in Hofbauer & Sigmund (1998) and Cressman (1996), respectively, where the analysis of ESSs in the interior of Δ is also emphasized. The second parts of both theorems contain the important concept of a *Nash equilibrium* (NE). In fact, any N -species ESS must be an N -species NE. An N -species NE is a p^* in Δ that satisfies $p^n \sum_{\ell=1}^N A^{n\ell} p^{*\ell} \leq p^{*n} \sum_{\ell=1}^N A^{n\ell} p^{*\ell}$ for all n and $p^n \in \Delta^n$. If a NE p^* is in the interior of Δ , then this is an equality for all n . Every N -species interaction system has at least one NE.

Theorem 1. (a) $p^* \in \Delta^1$ is a single-species ESS if and only if $pAp < p^*Ap$ for all $p \in \Delta^1$ sufficiently close but not equal to p^* .

(b) A p^* in the interior of Δ is a single-species ESS if and only if p^* is a NE and $\xi A \xi < 0$ for all non-zero $\xi \in X^1 \equiv \{(\xi_1, \dots, \xi_{m_1}) \mid \sum \xi_i = 0\}$.

Theorem 2. (a) $p^* \in \Delta^1 \times \Delta^2$ is a two-species ESS if and only if for all $p \in \Delta^1 \times \Delta^2$ sufficiently close but not equal to p^* , either $p^1(A^{11}p^1 + A^{12}p^2) < p^{*1}(A^{11}p^1 + A^{12}p^2)$ or $p^2(A^{21}p^1 + A^{22}p^2) < p^{*2}(A^{21}p^1 + A^{22}p^2)$.

(b) The following four statements are equivalent if p^* is in the interior of $\Delta^1 \times \Delta^2$.

(i) p^* is a two-species ESS.

[§]Garay & Varga (2000) called an N -species ESS an “evolutionarily dynamically stable state”.

(ii) There exists an $\mathbf{r} > 0$ (i.e. $\mathbf{r} = (r_1, r_2)$ with $r_1 > 0$ and $r_2 > 0$) such that, for all $p \in \Delta^1 \times \Delta^2$ sufficiently close but not equal to p^* ,

$$\begin{aligned} & r_1 p^1 (A^{11} p^1 + A^{12} p^2) + r_2 p^2 (A^{21} p^1 + A^{22} p^2) \\ & < r_1 p^{*1} (A^{11} p^1 + A^{12} p^2) \\ & \quad + r_2 p^{*2} (A^{21} p^1 + A^{22} p^2). \end{aligned} \quad (2)$$

(iii) p^* is a NE and there exists an $\mathbf{r} > 0$ such that $r_1 \xi_1 (A^{11} \xi_1 + A^{12} \xi_2) + r_2 \xi_2 (A^{21} \xi_1 + A^{22} \xi_2) < 0$ for all non-zero $(\xi_1, \xi_2) \in X^1 \times X^2$.

(iv) p^* is a NE and $\{\xi_n A^{n\ell} \xi_\ell\}_{n,\ell=1,2}$ is a 2×2 B -matrix for all non-zero ξ_1 and ξ_2 in X^1 and X^2 , respectively.

Remark 1. There are many equivalent conditions (Hofbauer & Sigmund, 1998) for the class of B -matrices. We will use the following two characterizations in this paper. An $m \times m$ matrix B is a B -matrix if $x_i (B\mathbf{x})_i < 0$ for some i whenever $\mathbf{x} \geq \mathbf{0}$ and $\mathbf{x} \neq \mathbf{0}$. This has obvious biological significance for the m -species population dynamic $\dot{x}_i = x_i (B\mathbf{x})_i$ where $x_i \geq 0$ represents the size of the i th species. B is a B -matrix if and only if, the origin is globally asymptotically stable for this dynamic in the first orthant. We will also use the fact that the transpose of a B -matrix is a B -matrix.

The B -matrix condition in part (iv) of Theorem 2(b) can also be expressed in terms of the class of P -matrices. Specifically $\{\xi_n A^{n\ell} \xi_\ell\}_{n,\ell=1,m}$ is a B -matrix for all non-zero ξ_1, \dots, ξ_m in X^1, \dots, X^m , respectively, if and only if $\{-\xi_n A^{n\ell} \xi_\ell\}_{n,\ell=1,m}$ is an $m \times m$ P -matrix for all non-zero ξ_1, \dots, ξ_m in X^1, \dots, X^m , respectively. To see this, clearly, B is a B -matrix if $-B$ is a P -matrix. Conversely, if $-B \equiv \{-\xi_n A^{n\ell} \xi_\ell\}_{n,\ell=1,m}$ is not a P -matrix, then $-\sum_\ell x_n \xi_n A^{n\ell} \xi_\ell x_\ell \leq 0$ for all n for some $\mathbf{x} \neq \mathbf{0}$. For every $x_\ell < 0$, replace ξ_ℓ by $\hat{\xi}_\ell = -\xi_\ell \in X^\ell$ (otherwise, set $\hat{\xi}_\ell = \xi_\ell$). Then $\sum_n |x_n| \hat{\xi}_n A^{n\ell} \hat{\xi}_\ell |x_\ell| \geq 0$ and so $\{\hat{\xi}_n A^{n\ell} \hat{\xi}_\ell\}_{n,\ell=1,m}$ is not a B -matrix.

