

A *G*-function approach to fitness minima, fitness maxima, evolutionarily stable strategies and adaptive landscapes

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ABSTRACT

We use a fitness-generating function (*G*-function) approach to evolutionary games. The *G*-function allows for simultaneous consideration of strategy dynamics and population dynamics. In contrast to approaches using a separate fitness function for each strategy, the *G*-function automatically expands and contracts the dimensionality of the evolutionary game as the number of extant strategies increases or decreases. In this way, the number of strategies is not fixed but emerges as part of the evolutionary process. We use the *G*-function to derive conditions for a strategy's (or a set of strategies) resistance to invasion and convergence stability. In hopes of relating the proliferation of ESS-related terminology, we define an ESS as a set of strategies that is both resistant to invasion and convergent-stable. With our definition of ESS, we show the following: (1) Evolutionarily unstable maxima and minima are not achievable from adaptive dynamics. (2) Evolutionarily stable minima are achievable from adaptive dynamics and allow for adaptive speciation and divergence by additional strategies – in this sense, these minima provide transition points during an adaptive radiation and are therefore unstable when subject to small mutations. (3) Evolutionarily stable maxima are both invasion-resistant and convergent-stable. When global maxima on the adaptive landscape are at zero fitness, these combinations of strategies make up the ESS. We demonstrate how the number of co-existing strategies (coalition) emerges when seeking an ESS solution. The Lotka-Volterra competition model and Monod model of competition are used to illustrate combinations of invasion resistance and convergence stability, adaptive speciation and evolutionarily 'stable' minima, and the diversity of co-existing strategies that can emerge as the ESS.

Keywords: adaptive landscapes, evolutionarily stable strategy, fitness, frequency-dependent selection, *G*-function, game theory, speciation, strategy dynamics.

INTRODUCTION

Evolutionarily stable strategies (ESS; Maynard Smith and Price, 1973) may be the likely outcome of evolution by natural selection. However, under adaptive dynamics, evolution may be unable to attain an ESS or evolution may result in evolutionarily stable points

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that are distinctly non-ESS. Eshel (1983, 1986), Taylor (1989) and others have noted that Maynard Smith's pioneering definition of an ESS only addresses strategies that cannot be invaded by rare, alternative strategies (= heritable phenotypes). However, an uninvadable strategy need not be convergent-stable (Eshel, 1996) in the sense that evolution by natural selection in the neighbourhood of the strategy need not result in the return of the population to that strategy following a perturbation. Our approach has been to define an ESS as a set of strategies that is both uninvadable and convergent-stable (Vincent and Brown, 1988; Vincent *et al.*, 1993; Brown, 1999; see Vincent *et al.*, 1999, for a technical discussion of this point). By so doing, we provide a framework for studying evolution that is compatible with earlier work, yet addresses complications that arise under adaptive dynamics.

Using the convergent-stable strategies (CSS) notion, Abrams *et al.* (1993b) and others (Brown and Pavlovic, 1992; Metz *et al.*, 1996; Geritz *et al.*, 1997, 1998; Meszena and Czibula, 1998; Mitchell, in press; Rees and Westboy, 1997) raised the possibility that mathematical models of evolutionary games may possess evolutionarily stable minima and evolutionarily unstable maxima. These possibilities arise from adaptive dynamics changing the strategy value of a monomorphic population under mathematical models that assume the following:

- the population's strategy is a continuous quantitative trait;
- the population's strategy changes in proportion to the slope of the adaptive landscape gradient (Brown and Vincent, 1987a; Charlesworth, 1990; Vincent, 1990; Abrams *et al.*, 1993b; Vincent *et al.*, 1993; Dieckmann and Law, 1996);
- there is no phenotypic (or genotypic) variation on the strategy;
- the dynamics of evolution is much slower than the dynamics of population sizes;
- the stability is local.

Stable minima which are convergent-stable (Metz *et al.*, 1996) are invadable because they are not ESSs. An evolutionarily unstable maximum arises from the possibility that a strategy when common throughout the population may be uninvadable but not convergent-stable. The possibility that such phenomena actually exist in nature has been advanced in some of these citations.

Our goals are three-fold. First, we revisit the requirements for a strategy (or a coalition of strategies) to be uninvadable and the requirements for the strategy to be convergent-stable. We define an ESS as a coalition of strategies that is both uninvadable and convergent-stable. We restrict ourselves to population dynamics that lead to stable equilibria with respect to the population sizes of each extant strategy (see Brown and Vincent, 1987b). In developing the conditions for convergence stability, we aim to clarify and correct ambiguities and omissions in the (often cited) conditions given by Abrams *et al.* (1993b), Metz *et al.* (1996) and others.

Second, we use a series of propositions to understand the adaptive dynamics that are likely to occur in the neighbourhood of evolutionarily stable maxima and evolutionarily stable minima. We show that, in both cases, it is possible for two strategies to co-exist at positive population sizes on either side of a peak or valley of the adaptive landscape. In the case of a peak, adaptive dynamics cause the strategies to converge on the evolutionarily stable maximum. In the case of a valley, adaptive dynamics result in the divergence of the two strategies. Because an evolutionarily stable minimum is only convergent-stable and not invasion-resistant, the tiniest amount of heritable variation within the population will

lead to an escape from the convergent-stable minimum point on the adaptive landscape. Populations at a stable minimum are extremely vulnerable to invasion and allow for sympatric speciation (i.e. competitive speciation; Rosenzweig, 1978). Thus, it is unlikely that such minima exist in nature.

Third, we consider examples of evolutionary games that exhibit the stability properties and adaptive dynamics under consideration.

Throughout, we use the fitness-generating function (G -function) to analyse evolutionary games, the ESS definition, adaptive dynamics, and the necessary conditions for invasion resistance and convergence stability. The G -function is a generalization of what is usually called individual fitness (e.g. Abrams *et al.*, 1993b). The G -function clearly separates the contributions to fitness of the individual's strategy, the strategies of others, and the population sizes of each strategy. The G -function also provides a unified approach to studying any number of extant and ESS strategies. In this way, the number of strategies (or species, or distinct phenotypes) is not fixed, but rather emerges as a property of the ESS or of the adaptive dynamics.

THE G -FUNCTION METHOD

We first outline the G -function approach to analysing evolutionary games (Vincent *et al.*, 1996) (see Vincent *et al.* for the proof of the theorem as stated here). This approach has an important feature: it allows us to determine the number of species that co-exist at an ESS. An ESS solution dictates the strategy values and the number of different values that co-exist. By our definition, a species is a collection of individuals that have practically identical values for their evolutionary strategy. This assumes that the extant variability in strategies around the species mean strategy is relatively tiny compared to the species' complete set of evolutionarily feasible strategies. For simplicity, we confine the discussion to those biological situations that require only a single G -function (but see Brown and Vincent, 1987c, and citations therein).

The ESS maximum principle

Assume there are a finite but arbitrary number r of different strategy values (e.g. species) $\mathbf{u} = [\mathbf{u}_1, \dots, \mathbf{u}_r]^T$ in a population. The strategies \mathbf{u}_i may be scalars u_i or vectors $\mathbf{u}_i = [u_{i1}, \dots, u_{is}]^T$ with s components. Each strategy \mathbf{u}_i is required to lie in the same subset $\mathcal{U} \subseteq \mathcal{R}^s$. We will shorten this latter requirement to read $\mathbf{u} \in \mathcal{U}$ (every component of \mathbf{u} must lie in \mathcal{U}). Although it is often assumed that $\mathcal{U} = \mathcal{R}^s$ (indeed, we will eventually make that assumption here), more generally the strategy set must be bounded for any real system. For example, in matrix games where the strategies are probabilities, it is clear what the bounds on the strategy set \mathcal{U} must be.

