

Evolutionary game theory: ESS, convergence stability, and NIS

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ABSTRACT

Question: How are the three main stability concepts from evolutionary game theory – evolutionarily stable strategy (ESS), convergence stability, and neighbourhood invader strategy (NIS) – related to each other? Do they form a basis for the many other definitions proposed in the literature?

Mathematical methods: Ecological and evolutionary dynamics of population sizes and heritable strategies respectively, and adaptive and NIS landscapes.

Results: Only six of the eight combinations of ESS, convergence stability, and NIS are possible. An ESS that is NIS must also be convergence stable; and a non-ESS, non-NIS cannot be convergence stable. A simple example shows how a single model can easily generate solutions with all six combinations of stability properties and explains in part the proliferation of jargon, terminology, and apparent complexity that has appeared in the literature. A tabulation of most of the evolutionary stability acronyms, definitions, and terminologies is provided for comparison.

Key conclusions: The tabulated list of definitions related to evolutionary stability are variants or combinations of the three main stability concepts.

Keywords: adaptive landscape, convergence stability, Darwinian dynamics, evolutionary game stabilities, evolutionarily stable strategy, neighbourhood invader strategy, strategy dynamics.

INTRODUCTION

Evolutionary game theory has and continues to make great strides. Increasingly, evolution by natural selection is seen as a game, and the mathematics of game theory as the language of Darwinian evolution. Yet, it rarely receives a central position in textbooks on evolution or even evolutionary ecology. And, as we enter the twenty-first century, the promise and intricacies of evolutionary game theory still elude many evolutionists and evolutionary

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ecologists. Progress has created an expanding jargon of evolutionary game theory that may prevent many from appreciating, understanding, and applying game theory to questions of natural selection. Recent advances permit an evaluation of what has become a Tower of Babel of terms. These sometimes complementary and sometimes competing terminologies can be reduced to three attributes of evolutionary stability (Geritz, 1998; Waxman and Gavrillets, 2005). These attributes are: resistance to invasion, convergence stability, and neighbourhood invasibility.

To be evolutionarily stable, a strategy must be resistant to invasion by alternative strategies. This logical attribute formed the cornerstone of the original definition for an evolutionarily stable strategy (ESS) (Maynard-Smith and Price, 1973; Maynard-Smith, 1982). An ESS was conceived by Maynard Smith and Price as a strategy which, when common, could not be invaded by any rare alternative strategy. Resistance to invasion leads to the concept of the ESS maximum principle in which such a strategy must reside on the peak of its adaptive landscape (Vincent and Brown, 2005). The adaptive landscape plots fitness as a function of the focal individual's strategy and it is a valuable tool for visualizing all three attributes of evolutionary stability.

By itself, the requirement of resistance to invasion proved inadequate for characterizing Maynard Smith's ESS as a likely outcome of evolution by natural selection. Such a strategy might be unbeatable, hence the spawning of the idea of an unbeatable strategy (Hamilton, 1967), but it might not be favoured given that the current population is using a nearby strategy. For example, an unbeatable strategy might not be convergence stable. Originally, convergence stability arose from the concept of continuously stable strategy (CSS) (Eshel and Motro, 1981; Eshel, 1983, 1996). In fact a CSS is an ESS that is convergence stable. A strategy is convergence stable if strategies successively closer to it can invade a population using any nearby strategy value.

Since Eshel's pioneering work, the notion of convergence stability has been refined into formal strategy dynamics that describe how the mean value of a population's strategy might change with time as the strategy value 'climbs' its adaptive landscape (Vincent *et al.*, 1993). Interestingly, convergence stability by itself may actually drive a strategy to a point of minimum fitness on the adaptive landscape, giving rise to the possibility of an evolutionarily stable minimum (Abrams *et al.*, 1993). The property of convergence stability and the evolution to minima of the adaptive landscape has initiated research in adaptive dynamics (Metz *et al.*, 1996) and evolutionary branching (Geritz *et al.*, 1998) respectively.