Clearly, parts (a) and (b) of Theorem 2 restrict to the respective parts of Theorem 1 when species

|| Recall (Hofbauer & Sigmund, 1998) that an $m \times m$ matrix B is a P -matrix if all its principal minors (i.e. the determinant of all $k \times k$ submatrices, with $1 \leq k \leq m$, formed by those entries in k arbitrary rows and the corresponding k columns) are positive. This is equivalent to $x_i (B\mathbf{x})_i > 0$ for some i whenever $\mathbf{x} \neq \mathbf{0}$.

two is fixed at p^{*2} [i.e. when $p^2 = p^{*2}$ in part (a) and $\xi_2 = 0$ in part (b)].

Several concepts for evolutionary stability stronger than those in Theorem 2 have appeared in the literature for two (or more) species frequency-dependent interactions. For instance, Taylor (1979) considered those $p^* \in \Delta^1 \times \Delta^2$ for which

$$\begin{aligned} & p^1 (A^{11} p^1 + A^{12} p^2) + p^2 (A^{21} p^1 + A^{22} p^2) \\ & < p^{*1} (A^{11} p^1 + A^{12} p^2) + p^{*2} (A^{21} p^1 + A^{22} p^2) \end{aligned} \quad (3)$$

for all $p \in \Delta^1 \times \Delta^2$ sufficiently close but not equal to p^* . Clearly, for interior p^* , eqn (3) is the special choice of weights $r_1 = r_2$ in eqn (2) whereas arbitrary positive weights provide a better formulation by Theorem 2(b).

Still stronger is the *strict N -species ESS* concept whereby, for all n ,

$$p^n \sum_{\ell=1}^N A^{n\ell} p^\ell < p^{*n} \sum_{\ell=1}^N A^{n\ell} p^\ell \quad (4)$$

for all p^n sufficiently close but not equal to p^{*n} . Garay & Varga (2000) showed that mixed phenotypes can only be a strict N -species ESS if inter-specific payoffs decompose into the sum of two components, one that depends only on one's own strategy choice and the other that depends only on the strategy choice of the opponent (an unlikely event for interesting inter-specific interactions). Furthermore, there is the strongest concept of a *strict N -species NE* $p^* \in \Delta$ whereby, for all n ,

$$p^n \sum_{\ell=1}^N A^{n\ell} p^{*\ell} < p^{*n} \sum_{\ell=1}^N A^{n\ell} p^{*\ell} \quad (5)$$

for all p^n sufficiently close but not equal to p^{*n} . Every strict N -species NE is a vertex of Δ (i.e. a pure strategy for each species).

A final intermediate concept will be important for describing other N -species ESSs on the boundary of Δ (see Theorem 5). A *quasi-strict NE* $p^* \in \Delta$ is a NE satisfying, for all n , $p^n \sum_{\ell=1}^N A^{n\ell} p^{*\ell} < p^{*n} \sum_{\ell=1}^N A^{n\ell} p^{*\ell}$ whenever p^n is not in support of p^{*n} (i.e. not in the face of Δ^n for which p^{*n} is interior). By default, a vertex of Δ is a strict NE if and only if it is quasi-strict and every interior NE

is quasi-strict. In particular, since it is well-known that not every interior NE is an ESS even when $N = 1$, there are quasi-strict NE that are not N – species ESSs (and vice versa). We first concentrate on these interior N –species ESSs (see Theorems 3 and 4). Our first main result is

Theorem 3. *A p^* in the interior of Δ is an N -species ESS if and only if p^* is a NE and $\{\xi_n A^{n\ell} \xi_\ell\}_{n,\ell=1,\dots,N}$ is an $N \times N$ B -matrix for all non-zero ξ_1, \dots, ξ_N in X^1, \dots, X^N , respectively.*