Let x_i be the density (i.e. the number of individuals) of strategy type \mathbf{u}_i at time t for $i = 1, \dots, r$ and $\mathbf{x} = [x_1, \dots, x_r]^T$ be the vector of all such densities. Assume that changes in population sizes are given by

$$\dot{x}_i = x_i H_i[\mathbf{u}, \mathbf{x}] \quad i = 1, \dots, r \tag{1}$$

where H_i is the fitness of individuals x_i using strategies \mathbf{u}_i . The individual fitness function $H_i[\mathbf{u}, \mathbf{x}]$ is assumed to be continuous (it is in practice usually continuously differentiable) in \mathbf{x} in the non-negative orthant

$$\mathbb{O}^r = \{\mathbf{x} \in \mathcal{R}^r \mid \mathbf{x} = [x_1, \dots, x_r], x_i \geq 0\}$$

and also continuous in \mathbf{u} if \mathcal{U} has a given topology.

In what follows we assume that, for any $\mathbf{u} \in \mathcal{U}$, there exists an equilibrium solution $\mathbf{x}^* \in \mathbb{O}^r$ satisfying $x_i^* H_i[\mathbf{u}, \mathbf{x}^*] = 0$ for $i = 1, \dots, r$. If, for some i , the equilibrium condition is satisfied by the non-trivial solution $H_i[\mathbf{u}, \mathbf{x}^*] = 0$ with $x_i^* > 0$, then the equilibrium solution is called an ‘ecological equilibrium point’. Reorder the i index if necessary so that all non-trivial solutions are listed first. Thus, at an ecological equilibrium point, there exists a $\sigma \geq 1$ such that the equilibrium solution is given by

$$\begin{aligned} H_i[\mathbf{u}, \mathbf{x}^*] &= 0 \text{ with } x_i^* > 0 && \text{for } i = 1, \dots, \sigma \\ x_i^* &= 0 && \text{for } i = \sigma + 1, \dots, r \end{aligned} \quad (2)$$

The strategies corresponding to the non-trivial solutions are designated by

$$\mathbf{u}_c = [\mathbf{u}_1, \dots, \mathbf{u}_\sigma]^T$$

with the remaining strategies designated by

$$\mathbf{u}_m = [\mathbf{u}_{\sigma+1}, \dots, \mathbf{u}_r]^T$$

For the definition that follows, we will require certain properties that are similar to asymptotic stability for the ecological equilibrium point. We cannot assume that \mathbf{x}^* is asymptotically stable at the onset, since \mathbf{x}^* will, in general, lie on the boundary of \mathbb{O}^r and trajectories starting at neighbouring points not in \mathbb{O}^r are of no interest and need not approach \mathbf{x}^* . Rather, we require that every trajectory starting in $\mathbb{O}^r \cap \mathcal{B}$, where \mathcal{B} is an open ball about \mathbf{x}^* , remains in \mathbb{O}^r for all time and converges to \mathbf{x}^* as $t \rightarrow \infty$. An ecological equilibrium point which satisfies these properties is called an ‘ecologically stable equilibrium point’ (ESE). If \mathcal{B} can be made arbitrarily large, then \mathbf{x}^* is said to be a global ESE; otherwise, it is a local ESE. These considerations ensure that the ESE consists of positive population densities.

Definition 1. *The vector $\mathbf{u}_c \in \mathcal{U}$ is an ESS for the ecological equilibrium point $\mathbf{x}^* \in \mathbb{O}^r$ if, for any $r > \sigma$ and any $\mathbf{u}_m \in \mathcal{U}$, \mathbf{x}^* is an ecologically stable equilibrium point.*

Definition 1 incorporates Maynard-Smith and Price’s (1973) pioneering concept that an ESS cannot be invaded by rare mutants. In fact, the ESS coalition of σ strategy types \mathbf{u}_c is stable against simultaneous invasion by any possible set of mutant strategies \mathbf{u}_m . The mutant strategy types need not use strategies near those used by members of the coalition. In this sense, the ESS is always global with respect to \mathcal{U} . In addition, the ESS has the property that \mathbf{x}^* is a locally stable equilibrium point regardless of the increased dimension of \mathbf{x} and $\mathbf{u} = [\mathbf{u}_c, \mathbf{u}_m]$. Thus, according to the above definition, an ESS is not only uninvadable (like Maynard Smith’s original definition) but it must also be convergent-stable (like the CSC of Eshel, 1983, 1996; see Vincent *et al.*, in prep.). If \mathbf{x}^* is a local ESE, then the mutants must be rare. If \mathbf{x}^* is a global ESE, then the mutants need not be rare. The requirement that an ESS is resistant to invasion gives rise to the ESS Maximum Principle (as stated below).

We favour this formal definition of an ESS for three reasons. First, while it is stronger than Maynard-Smith and Price’s (1973) original definition, our definition ensures that ESSs are the likely outcome of evolution by natural selection. It is not enough that a strategy may be uninvadable, if it is unattainable via adaptive dynamics by natural selection. Second, the

absence of convergence stability from Maynard-Smith and Price's definition has led to a proliferation of terms; for example, EUB and CSC of Eshel (1983, 1996), δ and m -stability of Taylor (1989) (see also discussions in Metz *et al.*, 1996; Geritz *et al.*, 1997, 1998). We believe that this proliferation of terms obscures the main features of evolutionary game theory. Definition 1 collects these important works and terms into a useful definition for the ESS as a set of strategies that is resistant to invasion by rare alternative strategies and that is convergent-stable in the neighbourhood of the ESS. Third, Definition 1 is constructive. The maximum principle emerges from this definition in a natural way, which provides us with a method of finding ESS (including the number of strategies that is required for the ESS).

The ESS Maximum Principle (Theorem 1 below) is based on the existence of a fitness-generating function G defined as follows.

Definition 2. A function $G(\cdot): \mathcal{U} \times \mathcal{U}^r \times \mathbb{C}^r \rightarrow \mathbb{R}$ is a G-function for (1) if, for every $i = 1, \dots, r$,

$$G(\mathbf{u}_i, \mathbf{u}, \mathbf{x}) \equiv H_i[\mathbf{u}, \mathbf{x}]$$

We write the G -function in terms of the virtual variable \mathbf{v} as $G(\mathbf{v}, \mathbf{u}, \mathbf{x})$. Replacing \mathbf{v} by the strategy used by individuals of strategy type \mathbf{u}_i results in the fitness function for these individuals. Thus, \mathbf{v} represents the strategy of an arbitrary individual, whereas \mathbf{u}, \mathbf{x} defines the current biotic environment.

Theorem 1 (ESS Maximum Principle). Let $G(\mathbf{v}, \mathbf{u}, \mathbf{x})$ be a G-function for (1). If $\mathbf{u}_e = [\mathbf{u}_1^*, \dots, \mathbf{u}_\sigma^*]$ is an ESS for the ecological equilibrium point $\mathbf{x}^* \in \mathbb{C}^r$, then $G(\mathbf{v}, \mathbf{u}^*, \mathbf{x}^*)$ must take on its maximum value as a function of $\mathbf{v} \in \mathcal{U}$ at $\mathbf{v} = \mathbf{u}_1^*, \dots, \mathbf{u}_\sigma^*$. Furthermore, $\max G(\mathbf{v}, \mathbf{u}^*, \mathbf{x}^*) = 0$ at $\mathbf{v} = \mathbf{u}_1^*, \dots, \mathbf{u}_\sigma^*$.