A concept similar to but distinct from convergence stability is that of neighbourhood invader strategy (NIS) (Apaloo, 1997; see also, for example, McKelvey and Apaloo, 1995; Geritz *et al.*, 1998; Apaloo *et al.*, 2005). A NIS is a strategy that can invade any population with a nearby strategy value. This concept of NIS considers the alternative strategy to be common, and the NIS to be the rare strategy. Whereas a point that is resistant to invasion results in a maximum principle, the NIS results in a minimum principle. When the fitness of the focal individual using the NIS is plotted as a function of the resident strategy, fitness takes on a minimum when the resident strategy is also the NIS.

Here we use the fitness-generating function concept (*G*-function) to evaluate all three facets of evolutionary stability embodied by resistance to invasion, convergence stability, and neighbourhood invasibility. We will see how eight possible combinations from the presence or absence of these properties was anticipated (Geritz *et al.*, 1998). However, although somewhat different, these three properties are not entirely independent of each other. In fact, only six combinations can actually occur. For example, an ESS that is NIS must also be convergence stable.

The explicit consideration of population dynamics illustrates the interaction of ecological and evolutionary processes in determining the outcomes of natural selection. The fitness-generating function starts as an ecological model of population dynamics with changes in population size as an explicit part of the modelling. The adaptive landscape changes both in response to the population's strategy value and also in response to population size. By not explicitly considering population size, the fitness landscapes of Waxman and Gavrillets (2005) are ecologically unrealistic and miss the interplay between strategy and population dynamics.

In what follows, we explicitly consider the combined effects of strategy and population dynamics. We examine each facet of evolutionary stability. We provide definitions, necessary and sufficient conditions, and worked examples. To make the properties of evolutionary stability more transparent and accessible, we illustrate the concepts graphically as adaptive landscapes, and we introduce the concept of the NIS landscape. The adaptive landscape plots fitness (per capita growth rate) as a function of the strategy of a focal individual within a given community of populations and strategies (Vincent *et al.*, 1993), whereas the NIS landscape plots the fitness of a focal (or fixed) individual within a varying community of populations and strategies. In the Discussion, we address the practical significance of the ESS, convergence stability, and NIS concepts. Besides being of theoretical interest for evolutionary games, an understanding of all three has practical importance in so far as actual species may reside at or evolve in response to evolutionary equilibria that possess one, two or three of these properties. We will discuss how each or combinations of each influence the evolutionary process. We end by evaluating the Babel of stability definitions spawned by evolutionary game theory in terms of the three stability concepts of ESS, NIS, and convergence stability. There is a lot of jargon. But in the end, an understanding of resistance to invasion, convergence stability, and neighbourhood invisibility clarifies how evolutionary game theory provides a framework for modelling the outcomes of evolution by natural selection.

THE EVOLUTIONARY GAME AS A G-FUNCTION

As proposed by Darwin, evolution by natural selection follows from three facts of living organisms. First, natural selection requires heritable variation. Individuals (players) possess heritable traits (strategies) and individuals may vary in their strategy values (usually as a result of genetic mutation and variability). Second, there is a struggle for existence. That is, individuals have fitness defined as the per capita growth rate, and there are limits to growth. Above some population size, per capita growth rate declines with population size. This recognizes an ecological dynamic where population sizes change with time. Third, the strategy of the individual and the strategies of others influence fitness. Changes in the population sizes lead to changes in the frequencies (evolution) of the strategies present, which establishes evolutionary dynamics. The strategies conferring higher per capita growth rates will increase in frequencies at the expense of those with lower than average per capita growth rates. We refer to the combined ecological and evolutionary dynamics as Darwinian dynamics (Vincent and Brown, 2005).