Proof. Suppose p^* is in the interior of Δ and $\{\xi_n A^{n\ell} \xi_\ell\}_{n,\ell=1,\dots,N}$ is an $N \times N$ B -matrix for all non-zero ξ_1, \dots, ξ_N in X^1, \dots, X^N , respectively. Fix a $p \in \Delta$ which yields non-zero ξ_1, \dots, ξ_N in X^1, \dots, X^N , respectively, satisfying $p^n \equiv p^{*n} + \xi_n$. Then the dynamic (1) becomes

$$\begin{aligned} \dot{\varepsilon}_n &= \varepsilon_n(1 - \varepsilon_n) \xi_n \sum_{\ell=1}^N A^{n\ell} \xi_\ell \varepsilon_\ell \\ &= \varepsilon_n(1 - \varepsilon_n) \sum_{\ell=1}^N B_{n\ell} \varepsilon_\ell, \end{aligned} \quad (6)$$

where $B_{n\ell} = \xi_n A^{n\ell} \xi_\ell$. The Taylor expansion of this dynamic about the origin up to second-order terms (there are no linear terms) is $\dot{\varepsilon}_n = \varepsilon_n \sum_{\ell=1}^N B_{n\ell} \varepsilon_\ell$. By Remark 1, the origin is globally asymptotically stable for this “quadratic” dynamic. By Molchanov’s Theorem (Khazin & Shnol, 1991), the origin is l.a.s. for eqn (6) [i.e. p^* is l.a.s. for eqn (1)].

Suppose p^* in the interior of Δ is an N –species ESS. Fix non-zero ξ_1, \dots, ξ_N in X^1, \dots, X^N , respectively, and let $B_{n\ell} = \xi_n A^{n\ell} \xi_\ell$. By Remark 1, if B is not a B -matrix, then neither is the transpose B^t and so there is a non-zero $\mathbf{q} \geq \mathbf{0}$ such that $(\mathbf{q}B)_n = (B^t\mathbf{q})_n \geq 0$ whenever $q_n \neq 0$. Introduce the change of variable given by $\mu_n \equiv \varepsilon_n/(1 - \varepsilon_n)$ and consider $Q(\boldsymbol{\mu}) \equiv \prod_{\{n|q_n \neq 0\}} (\mu_n)^{q_n}$. $Q(\boldsymbol{\mu})$ is positive in the interior of the invariant face $\{\boldsymbol{\mu} \geq \mathbf{0} | \mu_n = 0 \text{ whenever } q_n = 0\}$ and 0 at $\boldsymbol{\mu} = \mathbf{0}$. From eqn (6),

$$\begin{aligned} \dot{Q}(\boldsymbol{\mu}) &= \sum_{\{n|q_n \neq 0\}} \frac{q_n}{\mu_n} \dot{\mu}_n Q(\boldsymbol{\mu}) \\ &= Q(\boldsymbol{\mu}) \sum_{\{n|q_n \neq 0\}} \frac{q_n}{\mu_n} \frac{\dot{\varepsilon}_n}{(1 - \varepsilon_n)^2} \end{aligned}$$

$$\begin{aligned} &= Q(\boldsymbol{\mu}) \sum_{\{n|q_n \neq 0\}} q_n (B\varepsilon)_n \\ &= Q(\boldsymbol{\mu}) \mathbf{q} \cdot B\varepsilon \geq 0. \end{aligned}$$

Thus, any initial point in the interior of this invariant face cannot evolve to $\boldsymbol{\mu} = \mathbf{0}$ and so p^* is not l.a.s. for eqn (1). \square

As pointed out in the following section (see the discussion surrounding Example 1), it is no longer true that, for $N \geq 3$, an interior ESS satisfies $\sum_{n,\ell=1}^N r_n \xi_n A^{n\ell} \xi_\ell < 0$ for some $\mathbf{r} > \mathbf{0}$ as in Theorem 2(b). This latter stronger condition is analogous to the Volterra–Lyapunov (VL) stability concept[¶] for the evolution of N –species population sizes and so leads naturally to the following definition.

Definition 2. The N –species interaction system of matrices $\{A^{n\ell}\}_{n,\ell=1,\dots,N}$ is *RL-stable* (Replicator–Lyapunov stable) if, for some $\mathbf{r} > \mathbf{0}$, $\sum_{n,\ell=1}^N r_n \xi_n \cdot A^{n\ell} \xi_\ell < 0$ for all non-zero (ξ_1, \dots, ξ_N) in $X \equiv X^1 \times \dots \times X^N$.

By the following theorem, RL-stability implies that there is a unique NE p^* . By Theorems 1(b) and 2(b), if p^* is in the interior and $N = 1$ or 2, the interaction system is RL-stable if and only if p^* is an N -species ESS. It is also clear that the concepts given in conditions (3)–(5) are closely related to local versions of Definition 2 [i.e. for all (ξ_1, \dots, ξ_N) in $X \equiv X^1 \times \dots \times X^N$ that are sufficiently small and satisfy $p^{*n} + \xi_n \in \Delta^n$ for all n]. In particular, then, it is not difficult to show that

$$\sum_n r_n \left(\sum_{\ell} (p^{*n} - x^n) A^{n\ell} x^\ell \right) > 0 \quad (7)$$

for all $x \in \Delta$ sufficiently close but not equal to p^* (and for all $x \in \Delta$ different from p^* if p^* is interior). This formulation leads to the following biological interpretation of RL-stability based on the Darwinian tenet that a phenotype with a fitness greater than the average population fitness will