The ESS Maximum Principle is a necessary condition for an ESS, since it was derived by assuming that \mathbf{x}^* is a local ESE. It has a simple geometric interpretation when the strategies are scalars. Let an adaptive landscape be defined as a plot of $G(\mathbf{v}, \mathbf{u}, \mathbf{x})$ with respect to \mathbf{v} . According to the ESS Maximum Principle, each strategy of an ESS must be a global (with respect to $\mathbf{v} \in \mathcal{U}$) maximum of the adaptive landscape. For example, suppose that \mathbf{u}_e is an ESS with two scalar strategies u_1^* and u_2^* . If we substitute \mathbf{u}^* and \mathbf{x}^* into G and plot G as a function of v , its global maximum must occur at u_1^* and u_2^* with a value of zero. Furthermore, if \mathcal{U} is unbounded, then the ESS Maximum Principle results in the following necessary conditions:

$$\begin{aligned} \frac{\partial G(v, \mathbf{u}^*, \mathbf{x}^*)}{\partial v} \Big|_{v=u_1^*} &= \frac{\partial G(v, \mathbf{u}^*, \mathbf{x}^*)}{\partial v} \Big|_{v=u_2^*} = 0 \\ \frac{\partial^2 G(v, \mathbf{u}^*, \mathbf{x}^*)}{\partial v^2} \Big|_{v=u_1^*} &\leq 0 \\ \frac{\partial^2 G(v, \mathbf{u}^*, \mathbf{x}^*)}{\partial v^2} \Big|_{v=u_2^*} &\leq 0 \end{aligned}$$

An ESS must be invasion-resistant, and the above conditions can be thought of as the necessary conditions for insuring that \mathbf{u}^* is resistant to invasion by any $\mathbf{u} \in \mathcal{U}$.

Strategy dynamics

Adaptive dynamics consider how the strategy of the i th population, u_i , changes in response to the direction and magnitude of the fitness gradient on the adaptive landscape. Under the above assumptions regarding population dynamics and some assumptions regarding the distribution and redistribution of heritable strategies about the population's mean strategy, the strategy or mean strategy value of the i th population evolves according to (Charlesworth, 1990; Vincent, 1990, 1994; Abrams *et al.*, 1993a,b; Vincent *et al.*, 1993; Metz *et al.*, 1996; Cohen and Vincent, 1997; Geritz *et al.*, 1997, 1998):

$$\dot{u}_i = k \left. \frac{\partial G(v, \mathbf{u}, \mathbf{x})}{\partial v} \right|_{v=u_i} \quad (3)$$

where $k = h\sigma^2$ is a 'speed' term equal to the product of $h(0, 1)$, a heritability coefficient, and σ^2 , which is some measure of genetic variance. The strategy u_i is the mean strategy value of the population x_i . The dynamics of the strategy depends on the gradient of G . All of the strategies of \mathbf{u} with positive population sizes evolve by climbing the adaptive landscape. We use the term 'strategy dynamics' when referring to a specific model for the adaptive dynamics, for example, as given by (3).

The individual fitness function vs the G -function

Before examining strategy dynamics more closely, we highlight some of the differences between the G -function approach and the frequently used individual fitness approach (e.g. Eshel, 1983; Taylor, 1989; Abrams *et al.*, 1993b) to the study of evolutionary games. We refer to this alternate approach as the individual fitness function approach, or the F -function approach. The G -function approach, as sketched above, uses the fitness-generating function to model both the population dynamics and the strategy dynamics as a coupled system of equations. The F -function approach considers only strategy dynamics in terms of fitness functions. As we show below, the two approaches are equivalent only under special circumstances.

Consider scalar strategies. Then, by definition, the fitness of any individual using a strategy u_i is given by

$$G(v, \mathbf{u}, \mathbf{x})|_{v=u_i}$$

where \mathbf{u} is the vector of all strategies in the population and \mathbf{x} is the vector of all densities in the population. We can also formulate the dynamics in terms of the frequencies $p_i = x_i/N$, where $N = \sum x_i$ is the total population density. We can then write the fitness function as

$$G(v, \mathbf{u}, \mathbf{p}, N)|_{v=u_i}$$

When seeking an ESS coalition of one ($p_1 = 1$), we write the G -function as

$$G(v, u_1, N)$$

For a constant N , we would then write

$$G(v, u_1)$$

which is now similar to the F -function. To see this, consider the case where u_2 is a single mutant strategy at low frequency in a population of other individuals using strategy u_1 .

Assume that the strategy space is continuous and unbounded. With the G -function approach we write

$$G(v, u_1, u_2, p_1, p_2)$$

However, for this same case, the F -function approach would characterize the fitness of a mutant as

$$F(u_2, u_1)$$

where, in this case, u_1 is the mean strategy used by the population as a whole.

If the population is not at the ESS, the strategy dynamics for the coalition of one strategy is given by

$$\dot{u}_1 = k \left. \frac{\partial G}{\partial v} \right|_{v=u_1}$$

Using the F -function approach, the strategy dynamics is given by

$$\dot{u}_1 = k \left. \frac{\partial F}{\partial u_2} \right|_{u_2=u_1}$$

When G and F are of the same functional form, both methods will yield the same strategy dynamics; that is, the equilibrium values for u_1 and u_2 will be the same and, indeed, will have the same meaning. However, it is only in the case described (ESS of 1 strategy and N constant) that the same results are obtained. The need for, and the potential of, using the G -function approach becomes apparent when N is not constant and/or when the ESS contains two or more strategies.

Note that although the equilibrium solutions obtained using strategy dynamics yield an ESS candidate, the G -function approach provides an alternative way for finding candidates. For example, in the case where the ESS is a coalition of one on the interior of the strategy set, an ESS candidate solution is obtained from the necessary conditions

$$\left. \frac{\partial G}{\partial v} \right|_{v=u_1} = 0 \quad \text{and} \quad \left. \frac{\partial^2 G}{\partial v^2} \right|_{v=u_1} \leq 0$$

TOTAL SYSTEM DYNAMICS FOR A COALITION OF ONE

With the G -function approach, we write the coupled dynamics of the density and strategy as follows:

$$\dot{x}_1 = x_1 G(v, u_1, x_1) \Big|_{v=u_1} \tag{4}$$

$$\dot{u}_1 = k \left. \frac{\partial G(v, u_1, x_1)}{\partial v} \right|_{v=u_1} \tag{5}$$

Let us examine the stability of these equations in the neighbourhood of an ESS solution. Assuming that \mathcal{U} is unbounded and using the ESS Maximum Principle, we solve the necessary conditions

$$G(v, u_1, x_1) \Big|_{v=u_1} = 0 \tag{6}$$

$$\partial G(v, u_1, x_1)/\partial v|_{v=u_1} = 0 \tag{7}$$

which yield the solutions $x_1 = x_1^*$, $v = u_1 = u_1^*$.