The concept of the fitness-generating function, G , models these three facets of Darwinian dynamics. We describe a general evolutionary game using the function

$$G(v, \mathbf{u}, \mathbf{x}),$$

where the vector $\mathbf{u} = [u_1, \dots, u_{n_s}]$ represents the different scalar strategies found among a community of n_s different types or species. The vector $\mathbf{x} = [x_1, \dots, x_{n_s}]$ represents the current population sizes of each of these types where x_i and u_i , $i = 1, \dots, n_s$, give the density and strategy respectively of individuals of type i . Setting $v = u_i$ ‘generates’ the fitness function for the i^{th} species. The above function can be quite general. Here we consider only scalar-valued strategies. This formulation will permit extensions to vector-valued strategies and equilibria with more than one species, but this remains beyond our current scope. By using a single G -function, we are able to represent all species that share the same set of evolutionarily feasible strategies, and experience the same ecological consequences of possessing a given strategy. Hence, different species are identified by their differing strategies and not by their different strategy sets [for models with two rather than one G -function, see Brown and Vincent (1992)].

The fitness-generating function models the population dynamics and strategy dynamics of species i respectively according to:

$$\frac{dx_i}{dt} = x_i G|_{v=u_i} \quad \text{and} \quad \frac{du_i}{dt} = k \frac{\partial G}{\partial v} \Big|_{v=u_i}.$$

For strategy dynamics, we have multiplied the fitness gradient by an evolutionary ‘speed’ constant, k , meant to represent some measure of heritability and additive genetic variance, in line with Fisher’s fundamental theorem of natural selection. This speed term may be influenced by mutation rates, population size, population structure, and the underlying genetics of inheritance. For instance, in the canonical equation of adaptive dynamics (Dieckmann and Law, 1996), the speed term increases linearly with population size. For many quantitative analyses (Charlesworth, 1990; Falconer and Mackay, 1996) and individual-based models of mutation and evolution (Johannson, 2008), the evolutionary speed constant is largely unaffected by a range of population sizes.

For the remainder of this article, it is assumed that population dynamics converge to a stable equilibrium with a given strategy’s population size either approaching zero or approaching some positive population size for at least one species. In the G -function approach, the stability of populations sizes is defined as ecologically stable equilibrium (Vincent and Brown, 2005). The assumption of stable population dynamics is not absolutely necessary but it eases the task of discussing and illustrating the three aspects of evolutionary stability. Each combination of strategies, \mathbf{u} , will have an associated vector of equilibrium population sizes, \mathbf{x}^* , where each strategy’s equilibrium population size must be greater than or equal to zero: $x_i^* \geq 0$. Any value for u will have one (if a global equilibrium) or more (if a local equilibrium) values of x^* associated with it. But only certain combinations of u_i ’s will have positive equilibrium population sizes. Depending upon the model and its parameters, there will likely be an upper limit to the number of species that can co-exist at positive population sizes. The number of co-existing species will depend on each species’ strategy value.

ESS maximum principle: resistance to invasion

We divide the strategies of the vector $\mathbf{u} = [u_1, \dots, u_{n_s}]$ into two groups, a *coalition vector*, $\mathbf{u}_c = [u_1, \dots, u_{n_s^*}]$, and a *mutant vector*, $\mathbf{u}_m = [u_{s^*+1}, \dots, u_{n_s}]$, where $n_{s^*} \geq 1$ when considering evolutionary stability. In the following developments, the coalition vector represents the strategies that might possess some form of evolutionary stability. At the very least, these

strategies must be able to persist together at positive population sizes. Since evolutionary stability is in reference to how this coalition vector performs in the face of alternative strategies, the mutant vector represents the alternative strategies that ‘challenge’ the evolutionary stability of the coalition vector. If the coalition vector can pass muster against all possible mutant vectors, the coalition vector may be evolutionarily stable. The distinction between the coalition and mutant vectors will be useful for each of the following definitions of evolutionary stability.