[¶]An $N \times N$ matrix B is VL-stable (Volterra–Lyapunov stable) if, for some $\mathbf{r} > \mathbf{0}$, $\sum_{n,\ell=1}^N r_n x_n B_{n\ell} x_\ell < 0$ for all non-zero x (see Hofbauer & Sigmund, 1998).

propagate. Here, we introduce the notion of *relative advantage* (see Garay & Varga, 2000) of p^{*n} within its own species defined as $\sum_{\ell} p^{*n} A^{n\ell} x^{\ell} - \sum_{\ell} x^n A^{n\ell} x^{\ell}$. From this perspective, eqn (7) becomes the statement that the weighted sum (with weights r_n) of the relative advantages of the resident phenotypes p^{*n} is positive. That is, in this sense, RL-stability implies that the resident state is “better” than the perturbed one, if the perturbation is small enough.

Theorem 4. *If $\{A^{n\ell}\}_{n,\ell=1,\dots,N}$ is an RL-stable interaction system of matrices, then there exists a unique NE $p^* \in \Delta$. This p^* is an N -species ESS that is g.a.s. for the dynamic (1) with respect to any mutant strategy $p \in \Delta \setminus \{p^*\}$.*

Proof. By the general theory of NE, there exists at least one NE $p^* \in \Delta$. Suppose that $q^* \in \Delta$ is also a NE and consider $\xi_n \equiv q^{*n} - p^{*n}$ for all n . Then

$$\begin{aligned} 0 &\leq \sum_n r_n \left(\sum_{\ell} (p^{*n} - q^{*n}) A^{n\ell} p^{*\ell} \right. \\ &\quad \left. + \sum_{\ell} (q^{*n} - p^{*n}) A^{n\ell} q^{*\ell} \right) \\ &= \sum_n r_n \left(\sum_{\ell} (p^{*n} - q^{*n}) A^{n\ell} (p^{*\ell} - q^{*\ell}) \right) \\ &= \sum_n r_n \left(\sum_{\ell} \xi_n A^{n\ell} \xi_{\ell} \right), \end{aligned}$$

which contradicts the definition of RL-stability unless $\xi_n = 0$ for all n . That is, RL-stability implies that a unique NE p^* exists.

For any mutant strategy $p \in \Delta \setminus \{p^*\}$, the dynamic (1) is

$$\begin{aligned} \dot{\varepsilon}_n &= \varepsilon_n (1 - \varepsilon_n) \xi_n \sum_{\ell=1}^N A^{n\ell} \varepsilon_{\ell} \xi_{\ell} \\ &\quad + \varepsilon_n (1 - \varepsilon_n) (p^n - p^{*n}) \sum_{\ell=1}^N A^{n\ell} p^{*\ell} \\ &\leq \varepsilon_n (1 - \varepsilon_n) \xi_n \sum_{\ell=1}^N A^{n\ell} \varepsilon_{\ell} \xi_{\ell}, \end{aligned}$$

where $\xi_n \equiv p^n - p^{*n}$. To show stability, consider the Lyapunov function

$$V(\varepsilon) \equiv \prod_n (1 - \varepsilon_n)^{r_n},$$

which is positive for all $0 \leq \varepsilon_n < 1$ and has an isolated maximum at $\varepsilon = \mathbf{0}$. Then, by RL stability,

$$\begin{aligned} \dot{V}(\varepsilon) &= V(\varepsilon) \sum_{n=1}^N r_n \frac{-\dot{\varepsilon}_n}{(1 - \varepsilon_n)} \\ &\geq -V(\varepsilon) \sum_{n=1}^N r_n \varepsilon_n \xi_n \sum_{\ell=1}^N A^{n\ell} \varepsilon_{\ell} \xi_{\ell} > 0 \end{aligned}$$

unless $\varepsilon_n \xi_n = 0$ for all n . Thus, p^* g.a.s. for the dynamic (1). \square

Remark 2. It is also true that, if $\{\xi_n A^{n\ell} \xi_{\ell}\}_{n,\ell=1,\dots,N}$ is an $N \times N$ B -matrix for all non-zero ξ_1, \dots, ξ_N , in X^1, \dots, X^N , respectively, then there exists a unique NE $p^* \in \Delta$. This p^* is an N -species ESS by Theorem 3 and so automatically l.a.s. for the dynamic (1) with respect to any mutant strategy $p \in \Delta \setminus \{p^*\}$. We conjecture that p^* is actually g.a.s. in this case but have no proof of this for $N > 2$ even when p^* is in the interior of Δ . The converse of Theorem 3 is not true for boundary N -species ESSs (i.e. a boundary N -species ESS need not correspond to an $N \times N$ B -matrix). For instance, with $N = 1$, the pure strategy ESSs of the coordination game do not generate a 1×1 B -matrix $\xi A \xi$ since $\xi A \xi > 0$ if $\xi \neq \mathbf{0}$.