Next, we develop the necessary conditions for convergence stability. The perturbation equations for (4) and (5) are given by

$$\begin{aligned} \delta \dot{x}_1 &= \left[G(u_1^*, u_1^*, x_1^*) + x_1^* \frac{\partial G(u_1^*, u_1^*, x_1^*)}{\partial x_1} \right] \delta x_1 + x_1^* \left[\frac{\partial G(u_1^*, u_1^*, x_1^*)}{\partial v} + \frac{\partial G(u_1^*, u_1^*, x_1^*)}{\partial u_1} \right] \delta u_1 \\ \delta \dot{u}_1 &= \sigma^2 \left[\frac{\partial^2 G(u_1^*, u_1^*, x_1^*)}{\partial x_1 \partial v} \delta x_1 + \left(\frac{\partial^2 G(u_1^*, u_1^*, x_1^*)}{\partial v^2} + \frac{\partial^2 G(u_1^*, u_1^*, x_1^*)}{\partial u_1 \partial v} \right) \delta u_1 \right] \end{aligned}$$

where it is understood that the arguments are replaced by $x_1 = x_1^*$, $v = u_1 = u_1^*$ after all of the partial derivatives are performed. Using the necessary conditions (6) and (7), the first equation becomes

$$\delta \dot{x}_1 = x_1^* \left[\frac{\partial G(u_1^*, u_1^*, x_1^*)}{\partial x_1} \delta x_1 + \frac{\partial G(u_1^*, u_1^*, x_1^*)}{\partial u_1} \delta u_1 \right]$$

Since $x_1^* > 0$ and $\sigma^2 > 0$, the stability of the coupled equations (4) and (5) is determined by the eigenvalues of the matrix

$$\begin{bmatrix} \frac{\partial G(u_1^*, u_1^*, x_1^*)}{\partial x_1} & \frac{\partial G(u_1^*, u_1^*, x_1^*)}{\partial u_1} \\ \frac{\partial^2 G(u_1^*, u_1^*, x_1^*)}{\partial x_1 \partial v} & \frac{\partial^2 G(u_1^*, u_1^*, x_1^*)}{\partial v^2} + \frac{\partial^2 G(u_1^*, u_1^*, x_1^*)}{\partial u_1 \partial v} \end{bmatrix}$$

The stability analysis can be simplified if we assume that the local ecological dynamics on population sizes (equation 4) is very fast relative to that of the evolutionary dynamics on strategy values (equation 5); that is, the dynamics of (4) occurs in ecological time (fast) whereas the dynamics of (5) occurs in evolutionary time (slow). Provided that (4) is stable, this means that instead of solving the differential equation (4) to get x_1 , we can solve the algebraic equation

$$G(u_1, u_1, x_1) = 0 \tag{8}$$

for x_1 to give a relationship of the form

$$x_1 = f(u_1) \tag{9}$$

and substitute into (5) to determine the strategy dynamics as a function of v and u_1 only. In this case, the perturbation equation for u_1 becomes

$$\delta \dot{u}_1 = k \left(\frac{\partial^2 G(u_1^*, u_1^*, x_1^*)}{\partial v^2} + \frac{\partial^2 G(u_1^*, u_1^*, x_1^*)}{\partial u_1 \partial v} + \frac{\partial^2 G(u_1^*, u_1^*, x_1^*)}{\partial x_1 \partial v} \frac{\partial f(u_1^*)}{\partial u_1} \right) \delta u_1$$

Thus, for stable strategy dynamics, it is necessary that

$$\frac{\partial^2 G(u_1^*, u_1^*, x_1^*)}{\partial v^2} + \frac{\partial^2 G(u_1^*, u_1^*, x_1^*)}{\partial u_1 \partial v} + \frac{\partial^2 G(u_1^*, u_1^*, x_1^*)}{\partial x_1 \partial v} \frac{\partial f(u_1^*)}{\partial u_1} < 0 \quad (10)$$

Note that, if the above fast assumption and stability on x_1 do not apply, then the following stability results need not be valid. Denote the first term in equation (10) by A , the second by B , and the third by C .

Equation (10) is the condition for convergence stability. This condition contains the convergence conditions that are widely used (e.g. Abrams *et al.*, 1993b; Metz *et al.*, 1996). For example, Abrams *et al.* (1993b) ignore the term C and only consider $A + B < 0$ as the condition for convergence stability. Metz *et al.* (1996) subsume the term C into term B . Keeping term C separate from B highlights the interaction between strategy dynamics and population dynamics in influencing the convergence stability of an ESS. Furthermore, using the G -function, these conditions are clearer and easier to interpret and expand to two or more strategies when formulated as a G -function than as separate F -functions. It is the very fact that the dynamics of x_1 is fast (compared to that of u_1) that forces us to include the C term in equation (10).

The term $C = 0$ can occur under two special circumstances. In the first, population size may be independent of strategies and strategy dynamics: $\partial f / \partial u_1 = 0$. This is unlikely, because strategies increase in frequency precisely because they have higher fitness in the current population. Thus, changes in fitness and strategy values will generally also change equilibrium population sizes. Under strictly density-dependent selection, the strategies of the ESS will maximize equilibrium population size. Under many forms of frequency-dependent selection, the ESS usually does not represent the strategy or coalition of strategies that will maximize equilibrium population size. A second way for $C = 0$ occurs when population size is made implicit in the G -function by substituting $f(u_1)$ for x_1^* directly into G before evaluating the necessary conditions. In this way, the term B will implicitly subsume C and $A + B < 0$ becomes the correct necessary condition for convergence stability (see Metz *et al.*, 1996).

Although the necessary condition for convergence stability contains A , which also figures in the necessary conditions for invasion resistance, the conditions for convergence stability and invasion resistance are somewhat independent of each other. One may be satisfied while the other is not. This leads to four possibilities when evaluating strategies that are evolutionary singularities in the sense that $\partial G(v, u_1, x_1) / \partial v|_{v=u_1} = 0$:

1. An evolutionarily stable maximum results when u_1 is both resistant to invasion ($A < 0$) and convergent-stable ($A + B + C < 0$). If this strategy is a global maximum of the adaptive landscape, then the evolutionarily stable maximum is also an ESS.
2. An evolutionarily stable minimum (Abrams *et al.*, 1993b) occurs when u_1 is not resistant to invasion ($A > 0$) but is convergent-stable ($B + C < 0$ and $|B + C| > A$).
3. An evolutionarily unstable maximum (Eshel, 1983; Abrams *et al.*, 1993b; Taylor and Day, 1997) results when u_1 is resistant to invasion ($A < 0$) but is not convergent-stable ($B + C > 0$ and $B + C > |A|$).
4. An evolutionarily unstable minimum results when u_1 is not resistant to invasion ($A > 0$) and not convergent-stable ($A + B + C > 0$).

When considering a coalition of two strategies, the conditions for invasion resistance remain the same as when considering a single strategy – each strategy of the ESS coalition

must be a global maximum of the adaptive landscape when the landscape is evaluated for populations at the ESS. However, the conditions for convergence stability become complex (see Appendix).

Interestingly, under the fast equilibrium ecological dynamics on x_i , the slow ‘hill’-climbing dynamics on u_i is akin to an inclined treadmill that is pinned to the adaptive landscape but allowed to slide along the line $G=0$. The strategy constantly moves up the landscape but, as it does so, populations are always at equilibrium. As strategies evolve, the landscape changes, until a strategy reaches a point of zero gradient that can be a minimum, a maximum, or an inflection point on the adaptive landscape. As we shall soon show, at a maximum the strategy is under stabilizing selection and at a minimum it experiences disruptive selection.

STABLE MINIMA?

The number of combinations that form the matrix – which need to be analysed for maxima and minima – for a coalition of 2 or more is horrendous (see Appendix). It is not an approach that one would wish to pursue for the general case. Furthermore, one need not take such an approach because, as we prove next, stable minima cannot exist under adaptive speciation if the time scale of evolution is slow compared with the dynamics of population density. Recall that this difference in time scale allows us to use equation (8) to obtain x_i^* . In other words, the strategies evolve with populations always at equilibrium (with $G=0$) for any number of mutant strategies.

This is easy to visualize for scalar strategies in terms of an adaptive landscape. The adaptive landscape is simply a plot of the G -function versus the virtual variable v with u and x held fixed. Between any two strategies there must always lie a minimum or a maximum of the G -function. Figure 1 demonstrates this idea for a minimum: At first we have a ‘stable’ minimum; a small (ε) mutant strategy is then added. Because this strategy must fall on $G=0$, a minimum (in this case) happens to occur between the two strategies. Note also that the shape of the adaptive landscape changes as a result of this addition.