We write the vector of strategies as

$$\mathbf{u} = [\mathbf{u}_c, \mathbf{u}_m].$$

Rather than considering the \mathbf{x}^* associated with \mathbf{u} , it will be useful to consider the stable population sizes associated with the coalition vector in the absence of any individual from the mutant vector, as well as the ecologically stable equilibrium associated with the mutant vector in the absence of any individuals from the coalition vector. We will write these as $[\mathbf{x}_c^*, \mathbf{0}]$ and $[\mathbf{0}, \mathbf{x}_m^*]$, respectively. The equilibrium point associated with the mutant vector does not require that each mutant strategy be able to persist at a positive population size with the other mutant strategies. However, each member of the coalition vector at \mathbf{x}_c^* must have a positive population size. At an equilibrium

$$G(v, [\mathbf{u}_c, \mathbf{u}_m], [\mathbf{x}_c^*, \mathbf{0}])|_{v=u_i} = \mathbf{0} \quad \text{for } i = 1, \dots, n_{s^*}.$$

The coalition vector represents one or more strategies that can co-exist, with each strategy at a positive population size. Candidate solutions for evolutionary stability must at the very least be a coalition vector. The mutant vector allows us to add a perturbation to an ecological system comprised of a coalition vector. Strategies in the mutant vector may be close in value to strategies of the coalition vector or quite distant and may occur with large or very small population sizes. As the ecological dynamics produce changes in population sizes, these strategies of the mutant vector may die off by having their populations sizes go to zero or some of them may successfully invade. Successful invaders will result in a new coalition vector that either maintains the previous species or results in the extinction of one or more members of the previous coalition vector. While the strategies of the coalition vector can co-exist with each other in the absence of the mutant vector, there is no guarantee that all or even some of the strategies of the coalition vector can persist in the face of an invasion from individuals in the mutant vector.

We now examine additional properties of \mathbf{u}_c that become necessary for this combination of strategies to be resistant to invasion, NIS, and convergence stable. However, in the following developments, we will assume that \mathbf{u}_c and \mathbf{u}_m are both composed of just a single type, that is $n_{s^*} = 1$ and $n_s = 2$, written as u_c and u_m respectively. As with the assumption of scalar strategies, the reason for making this additional assumption is so that we can focus on the three main features of the evolutionary game rather than on the complexities introduced by allowing for vector strategies and ESS coalitions greater than one.

For the fitness-generating function, this property of evolutionary stability follows directly from the general definition for an ESS (Vincent and Brown, 2005). Let \mathcal{U} be the strategy set.

Definition 1 (ESS-scalar). *A coalition strategy $u_c \in \mathcal{U}$ is said to be an evolutionarily stable strategy (ESS) for the equilibrium point $\mathbf{x}^* = [x_c^*, x_m^*] = [x_c^*, 0]$ if, for all feasible strategies u_m , \mathbf{x}^* remains as the stable equilibrium with respect to population dynamics. It is said to be a local (global) ESS if \mathbf{x}^* is a local (global) ecologically stable equilibrium.*

The following ESS maximum principle (Vincent and Brown, 2005) applies to both local and global ESS.

Theorem 2 (maximum principle-scalar). *If the strategy $u_c \in \mathcal{U}$ is an ESS for \mathbf{x}^* , then*

$$\max_{v \in \mathcal{U}} G(v, [u_c, u_m], [x_c^*, 0]) = G(v, [u_c, u_m], [x_c^*, 0])|_{v=u_c} = 0.$$

The ESS maximum principle is always global with respect to strategy space. In a world of u_c at x_c^* , the strategy $v = u_c$ must yield higher fitness than setting v to any other strategy in the feasible strategy space. This property of evolutionary stability can be seen graphically using the adaptive landscape where $G(v, [u_c, u_m], [x_c^*, 0])$ versus v must take on a global maximum at $v = u_c$.