Theorem 3 gives a complete static characterization of interior N -species ESSs. There is no corresponding complete static characterization of N -species ESSs on the boundary of Δ . We do have the following partial results though.

Definition 3. p^* is a regular N -species ESS if it is an N -species ESS that is a quasi-strict NE.

Regular ESSs for a single species were introduced by Taylor & Jonker (1978), who used the linearization technique to study their dynamic stability. Stability of an N -species quasi-strict NE p^* rests completely on an analysis of the dynamic (1) restricted to those mutant strategies

p that lie in the invariant face generated by the support of p^* since eigenvalues for the p^n outside this invariant face are guaranteed to be real and negative. This is the essential ingredient in the proof of the following theorem.

Theorem 5. p^* is a regular N -species ESS if and only if it is quasi-strict and $\{\xi_n A^{n\ell} \xi_\ell\}_{n,\ell=1,\dots,N}$ is an $N \times N$ B -matrix for all non-zero ξ_1, \dots, ξ_N in X^1, \dots, X^N , respectively, such that ξ_n is in support of p^{*n} for all n .

Proof. Suppose p^* is a regular N -species ESS. Then p^* is quasi-strict by Definition 3. Furthermore, p^* must be l.a.s. with respect to the invariant face of Δ for which p^* is interior. By Theorem 3, this implies $\{\xi_n A^{n\ell} \xi_\ell\}_{n,\ell=1,\dots,N}$ is an $N \times N$ B -matrix for all nonzero ξ_1, \dots, ξ_N in X^1, \dots, X^N , respectively, such that ξ_n is in support of p^{*n} for all n .

Now, suppose p^* is a quasi-strict NE and $\{\xi_n A^{n\ell} \xi_\ell\}_{n,\ell=1,\dots,N}$ is an $N \times N$ B -matrix for all nonzero ξ_1, \dots, ξ_N in X^1, \dots, X^N , respectively, such that ξ_n is in support of p^{*n} for all n . Given a different $p \in \Delta$, the linearization of the dynamic (1) for those n with p^n not in support of p^{*n} is

$$\dot{\varepsilon}_n = \varepsilon_n (p^n - p^{*n}) \sum_{\ell=1}^N A^{n\ell} p^{*\ell}.$$

That is, for these n , the only non-zero term in the Jacobian matrix of the linearization is the diagonal term $(p^n - p^{*n}) \sum_{\ell=1}^N A^{n\ell} p^{*\ell}$ and this is negative since p^* is a quasi-strict NE. Thus, l.a.s. is determined by restricting the dynamic for monomorphic invading populations p for which p^n is in support of p^{*n} (this includes the situation where $p^n = p^{*n}$). By Theorem 3, p^* must be l.a.s. since $\{\xi_n A^{n\ell} \xi_\ell\}_{n,\ell=1,\dots,N}$ is an $N \times N$ B -matrix for all non-zero ξ_1, \dots, ξ_N , in X^1, \dots, X^N , respectively, such that ξ_n is in support of p^{*n} for all n . Thus p^* is an N -species ESS which is regular since it is quasi-strict. \square

The characterization in Theorem 5 is especially appealing in the special case that p^{*n} is a pure strategy in Δ^n for some species n , say $n = N$. Then p^* is a regular N -species ESS if and only if, $p^N \sum_{\ell=1}^N A^{N\ell} p^{*\ell} < p^{*N} \sum_{\ell=1}^N A^{N\ell} p^{*\ell}$ for all $p^N \neq p^{*N}$

and p^* is a regular $(N - 1)$ -species ESS for the interaction system $\{\tilde{A}^{n\ell}\}_{n,\ell=1,\dots,N-1}$ where the entries in the matrix $\tilde{A}^{n\ell}$ are those of $A^{n\ell}$ plus the payoff to the row player against p^{*N} . This is the $(N - 1)$ -species interaction system induced by fixing species N at p^{*N} . The induction process can be continued if other components p^{*n} of p^* are pure strategies. In the extreme case that only one component of p^* is a mixed strategy (say for $n = 1$), p^* will be an N -species ESS if $p^1 \sum_{\ell=1}^N A^{1\ell} p^{*\ell} < p^{*1} \sum_{\ell=1}^N A^{1\ell} p^{*\ell}$ for all $2 \leq n \leq N$ and p^{*1} is a single-species ESS for the induced payoff matrix \tilde{A}^{11} .