Thus, assuming that G is twice differentiable everywhere, we make the following propositions for scalar strategies:

Proposition 1. *Consider the fast–slow system at equilibrium with u^* and $x^* > 0$. Replace u^* with*

$$u_1 = u^* + \varepsilon_1 \quad u_2 = u^* - \varepsilon_2$$

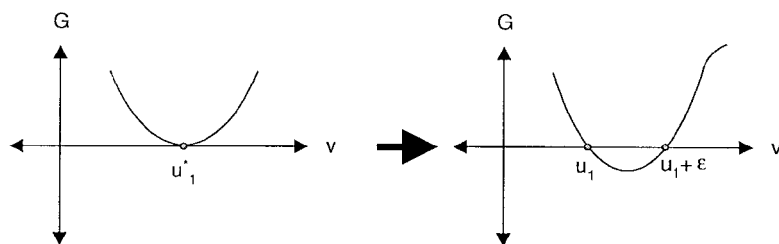


Fig. 1. Deviation from ‘stable’ minimum.

where ε_1 and ε_2 are arbitrarily small changes in strategy. If positive equilibrium densities x_1^* and x_2^* corresponding to u_1 and u_2 exist, then, since the G-function is a continuous function of its arguments, in the neighbourhood of u^* , x^* the shape of the adaptive landscape must remain relatively unchanged.

This proposition follows from the assumption that G is twice differentiable.

Proposition 2. *The only places where two strategies can be within ε of one another and co-exist at positive population sizes is in the neighbourhood of a maximal point, minimal point or inflection point.*

This proposition follows from the fact that only at these points is it possible for the adaptive landscape to maintain its local shape after adding a neighbouring strategy with both equilibrium densities positive. Figure 1 illustrates how it is possible to maintain the local shape at a minimal (or maximal or inflection) point with the addition of a neighbouring strategy.

Proposition 3. *In the neighbourhood of two co-existing strategies that are within ε of each other, the adaptive landscape must have a maximum or minimum which lies between the two strategies.*

It follows from this proposition that, under strategy dynamics, two strategies that are within ε of each other (and are close to a fixed point) will either diverge from the minimum or climb back to the same maximum. It further follows that, if the mutant strategy happens to appear when the resident strategy is at an inflection point, either a minimum or a maximum will occur between these two. If a minimum occurs, the strategies will climb away from it; if a maximum occurs, the strategies will climb towards it and we may end up at the inflection point again.

Proposition 4. *If an ESS coalition of one exists we can always find it, using strategy dynamics, by starting with a coalition of one at any feasible strategy and the corresponding positive equilibrium density. If a coalition of two exists we can always find it, using strategy dynamics, by starting with a coalition of three feasible strategies at positive equilibrium densities. If a coalition of three exists we can always find it starting with a coalition of five at positive equilibrium densities. And so on.*

The implication of these propositions is that, if one is willing to admit (however small) variance in the strategy within a population, then evolutionarily stable minima will result in speciation (of the strategy) into two strategies that will diverge to reach new maxima or minima of the landscape. If new stable evolutionarily minima are achieved, then the strategies will speciate again into two diverging strategies. This process of evolving to evolutionarily stable minima and speciating will continue until all co-existing strategies occupy local or global maxima of the adaptive landscape. This process provides a model of an adaptive radiation. In this sense – unless one refuses to admit mutations of (or invasions by) strategies – evolutionarily stable minima are not possible.

It is unlikely, but possible, that when two strategies are ε apart on both sides of an inflection point, and a maximum happens to emerge between these, the strategies will climb

towards that maximum, and we may end up with a single strategy at an inflection point again.

In closing this section, we wish to emphasize that here we are talking about adaptive speciation, minima and maxima on the adaptive landscape. We are not talking about minima and maxima of fitness. We assert that ESS are maxima of the G -function, and that evolutionarily stable minima of the G -function are possible in pathological cases only (where no variability in strategy values is allowed).

Next, we consider specific examples to illustrate the types of stability, adaptive dynamics and the propositions.

EXAMPLE: LOTKA-VOLTERRA COMPETITION

Here we use the Lotka-Volterra competition model analysed by Vincent *et al.* (1993) and Cohen and Vincent (1997). We show that for model parameters that dictate a coalition of two at ESS, the strategy/population dynamics with a coalition of one leads to a stable local minimum of the G -function. We also show that the addition of a mutant arbitrarily close to a stable minimum changes the adaptive landscape in such a way that strategy dynamics results in new local maxima of the G -function. Finally, we show that small variance moves the strategy from its local minimum to local maxima, and that getting out of local maxima requires large mutations far in value from the extant strategies.

Consider the following model:

$$K(u) = K_m \exp \left\{ -\frac{u^2}{2\sigma_k^2} \right\}$$

$$a(u, u_i) = 1 + \exp \left\{ -\frac{(u - u_i + \beta)^2}{2\sigma_a^2} \right\} - \exp \left\{ -\frac{\beta^2}{2\sigma_a^2} \right\}$$

$$G_f(v, \mathbf{u}, \mathbf{x}) = R - \frac{R}{K(v)} \sum_{j=1}^r a(v, u_j)x_j$$

Here we have

$$\dot{x}_i = x_i G_f(u_i, \mathbf{u}, \mathbf{x}) \quad i = 1, \dots, r \tag{11}$$

$$\dot{u}_i = k \left. \frac{\partial G_f(v, \mathbf{u}, \mathbf{x})}{\partial v} \right|_{v=u_i} \quad i = 1, \dots, r \tag{12}$$

where r is the number of strategies that will result in an ESS.

Getting out of a local minimum is easy

For the model outlined above and the parameter values

$$K_m = 100, R = 0.25, \sigma_k^2 = 12.5, \beta = 2, \sigma_a^2 = 4, h\sigma^2 = 0.2 \tag{13}$$

we get an ESS coalition of two (Vincent *et al.*, 1993). If instead we use a coalition of one ($r = 1$), then under fast-slow strategy dynamics, we get $x_1^* = 56.2914$ and $u_1^* = 3.79021$. A

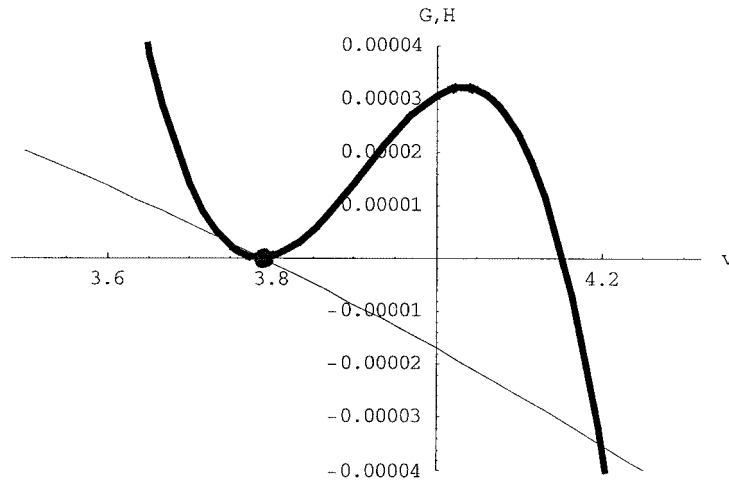


Fig. 2. Minimum on the adaptive landscape (bold line) and the corresponding fitness function (thin line).