The conditions for a strategy u_c (on the interior of the strategy set) to be resistant to invasion and satisfy the ESS maximum principle include

$$G(v, [u_c, u_m], [x_c^*, 0])|_{v=u_c} = 0 \quad (1)$$

$$\left. \frac{\partial G(v, [u_c, u_m], [x_c^*, 0])}{\partial v} \right|_{v=u_c} = 0 \quad (2)$$

$$\left. \frac{\partial G(v, [u_c, u_m], [x_c^*, 0])}{\partial x_c} \right|_{v=u_c, x_c=x_c^*} < 0 \quad (3)$$

Equation (1) requires that at equilibrium the fitness is zero. The equilibrium population size, x_c^* in terms of u_c , may be determined from this expression. Equation (2) represents a first-order necessary condition for G to take on a maximum with respect to v at $v = u_c$ and may be used to solve for x_c^* as a function of u_c . Thus we may write $G(v, [u_c, u_m], [x_c^*, 0])$ as $G(v, [u_c, u_m])$, which may be used to obtain simpler second-order conditions. Conditions (1) and (3) ensure that x_c^* is a stable equilibrium point with respect to the population dynamics. These three conditions are assumed to be satisfied when discussing ESS, NIS, and convergence stability.

Resistance to invasion also depends upon an additional (second-order) condition that determines whether the strategy is at a maximum or minimum of the adaptive landscape. This condition is written in terms of S_1 :

$$S_1 = \left. \frac{\partial^2 G(v, [u_c, u_m], [x_c^*, 0])}{\partial v^2} \right|_{v=u_c}. \quad (4)$$

If S_1 is positive, the adaptive landscape attains a minimum at the focal strategy and it is not resistant to invasion. If S_1 is negative, the focal strategy satisfies the ESS maximum principle and it is invasion resistant. Thus u_c and its corresponding equilibrium point x_c^* will be an ESS candidate if conditions (1)–(3) are all satisfied and S_1 is negative. For u_c to be an ESS, the maximum principle must additionally be satisfied.

NIS minimum principle: neighbourhood invader strategy

The neighbourhood invader strategy (NIS) concept views evolutionary stability from the perspective of whether the strategy u_c is capable of invading a population with a strategy close to u_c . Imagine a neighbouring strategy, u_m , at its equilibrium population size of x_m^* .

This means an individual using $v = u_m$ has a fitness of zero within the population. For u_c to be NIS, fitness must be positive for $v = u_c$ within the population adopting the strategy $u_m \neq u_c$, and at size x_m^* . We give the formal definition and its associated minimum principle (Apaloo, 1997) in the same context and notation as the ESS maximum principle. It is now essential to recall that in the NIS concept, it is the resident strategy that is varied. Thus x_m^* varies as u_m varies. This relationship occurs in the concept of convergence stability also. Therefore, in this and the next subsections, x_m^* must be considered as a function of u_m and we may write $G(v, [u_c, u_m], [0, x_m^*])$ as $G(v, [u_c, u_m])$, which may be used to obtain simpler second-order conditions.

Definition 3 (NIS-scalar). A strategy $u_c \in \mathcal{U}$ is said to be a neighbourhood invader strategy (NIS) for the equilibrium point $\mathbf{x}^* = [x_c^*, x_m^*] = [x_c^*, 0]$ if, when the population using u_c is rare ($x_c = \varepsilon \approx 0$), for any scalar strategy u_m in a close neighbourhood of u_c , $N(u_c)$ with $u_m \neq u_c$,

$$G(v, [u_c, u_m], [0, x_m^*])|_{v=u_c} > 0. \tag{5}$$

Theorem 4 (minimum principle-scalar). The strategy $u_c \in \mathcal{U}$ is an NIS for \mathbf{x}^* iff u_c is the unique solution to the minimization problem

$$\min_{u_m \in N(u_c)} G(v, [u_c, u_m], [0, x_m^*])|_{v=u_c} = G(v, [u_c, u_c], [0, x_c^*])|_{v=u_c} = 0.$$

The proof of this theorem follows trivially from the definition. The NIS need be local only with respect to strategy space. The NIS need not be able to invade a strategy u_m that is far from the value of u_c . In the above definition for NIS, if the neighbourhood of u_c , $N(u_c)$, over which the strategy u_c can invade u_m is global, i.e. $N(u_c) = \mathcal{U}$, then u_c is a global NIS, otherwise it is a local NIS. The property of the NIS can be seen graphically using what we will call the *NIS landscape*. For the strategy u_c to be an NIS, the NIS landscape evaluated at u_m and x_m^* with $u_m \neq u_c$, $u_m \in N(u_c)$ must be higher than zero at the point $v = u_c$.