3. Stability in Polymorphic Populations

The N -species ESS concept of Section 2 is based on a monomorphic resident N -species system where all individuals in species n play p^{*n} . However, the one and two-species ESS concepts are equally important for polymorphic models where the resident population may have individuals in some of the species using many different (mixed) strategies. The stability question now becomes whether the state p^* of the system that specifies the average phenotype in each species is l.a.s. in the corresponding polymorphic replicator dynamic. Cressman (1992, 1996) showed that, if p^* is an N -species ESS in the interior of Δ for $N = 1$ or 2 that is attainable as a state of the system, then it is globally asymptotically stable for the polymorphic replicator dynamic (a concept he called *strong stability*).

A particularly important special case is the following polymorphic model where all individuals must play pure strategies. Here a mixed strategy $p^* \in \Delta$ is no longer an individual strategy but represents the mean population strategy. That is, p_i^{*n} is now the frequency of individuals in species n who use the i -th pure strategy at all times. The N -species replicator dynamic on Δ becomes

$$\dot{p}_i^n = p_i^n \left(\sum_{\ell=1}^N (A^{n\ell} p^\ell)_i - p^n \sum_{\ell=1}^N A^{n\ell} p^\ell \right). \quad (8)$$

The following result is well known if $N = 1$ and shown by Cressman (1992, 1996) if $N = 2$.

Theorem 6. *If p^* is a one- or two-species ESS, then p^* is l.a.s. under (8) and, if p^* is in the interior of Δ , then p^* is g.a.s.*

However, if $N \geq 3$, Cressman (1992) also showed that there are N -species ESSs that are not stable under eqn (8) by giving a counterexample through constructing sufficient conditions on the linearization of eqn (8) to ensure instability. The following example makes this construction more explicit.

Example 1. Following Cressman (1992) but with our terminology, there is a three-species ESS in the interior of Δ where each species has two pure strategies that are unstable under eqn. (8). Explicitly, take the interaction system $\{A^{n\ell}\}_{n,\ell=1,\dots,3}$ to be

$$\begin{aligned} A^{11} &= \begin{bmatrix} 0 & 1 \\ 1 & 0 \end{bmatrix}, & A^{12} &= \begin{bmatrix} 0 & 0 \\ 0 & 0 \end{bmatrix}, & A^{13} &= \begin{bmatrix} 0 & 3 \\ 3 & 0 \end{bmatrix}, \\ A^{21} &= \begin{bmatrix} 0 & 3 \\ 3 & 0 \end{bmatrix}, & A^{22} &= \begin{bmatrix} 0 & 1 \\ 1 & 0 \end{bmatrix}, & A^{23} &= \begin{bmatrix} 0 & 0 \\ 0 & 0 \end{bmatrix}, \\ A^{31} &= \begin{bmatrix} 0 & 0 \\ 0 & 0 \end{bmatrix}, & A^{32} &= \begin{bmatrix} 0 & 3 \\ 3 & 0 \end{bmatrix}, & A^{33} &= \begin{bmatrix} 0 & 1 \\ 1 & 0 \end{bmatrix}. \end{aligned}$$

Since each species has two pure strategies, a $p = (p^1, p^2, p^3) \in \Delta$ can be specified by the first component p_1^n of each p^n [i.e. $p^n = (p_1^n, 1 - p_1^n)$]. Let p^* be given by $p_1^{*n} = \frac{1}{2}$. From the above payoff matrices, it is straightforward to verify that $p^n \sum_{\ell=1}^N A^{n\ell} p^{*\ell} = 2$ for all $1 \leq n \leq 3$ and $p^n \in \Delta^n$. Thus, p^* is an interior three-species NE. Since every $\xi_n \in X^n$ is of the form $(x, -x)$, the 3×3 matrix $\{\xi_n A^{n\ell} \xi_\ell\}_{n,\ell=1,\dots,3}$ is

$$B = \begin{bmatrix} -2x^2 & 0 & -6xz \\ -6xy & -2y^2 & 0 \\ 0 & -6yz & -2z^2 \end{bmatrix},$$

where $\xi_1 = (x, -x)$, $\xi_2 = (y, -y)$ and $\xi_3 = (z, -z)$. By Remark 1, this is a B -matrix for all non-zero x, y and z . To see this, assume without loss of generality that $x > 0$. Then $-2x^2 - 6xz \geq 0$ and $-6xy - 2y^2 \geq 0$ implies

$z < 0$ and $y \leq 0$ and so $-6yz - 2z^2 < 0$. Thus, p^* is an interior three-species ESS.

On the other hand, the linearization of eqn (8) about p^* shows that p^* is unstable. For the linearization, let $x = p_1^1 - p_1^{*1}, y = p_1^2 - p_1^{*2}$ and $z = p_1^3 - p_1^{*3}$. The linearization is

$$\begin{bmatrix} \dot{x} \\ \dot{y} \\ \dot{z} \end{bmatrix} = \frac{1}{2} \begin{bmatrix} -1 & 0 & -3 \\ -3 & -1 & 0 \\ 0 & -3 & -1 \end{bmatrix} \begin{bmatrix} x \\ y \\ z \end{bmatrix},$$

which has eigenvalues $-2, \frac{1}{4} \pm 3\sqrt{3}/4i$. Since two of these eigenvalues have positive real part, p^* is unstable.