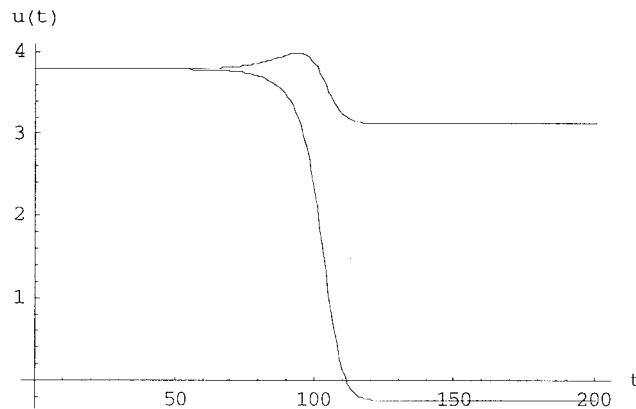


Fig. 3. Dynamics of \mathbf{u} with a coalition of two.

plot of $G(v, u_1^*, x_1^*)$ versus v in the neighbourhood of this strategy shows that the strategy is at a local minimum (Fig. 2).

Applying the stability condition (equation 10) results in a value of $A = 0.003$, $B = -0.023$ and $C = -3.7 \times 10^{-6}$ for the first, second and third terms in (10). Recall that the stability condition assumes that x dynamics is stable. To test this condition we compute $\partial G(u_1^*, u_1^*, x_1^*)/\partial x = -0.004$. Thus we conclude that the ESE is stable and it is valid to use (9). Next, we ran equations (11) with the initial conditions almost identical to the equilibrium solutions that were obtained with a system of 1 strategy. That is, we start with $u_1 = 2.79021$ and $u_2 = 2.79022$. The 10^{-4} difference among the strategies' initial conditions was sufficient to drive the solution to an ESS of $x_1^* = 39.2839$, $x_2^* = 51.0618$, $u_1^* = -0.239734$ and $u_2^* = 3.12943$ (Figs 3 and 4). Since we obtain proper local maxima, this is indeed an ESS.

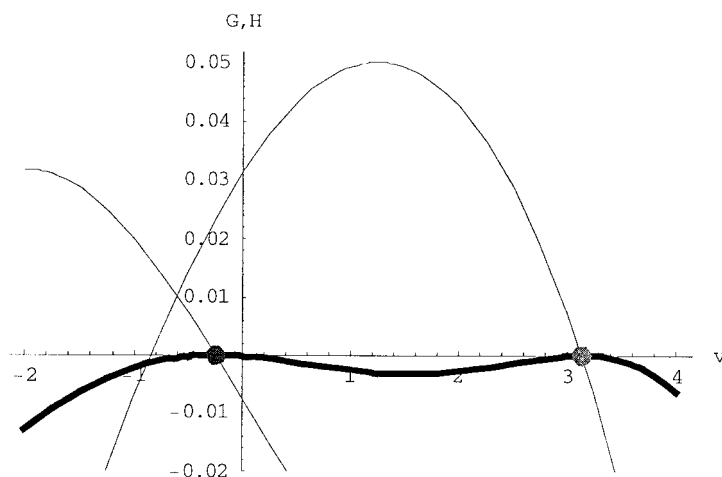


Fig. 4. The adaptive landscape (the G -function, bold line) for a coalition of two and the corresponding fitness functions H_1 and H_2 (thin lines).

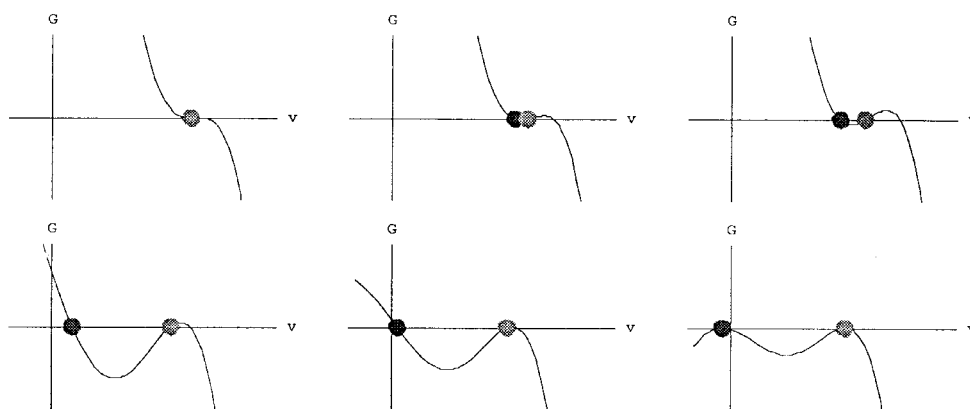


Fig. 5. Animation of adaptive landscape with a coalition of two.

Thus, at least for this model, the G -function approach to the solution with the correct number of strategies of the coalition pulls the system out of a local minimum. Figures 2 and 4 also demonstrate that minimum or maximum on the adaptive landscape (G) need not correspond to a minimum or maximum of the fitness functions (H).

It is important to realize that without considering the full local dynamics (including the correct number of coalition strategies) of the linearized system, one may draw the wrong conclusions about minima, maxima and local stability. This is particularly true because invasion by mutants (as we do here) changes the adaptive landscape (the G -function) and local stability analysis is not sufficient because we are now dealing with a different model: there are two more differential equations (for x_2 and u_2). To see how this works, we produced the following animation: The adaptive landscape changes as a single strategy approaches its local minimum. We then let a mutant (strategy value different from the local minimum by

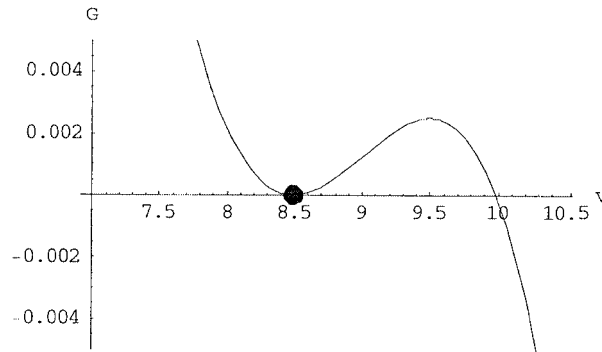


Fig. 6. Stable minimum on the adaptive landscape in an ESS coalition of three with only one strategy included in the model.

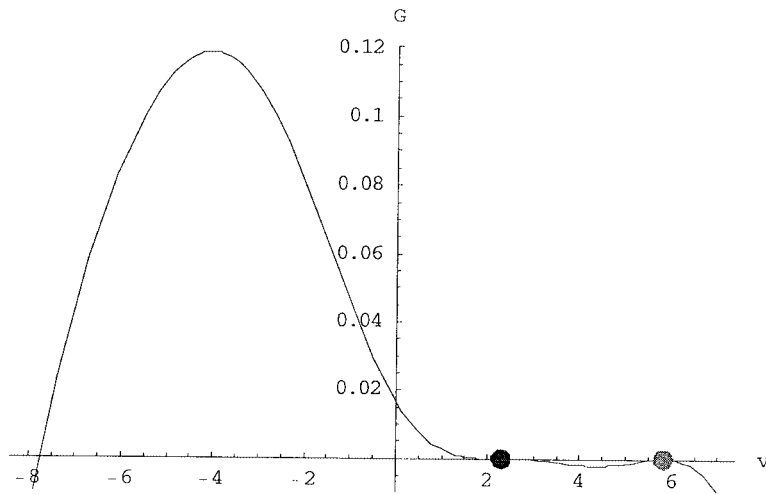


Fig. 7. Local maxima on the adaptive landscape for two strategies in a coalition of three ESS model.