The NIS minimum principle can be shown graphically on the NIS landscape, if we plot

$$G(v, [u_c, u_m], [0, x_m^*])|_{v=u_c}$$

versus u_m . On this curve,

$$G(v, [u_c, u_m], [0, x_m^*])|_{v=u_c} > 0$$

for all $u_m \neq u_c$ and when $u_m = u_c$

$$G(v, [u_c, u_c], [0, x_c^*])|_{v=u_c} = 0.$$

Hence, this curve takes on a minimum at $u_m = u_c$. Note how the NIS landscape mimics but is quite different from the adaptive landscape. The adaptive landscape fixes the strategy within the population and then evaluates the fitness consequence of varying the focal individual's strategy, v . The NIS landscape fixes the strategy of the focal individual and evaluates how this individual's fitness will be affected by collectively varying the strategy of others using strategy u_m . While these landscapes exist in different state spaces, they can be superimposed on the same graph if we let the horizontal axis be v for the adaptive landscape, and then let it be u_m for the NIS landscape.

For a strategy to be NIS, it must satisfy (1)–(3) just like the ESS maximum principle. The second-order condition is different and unique to the NIS minimum principle. It requires an

evaluation of how fitness of an individual using u_c ($v = u_c$) changes with a change in the resident strategy u_m away from u_c . We write this second-order condition in terms of S_2 . If we substitute into G the effect of u_m on the equilibrium population size, x_m^* , then S_2 may be written as

$$S_2 = \frac{\partial^2 G(v, [u_c, u_m])}{\partial u_m^2} \Big|_{v = u_m = u_c^*},$$

but a more extensive form that illustrates all of the evolutionary and ecological effects is:

$$S_2 = \left(\frac{\partial^2 G(v, [u_c, u_m], [0, x_m^*])}{\partial u_m^2} + 2 \frac{\partial^2 G(v, [u_c, u_m], [0, x_m^*])}{\partial u_m \partial x_m^*} \frac{\partial x_m^*}{\partial u_m} + \frac{\partial^2 G(v, [u_c, u_m], [0, x_m^*])}{\partial x_m^{*2}} \left(\frac{\partial x_m^*}{\partial u_m} \right)^2 + \frac{\partial G(v, [u_c, u_m], [0, x_m^*])}{\partial x_m^*} \frac{\partial^2 x_m^*}{\partial u_m^2} \right) \Big|_{v = u_m = u_c^*}$$

This more extensive form reveals both the direct effect of changing the value of the resident strategy, u_m (first term), and shows the indirect effects of changing u_m that accrue through effects on the population's equilibrium size, x_m^* (last three terms).

When S_2 is negative, the NIS landscape takes on a maximum at the focal strategy u_c and the strategy is not NIS. If S_2 is positive, the NIS landscape takes on a minimum at u_c and the NIS minimum principle is satisfied.

Convergence stability

We now give the definition for a strategy to be *convergence stable* (Christiansen, 1991). A convergence stable strategy is also referred to as *m-stable* by Taylor (1989). The concept of convergence stability is a part of the concept of continuously stable strategy, which was first developed by Eshel and Motro (1981).

Definition 5 (coverage stable-scalar). A strategy $u_c \in \mathcal{U}$ is said to be convergence stable for the equilibrium point $[x_c^*, x_m^*] = [x_c^*, 0]$ if there is a value $\varepsilon > 0$ such that for any strategy u_m with an associated equilibrium point $[0, x_m^*]$ in an ε neighbourhood of u_c , there is a value $\delta > 0$ such that for any strategy v at a δ vicinity of u_m with $u_m \neq u_c$,

$$G(v, [u_c, u_m], [0, x_m^*]) > 0 \text{ whenever } |v - u_c| < |u_m - u_c|. \quad (6)$$