The following result shows that the type of counterexample given above is impossible when the interaction system is RL-stable. Thus, the ESS and RL stability conditions are not equivalent if $N \geq 3$.

Theorem 7. *If the interaction system of matrices $\{A^{n\ell}\}_{n,\ell=1,\dots,N}$ is RL-stable, then there is a unique NE p^* . This p^* is an N -species ESS that is g.a.s. under eqn (8).*

Proof. By Theorem 4, there is a unique NE p^* and p^* is an N -species ESS. To show p^* is g.a.s. under eqn (8), consider

$$V(\mathbf{p}) \equiv \prod_{n=1}^N \prod_{i=1}^{m_n} (p_i^n)^{r_n p_i^{*n}},$$

where $(p_i^n)^{r_n p_i^{*n}}$ is taken to be 1 if $p_i^{*n} = 0$. $V(\mathbf{p})$ is a nonnegative function defined on Δ which has a global maximum at p^* . From eqn (8),

$$\begin{aligned} \dot{V}(\mathbf{p}) &= V(\mathbf{p}) \sum_{n=1}^N r_n (p^{*n} - p^n) \sum_{\ell=1}^N A^{n\ell} p^\ell \\ &\geq V(\mathbf{p}) \sum_{n=1}^N r_n (p^{*n} - p^n) \sum_{\ell=1}^N A^{n\ell} (p^\ell - p^{*\ell}) \\ &= -V(\mathbf{p}) \sum_{n=1}^N r_n \xi_n \sum_{\ell=1}^N A^{n\ell} \xi_\ell, \end{aligned}$$

where $\xi_n \equiv (p^n - p^{*n})$. Thus, $\dot{V}(\mathbf{p}) > 0$ unless $\xi_n = \mathbf{0}$ for all n or $V(\mathbf{p}) = 0$. Thus, p^* is g.a.s.

Note the similarity between this proof and that of Theorem 4. Both assert the existence of a global Lyapunov function. \square

4. Stability in the Polymorphic Setting with Mutation

We now consider a model where mutants are continuously introduced into each species. Specifically, suppose all individuals in species n mutate to the i -th pure strategy at a rate of $\mu_i^n > 0$ per unit time. The continuous-time N -species replicator dynamic with mutation is then

$$\dot{p}_i^n = p_i^n \left(\sum_{\ell=1}^N (A^{n\ell} p^\ell)_i - p^n \sum_{\ell=1}^N A^{n\ell} p^\ell \right) + \mu_i^n - p_i^n \mu^n, \quad (9)$$

where $\mu^n = \sum_{i=1}^{m_n} \mu_i^n$.** For RL-stable interaction systems, the following result shows that, while these persistent mutants will shift the equilibrium, they will neither destroy its uniqueness nor its global stability. On the other hand, Example 1 shows that the existence of an (interior) N -species ESS does not imply eqn (9) has a stable rest point if $N > 2$ since Example 1 will remain linearly unstable for all small mutation rates μ_i^n .

Theorem 8. *If the interaction system of matrices $\{A^{n\ell}\}_{n,\ell=1,\dots,N}$ is RL-stable, then for every choice of mutation rates $\mu_i^n > 0$, there is a unique and globally asymptotically stable rest point \hat{p} of eqn (9).*

Proof. The map from $p \in \Delta$ whose image has components

$$p_i^n \left(\sum_{\ell=1}^N (A^{n\ell} p^\ell)_i - p^n \sum_{\ell=1}^N A^{n\ell} p^\ell \right) + \mu_i^n - p_i^n \mu^n$$

is continuous from Δ into its interior. Thus, by Brouwer's fixed point theorem (Hofbauer &

**When $N = 1$ and A is a symmetric payoff matrix, this dynamic is the model of natural selection with mutation for "special mutation rates" analysed by Hofbauer & Sigmund (1998). Hofbauer (2000) proved the single species version of Theorem 8; namely, there is a g.a.s. interior rest point of eqn (9) for every payoff matrix that satisfies $\xi A \xi < 0$ for all non-zero $\xi \in X^1$ (and so has a unique ESS).