10^{-4} invade, and then follow the dynamics as both strategies achieve their maxima with the ‘correct’ number of strategies in the coalition (i.e. with an invasion) from local minimum to two maxima. The first three (top row, left to right) and last three (bottom row, left to right) frames of the animation are shown in Fig. 5 (see also Brown and Pavlovic, 1992). Readers may observe this animation at <http://turtle.gis.umn.edu/people/yc/ess/>

Getting out of a local maximum is hard

In this example, we maintain the parameter values as given in (13), except for $\sigma_k^2 = 28$. This results in a stable ESS of three strategies (Vincent *et al.*, 1993). We start with a coalition of one ($r = 1$) and arrive at a stable minimum (Fig. 6) where $x_1^* = 27.5938$ and $u_1^* = 8.49143$.

Next, we ran the model with a coalition of two strategies with the following initial conditions: $x_1^* = x_2^* = 27.5938$, $u_1^* = 8.49143$ and $u_2^* = 8.49145$. This leads to two stable maxima at $x_1^* = 54.6209$, $x_2^* = 31.9853$, $u_1^* = 2.28615$ and $u_2^* = 5.81482$ (Fig. 7). To get out of these maxima and reach the ESS, the initial condition on u_3 had to be changed by at least 0.286. Compare this (i.e. 2 vs 2.28615) with the 10^{-4} difference that was sufficient to get out of a minimum in the adaptive landscape. At the two local maxima, there is a valley between extant strategies and strategies that may exist higher on the landscape. In this configuration of local maxima, adaptive speciation due to, say, small mutation is insufficient to produce an ESS with three strategies.

EXAMPLE: EVOLUTIONARILY UNSTABLE MAXIMUM

An evolutionarily unstable maximum with a coalition of one strategy requires that the strategy is resistant to invasion (the evolutionarily unbeatable strategy of Eshel, 1996) but not convergent-stable. The following example is based on the Monod equation with the modification that the strategy of the individual and the strategy of others change the carrying capacity:

$$G(v, \mathbf{u}, \mathbf{x}) = \left(K - \frac{v^2}{a} + \frac{b \sum_{i=1}^r v u_i x_i}{\sum_{j=1}^r x_j} \right) - \sum_{i=1}^r x_i$$

In this model, an individual's carrying capacity is maximized (in the absence of competitors) when $v = 0$. However, carrying capacity in the presence of competitors has an increasing component generated by collective changes in the population's strategy away from 0. Population dynamics in this model is given by (11).

For a coalition of one, $u_1 = 0$ satisfies $\partial G / \partial v|_{v=u_1} = 0$ and $\partial^2 G / \partial v^2 = -2a$, which indicates a maximum on the adaptive landscape, and $\partial^2 G / \partial u \partial v = b$, $\partial^2 G / \partial v \partial x = 0$ and $x_1^*|_{u_1=0} = K$.

For $a > 0$, the strategy $u_1 = 0$ will be convergent-stable and the ESS for the model when $a > b/2$. The stabilizing selection from an individual maximizing carrying capacity in the absence of competitors cancels the directional selection effects of capitalizing on others' strategies. When $a < b/2$, then strategy $u_1 = 0$ is not convergent-stable and it is an evolutionarily unstable maximum. In this case, adaptive dynamics can never drive the population to this point. Instead, if $u_1 > 0$, then natural selection favours ever greater values for the strategy up to some maximum value. If $u_1 < 0$, then the opposite occurs and selection favours ever smaller values for the strategy. The model actually has two ESSs, each of which is locally stable. These ESSs are the two corner solutions: $u_1^* = u_{\max}$ and $u_1^* = u_{\min}$. Which ESS results depends upon the initial strategy values in the population. If the average strategy value in the population is greater than zero (or less than zero), then u_{\max} (or u_{\min}) is achieved.

EXAMPLES OF EVOLUTIONARILY STABLE MINIMA

Starting with the example of Brown and Pavlovic (1992), the literature offers several examples of evolutionarily stable minima (Metz *et al.*, 1996; Mitchell, in press). With the idea of evolutionarily branching trees, Geritz *et al.* (1997, 1998) see adaptive dynamics to

these stable minima as a means for speciation and diversification (Metz *et al.*, 1996). The evolutionary game with Lotka-Volterra competition models generates an evolutionarily stable minimum. It is likely that many (indeed, perhaps most) games with ESS coalitions of two or more strategies will exhibit adaptive dynamics to an evolutionarily stable minimum when the number of evolving strategies is artificially fixed at one: $r = 1$.

We used the Monod model of density-dependent population growth to construct an evolutionary game that exhibits an evolutionarily unstable maximum ($a > 0$, $a < b/2$). This same model has an evolutionarily stable minimum at $u^* = 0$ when $a < 0$ and $a > b/2$. The model has an evolutionarily unstable minimum at $u^* = 0$ when $a < 0$ and $a < b/2$. Adaptive dynamics can achieve the evolutionarily stable minimum when there is only a single, evolving strategy. The evolutionarily unstable minimum, like the evolutionarily unstable maxima, is unattainable via adaptive dynamics.

CONCLUSIONS

Different stability concepts have been advanced with respect to strategy dynamics (e.g. Eshel, 1983; Taylor, 1989; Abrams, 1993a,b). Some of these concepts relate to the dynamics of the mean strategy value in the population (e.g. Roughgarden, 1983; Abrams, 1993a; Vincent *et al.*, 1993). If one admits the definition that a strategy (and its dynamics) represents the mean strategy value in a population of phenotypes, then we have the following result.

Recall that, based on Definition 1 (the definition of ESS), if for any m -coalition strategies $\mathbf{x}^* \in (0, M]$ is an ESE, then these strategies are ESSs. This means that, for the x_{ij}^* phenotypes of x_i^* (asterisks denote ESE), we have

$$x_i^* = \sum_{j=1}^N x_{ij}^* \quad i = 1, \dots, \sigma$$

Now for small enough Δu we have

$$\bar{u}_i^* = \frac{1}{x_i^*} \sum_{j=1}^N x_{ij}^* (j - K) \Delta u \quad K \geq 0$$

This follows from the definition of mean strategy. In other words, we have

$$\bar{u}_i^* = \frac{1}{x_i^*} \sum_{j=1}^N x_{ij}^* j \Delta u - NK \Delta u$$

Thus, a necessary condition for the stability of \bar{u}_i^* is that \mathbf{x}^* is an ESE.

In light of the theory developed here, and with the requirement that any strategy dynamics must be accompanied by a model of population dynamics – even if one assumes that the population is stable in evolutionary time – we reconsidered the two examples of unstable maximum and stable minimum given by Abrams *et al.* (1993b). Re-analysis of these examples using the *G*-function approach indicated that they do not yield evolutionarily stable minima or evolutionarily unstable maxima. As our examples demonstrate, it is likely that adaptive minima are reached when the strategies considered in the model are not those which lead to an ESS. Thus, some of the results in the literature might be different if coalitions with more than one strategy were considered.

Furthermore, we consider mathematical models of evolutionary games incomplete when only strategy dynamics equations are presented. Equations for population dynamics should always be stated explicitly, even if one chooses to ignore such dynamics.

Frequency-dependent selection and evolutionary game theory have revealed a bestiary of possible outcomes from evolution by natural selection. It invites us to change our view of the world from one of fairly static adaptive landscapes to one in which the adaptive landscape changes as much as – or more than – the strategies themselves (as glimpsed by Rosenzweig, 1978). Subject to flexible adaptive landscapes, maxima may not be evolutionarily stable and minima may be evolutionarily stable. This realization has led to a proliferation of terms in the literature regarding whether a strategy can be invaded or whether a strategy is convergent-stable under adaptive dynamics. Here, we have shown that the spirit of Maynard Smith's ESS concept becomes embodied when the ESS definition requires that the strategies of the ESS are both resistant to invasion and convergent-stable. In this way, ESSs may be the likely outcome of evolution by natural selection. In particular, evolutionarily stable minima, which can be achieved through adaptive dynamics, are likely to be invaded or split by competitive speciation (Rosenzweig, 1978). This results in an increase in strategy diversity and increases the likelihood of achieving an ESS that contains more strategies than currently extant in the community.