There is no optimization principle for the convergence stability concept. The first-order necessary conditions for convergence stability are the same as those for resistance to invasion and NIS. In perturbing a strategy away from u_c , the adaptive landscape at $u_c + \delta$ has positive or negative slope depending on whether δ is negative or positive, respectively. The second-order condition is defined in terms of S_3 (Eshel, 1983). If we substitute into G the effect of u_m on x_m^* , then S_3 may be written as

$$S_3 = \frac{\partial^2 G(v, [u_c, u_m])}{\partial v^2} + \frac{\partial^2 G(v, [u_c, u_m])}{\partial u_m \partial v} \Big|_{v = u_m = u_c^*},$$

but a more extensive form that explicitly considers both evolutionary and ecological effects gives

$$S_3 = \left(\frac{\partial^2 G(v, [u_c, u_m], [0, x_m^*])}{\partial v^2} + \frac{\partial^2 G(v, [u_c, u_m], [0, x_m^*])}{\partial u_m \partial v} + \frac{\partial^2 G(v, [u_c, u_m], [0, x_m^*])}{\partial v \partial x_m^*} \frac{\partial x_m^*}{\partial u_m} \right) \Big|_{v=u_m=u_c}$$

where the first term describes effects mediated through the strategy of the focal individual, v , the second term considers the effects of changing the resident strategy, u_m , on the slope of the adaptive landscape, and the third term shows how changes in the equilibrium population size of the resident strategy, x_m^* , influence the fitness gradient.

When S_3 is positive, the strategy is not convergence stable and perturbations away from u_c will lead to strategy dynamics that diverge from u_c . When S_3 is negative, the strategy is convergence stable and strategy dynamics will return the population's strategy back to u_c following a perturbation.

An ESS that is also a NIS permits fortuitous mutational jumps to an ESS that may not be possible when the ESS is just convergence stable. Additionally, an ESS that is an NIS permits the strategy to approach the peak on the adaptive landscape continuously, since an ESS which is a NIS is also convergence stable (Apaloo, 1997). This point is one of the reasons why we are enthusiastic about the novel application of adaptive landscapes to comparing the NIS and convergence stability. As we show using the NIS landscape, the NIS is a minimum principle (minimizing G with respect to u). Interestingly, using the adaptive landscape this is similar to the ESS as a maximum principle (maximizing G with respect to v).

COMBINATIONS OF EVOLUTIONARY STABILITIES AND EXAMPLES

In what follows, we assume that the joint first-order conditions (1), (2), and (3) are satisfied.

1. The aspects of evolutionary stabilities and their separate second-order conditions lead to the following evolutionary stability classifications:

if $S_1 < 0$, then u_c is an ESS,

if $S_2 > 0$, then u_c is an NIS,

if $S_3 < 0$, then u_c is convergence stable.

2. The second-order conditions given in terms of S_1 , S_2 , and S_3 determine the type of evolutionary stability that a strategy will have. Ignoring cases where $S_i = 0$ for some i , and taking the resulting strict inequality conditions in groups of three, we have the eight configurations as shown in Table 1. If the signs of the second-order derivatives are taken in pairs, it may force or influence the sign of the third remaining second-order derivative. In fact, two of the eight combinations in Table 1 are not possible and they are marked with the symbol *. It is not possible to have a strategy that is both an NIS and resistant to invasion, and yet is not convergence stable (Apaloo, 1997). This observation implies that if $S_1 < 0$ and $S_2 > 0$, then $S_3 < 0$. In the second case, it is not possible to have a convergence stable strategy that is neither resistant to invasion nor NIS (see, for example, Figure 2 in Meszena *et al.*, 2001). This observation implies that if $S_3 < 0$, then $S_1 < 0$ and/or $S_2 > 0$.
3. In what follows, we provide an example to illustrate the various stabilities and their combinations. Consider a scalar valued strategy u that influences the carrying capacity K