Sigmund, 1998), eqn (9) has at least one rest point \hat{p} in the interior of Δ . To show \hat{p} is g.a.s. under eqn (9), consider again

$$V(\mathbf{p}) \equiv \prod_{n=1}^N \prod_{i=1}^{m_n} (p_i^n)^{r_n \hat{p}_i^n}$$

as in the proof of Theorem 7. Then, since \hat{p} is a rest point,

$$\begin{aligned} \dot{V}(\mathbf{p}) &= V(\mathbf{p}) \sum_{n=1}^N r_n (\hat{p}^n - p^n) \sum_{\ell=1}^N A^{n\ell} p^\ell \\ &\quad + \sum_i \frac{\hat{p}_i^n}{p_i^n} \mu_i^n - \mu^n \\ &= V(\mathbf{p}) \sum_{n=1}^N r_n \left[(\hat{p}^n - p^n) \sum_{\ell=1}^N A^{n\ell} (p^\ell - \hat{p}^\ell) \right. \\ &\quad \left. + (\hat{p}^n - p^n) \sum_{\ell=1}^N A^{n\ell} \hat{p}^\ell + \sum_i \frac{\hat{p}_i^n}{p_i^n} \mu_i^n - \mu^n \right] \\ &= V(\mathbf{p}) \sum_{n=1}^N r_n \left[(\hat{p}^n - p^n) \sum_{\ell=1}^N A^{n\ell} (p^\ell - \hat{p}^\ell) \right. \\ &\quad \left. - \sum_i (\hat{p}_i^n - p_i^n) \frac{\mu_i^n}{\hat{p}_i^n} + \sum_i \frac{\hat{p}_i^n}{p_i^n} \mu_i^n - \mu^n \right] \\ &= V(\mathbf{p}) \sum_{n=1}^N r_n \left[-\xi_n \sum_{\ell=1}^N A^{n\ell} \xi_\ell \right. \\ &\quad \left. + \sum_i \mu_i^n (\hat{p}_i^n - p_i^n) \left(\frac{1}{p_i^n} - \frac{1}{\hat{p}_i^n} \right) \right] \\ &= V(\mathbf{p}) \left[-\sum_{n=1}^N r_n \xi_n \sum_{\ell=1}^N A^{n\ell} \xi_\ell \right. \\ &\quad \left. + \sum_{n=1}^N \sum_{i=1}^{m_n} r_n \mu_i^n (\xi_{n,i})^2 \frac{1}{p_i^n \hat{p}_i^n} \right], \end{aligned}$$

where $\xi_n \equiv (p^n - \hat{p}^n)$. Thus, $\dot{V}(\mathbf{p}) > 0$ unless $\xi_n = \mathbf{0}$ for all n . Thus, \hat{p} is g.a.s. (and therefore unique as well). \square

5. Discussion

The analysis of evolutionary stability concepts in this paper is most clear for interior equilibria

and so we will restrict our discussion to this special case. In the spirit of the original approach by Maynard Smith & Price (1973) (and Taylor & Jonker, 1978) for a single species, we have developed intuitive static conditions and their relationship to dynamic stability. From the monomorphic setting, stability under rare mutations leads to the N -species ESS concept of Definition 1 and its complete characterization in terms of B -matrices in Theorem 3. However, from Example 1, it is clear that stability in the polymorphic setting is not equivalent to the N -species ESS concept. Of course, this is not surprising since it is well known that there are interior NE for the single species pure strategy model that are g.a.s. under the replicator dynamic (8) but not a single-species ESS. However, from the special cases of $N = 1$ and 2, we might have at least expected an N -species ESS to be g.a.s. under the replicator dynamic (8).

This led us to consider the stronger static concept of RL-stability which, in a single species, is the same as the ESS concept whereby the resident population has a positive relative advantage over the mutant. For N -species, RL-stability demands a positive “weighted” relative advantage of the whole resident system over the mutants (see Definition 2), a concept analogous to the well-known VL-stability criteria for Lotka–Volterra models from population dynamics (Hofbauer & Sigmund, 1998). Thus, from a mathematical perspective, the obstruction to generalizing the result that monomorphic stability implies polymorphic stability to interaction systems with more than two species seems to be precisely the difference between B -matrices and RL-stability when $N > 2$.

The main results of this paper from the biological viewpoint are, in brief, that first RL-stability implies g.a.s. of the monomorphic model under rare mutations, of the pure-strategy replicator dynamic (Theorem 7) and the pure-strategy model with continuous mutation (Theorem 8). Secondly, the local (or global) asymptotic stability of the monomorphic replicator dynamic (1) does not imply that of the polymorphic replicator dynamic (8) from Example 1. This latter result means that there is an essential difference between the biological understanding of the monomorphic and polymorphic cases for our

frequency-dependent model when there are more than two species.

From a different perspective, one could argue that it was only good fortune that Maynard Smith’s monomorphic uninvasibility concept in Definition 1 actually implies stability in the polymorphic setting when $N = 1$ and 2 (see Theorem 6). In some ways, the difference between stability in the monomorphic vs. polymorphic setting [i.e. eqn (1) vs. eqn (8)] is mirrored in the well-understood result that stability under the latter pure-strategy dynamic does not imply uninvasibility. This result, already established for $N = 1$ by Taylor & Jonker (1978), has not deterred the importance of the single-species ESS concept. We feel confident that the N -species ESS concept based on uninvasibility will prove equally durable.

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