We hope that the ESS definition, conditions for resistance to invasion and convergence stability, the adaptive dynamics, and the propositions developed here will facilitate discussion and modelling of evolution by natural selection.

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APPENDIX: DYNAMICS FOR A COALITION OF TWO

When system dynamics involves a coalition of two, the equations become more complicated. Simple extension of the results of a coalition of one – that is, equation (10) – to a coalition of two is not appropriate. Here is the analysis:

$$\begin{aligned}\dot{x}_1 &= x_1 G(v, \mathbf{u}, \mathbf{x}) \Big|_{v=u_1} \\ \dot{x}_2 &= x_2 G(v, \mathbf{u}, \mathbf{x}) \Big|_{v=u_2} \\ \dot{u}_1 &= h\sigma^2 \frac{\partial G(v, \mathbf{u}, \mathbf{x})}{\partial v} \Big|_{v=u_1} \\ \dot{u}_2 &= h\sigma^2 \frac{\partial G(v, \mathbf{u}, \mathbf{x})}{\partial v} \Big|_{v=u_2}\end{aligned}$$

$$G(v, \mathbf{u}, \mathbf{x})|_{v=u_1} = 0$$

$$G(v, \mathbf{u}, \mathbf{x})|_{v=u_2} = 0$$

$$\left. \frac{\partial G(v, \mathbf{u}, \mathbf{x})}{\partial v} \right|_{v=u_1} = 0$$

$$\left. \frac{\partial G(v, \mathbf{u}, \mathbf{x})}{\partial v} \right|_{v=u_2} = 0$$

These equations are solved to get x_1^* , x_2^* , u_1^* , u_2^* . The Taylor series expansion around the equilibrium solution is

$$\begin{aligned} \delta \dot{x}_1 &= x_1^* \left[\frac{\partial G(u_1^*, \mathbf{u}^*, \mathbf{x}^*)}{\partial x_1} \delta x_1 + \frac{\partial G(u_1^*, \mathbf{u}^*, \mathbf{x}^*)}{\partial x_2} \delta x_2 + \frac{\partial G(u_1^*, \mathbf{u}^*, \mathbf{x}^*)}{\partial u_1} \delta u_1 + \frac{\partial G(u_1^*, \mathbf{u}^*, \mathbf{x}^*)}{\partial u_2} \delta u_2 \right] \\ \delta \dot{x}_2 &= x_2^* \left[\frac{\partial G(u_2^*, \mathbf{u}^*, \mathbf{x}^*)}{\partial x_1} \delta x_1 + x_1 \frac{\partial G(u_2^*, \mathbf{u}^*, \mathbf{x}^*)}{\partial x_2} \delta x_2 + x_1 \frac{\partial G(u_2^*, \mathbf{u}^*, \mathbf{x}^*)}{\partial u_1} \delta u_1 + x_1 \frac{\partial G(u_2^*, \mathbf{u}^*, \mathbf{x}^*)}{\partial u_2} \delta u_2 \right] \\ \delta \dot{u}_1 &= \sigma^2 \left[\frac{\partial^2 G(u_1^*, \mathbf{u}^*, \mathbf{x}^*)}{\partial x_1 \partial v} \delta x_1 + \frac{\partial^2 G(u_1^*, \mathbf{u}^*, \mathbf{x}^*)}{\partial x_2 \partial v} \delta x_2 + \right. \\ &\quad \left. \left(\frac{\partial^2 G(u_1^*, \mathbf{u}^*, \mathbf{x}^*)}{\partial v^2} + \frac{\partial^2 G(u_1^*, \mathbf{u}^*, \mathbf{x}^*)}{\partial u_1 \partial v} \right) \delta u_1 + \frac{\partial^2 G(u_1^*, \mathbf{u}^*, \mathbf{x}^*)}{\partial u_2 \partial v^2} \delta u_2 \right] \\ \delta \dot{u}_2 &= \sigma^2 \left[\frac{\partial^2 G(u_2^*, \mathbf{u}^*, \mathbf{x}^*)}{\partial x_1 \partial v} \delta x_1 + \frac{\partial^2 G(u_2^*, \mathbf{u}^*, \mathbf{x}^*)}{\partial x_2 \partial v} \delta x_2 + \frac{\partial^2 G(u_2^*, \mathbf{u}^*, \mathbf{x}^*)}{\partial u_1 \partial v} \delta u_1 + \right. \\ &\quad \left. \left(\frac{\partial^2 G(u_2^*, \mathbf{u}^*, \mathbf{x}^*)}{\partial v^2} + \frac{\partial^2 G(u_2^*, \mathbf{u}^*, \mathbf{x}^*)}{\partial u_2 \partial v} \right) \delta u_2 \right] \end{aligned}$$

This solution then gives the following matrix:

$$\begin{bmatrix} \frac{\partial G(u_1^*, \mathbf{u}^*, \mathbf{x}^*)}{\partial x_1} & \frac{\partial G(u_1^*, \mathbf{u}^*, \mathbf{x}^*)}{\partial x_2} & \frac{\partial G(u_1^*, \mathbf{u}^*, \mathbf{x}^*)}{\partial u_1} & \frac{\partial G(u_1^*, \mathbf{u}^*, \mathbf{x}^*)}{\partial u_2} \\ \frac{\partial G(u_2^*, \mathbf{u}^*, \mathbf{x}^*)}{\partial x_1} & \frac{\partial G(u_2^*, \mathbf{u}^*, \mathbf{x}^*)}{\partial x_2} & \frac{\partial G(u_2^*, \mathbf{u}^*, \mathbf{x}^*)}{\partial u_1} & \frac{\partial G(u_2^*, \mathbf{u}^*, \mathbf{x}^*)}{\partial u_2} \\ \frac{\partial^2 G(u_1^*, \mathbf{u}^*, \mathbf{x}^*)}{\partial x_1 \partial v} & \frac{\partial^2 G(u_1^*, \mathbf{u}^*, \mathbf{x}^*)}{\partial x_2 \partial v} & \frac{\partial^2 G(u_1^*, \mathbf{u}^*, \mathbf{x}^*)}{\partial v^2} + \frac{\partial^2 G(u_1^*, \mathbf{u}^*, \mathbf{x}^*)}{\partial u_1 \partial v} & \frac{\partial^2 G(u_1^*, \mathbf{u}^*, \mathbf{x}^*)}{\partial u_2 \partial v} \\ \frac{\partial^2 G(u_2^*, \mathbf{u}^*, \mathbf{x}^*)}{\partial x_1 \partial v} & \frac{\partial^2 G(u_2^*, \mathbf{u}^*, \mathbf{x}^*)}{\partial x_2 \partial v} & \frac{\partial^2 G(u_2^*, \mathbf{u}^*, \mathbf{x}^*)}{\partial u_1 \partial v} & \frac{\partial^2 G(u_2^*, \mathbf{u}^*, \mathbf{x}^*)}{\partial v^2} + \frac{\partial^2 G(u_2^*, \mathbf{u}^*, \mathbf{x}^*)}{\partial u_2 \partial v} \end{bmatrix}$$

It is the eigenvalues of this matrix that need to be examined for local stability.