Table 1. Eight combinations of stability properties

$S_1 < 0$ $S_2 > 0$ $S_3 < 0$	ESS, NIS, convergence stable
$S_1 < 0$ $S_2 < 0$ $S_3 < 0$	ESS, not NIS, convergence stable
$S_1 < 0$ $S_2 > 0$ $S_3 > 0$	ESS, NIS, not convergence stable*
$S_1 > 0$ $S_2 > 0$ $S_3 > 0$	not ESS, NIS, not convergence stable
$S_1 < 0$ $S_2 < 0$ $S_3 > 0$	ESS, not NIS, not convergence stable
$S_1 > 0$ $S_2 < 0$ $S_3 < 0$	not ESS, not NIS, convergence stable*
$S_1 > 0$ $S_2 < 0$ $S_3 > 0$	not ESS, not NIS, not convergence stable
$S_1 > 0$ $S_2 > 0$ $S_3 < 0$	not ESS, NIS, convergence stable

* A combination that is not possible.

of a population growth model. Let there be a single resident strategy u_c with a positive equilibrium population size x_c^* and suppose that the fitness-generating function is given by the logistic growth equation:

$$G(v, [u_c, u_m], [x_c, 0]) = r \left(\frac{K(v, u_c) - x_c}{K(v, u_c)} \right), \quad (7)$$

where

$$K(v, u) = k - v^2 a + buv.$$

For this example, It can easily be shown that the candidate solution is $u_c = 0$ with the equilibrium population size x_c^* given by $x_c^* = k + (b - a)u_c^2$. In addition, the second-order partial derivatives result in $S_1 = -2a$, $S_2 = 2(a - b)$, and $S_3 = -(2a - b)$. Thus the singular point is an ESS if $a > 0$, an NIS if $a > b$, and convergence stable if $2a > b$.

As expected, only six of the eight combinations are possible for this model. The NIS that is resistant to invasion must also be convergence stable, and a convergence stable, non-NIS must be resistant to invasion and hence ESS. Through the non-independence of the three conditions, one sees in the NIS certain properties of convergence stability, and certain properties of the maximum principle in such a manner that all eight outcomes are not feasible. As shown in Fig. 1, variation of the values of the parameters a and b throughout the entire parameter space alters the stability properties of $u_c = 0$ through all six configurations mentioned above.

ALTERNATIVE SOLUTIONS

In the preceding example, there is a unique solution to the shared set of necessary conditions for the evolutionary stabilities. Here we examine a model in which alternative solutions can emerge from the same fitness-generating function. The model is based upon the logistic population growth, but the parameterization has been contrived to produce three candidate solutions that exhibit different stability properties.

We will consider population growth to be logistic as given by

$$\frac{dx_i}{dt} = rx_i \left(\frac{K(v, \mathbf{u}, \mathbf{x}) - \sum_{i=1}^{n_s} x_i}{K(v, \mathbf{u}, \mathbf{x})} \right) \Big|_{v=u_i}$$

and the strategy of the focal individual and that of others influence K according to (using the population frequency notation)

$$K(v, \mathbf{u}, \mathbf{x}) = 500 - \frac{v^2 \left(\sum_{i=1}^{n_s} p_i u_i \right)^2}{2} + 13v \left(\sum_{i=1}^{n_s} p_i u_i \right)^2 - 44v \left(\sum_{i=1}^{n_s} p_i u_i \right) u + 32v,$$

where

$$p_i = \frac{x_i}{\sum_{i=1}^{n_s} x_i}.$$

We can then form an explicit fitness-generating function by substituting the equation for K into the following general form:

$$G(v, \mathbf{u}, \mathbf{x}) = r \left(\frac{K(v, \mathbf{u}, \mathbf{x}) - \sum_{i=1}^{n_s} x_i}{K(v, \mathbf{u}, \mathbf{x})} \right).$$

This fitness-generating function yields three different candidate solutions of $u_1 = 1$, $u_2 = 4$, and $u_3 = 8$ obtained from solving (1)–(3).

All three of these solutions are resistant to invasion and reside at a maximum of their respective adaptive landscapes. In addition, they satisfy the condition that an ESS be

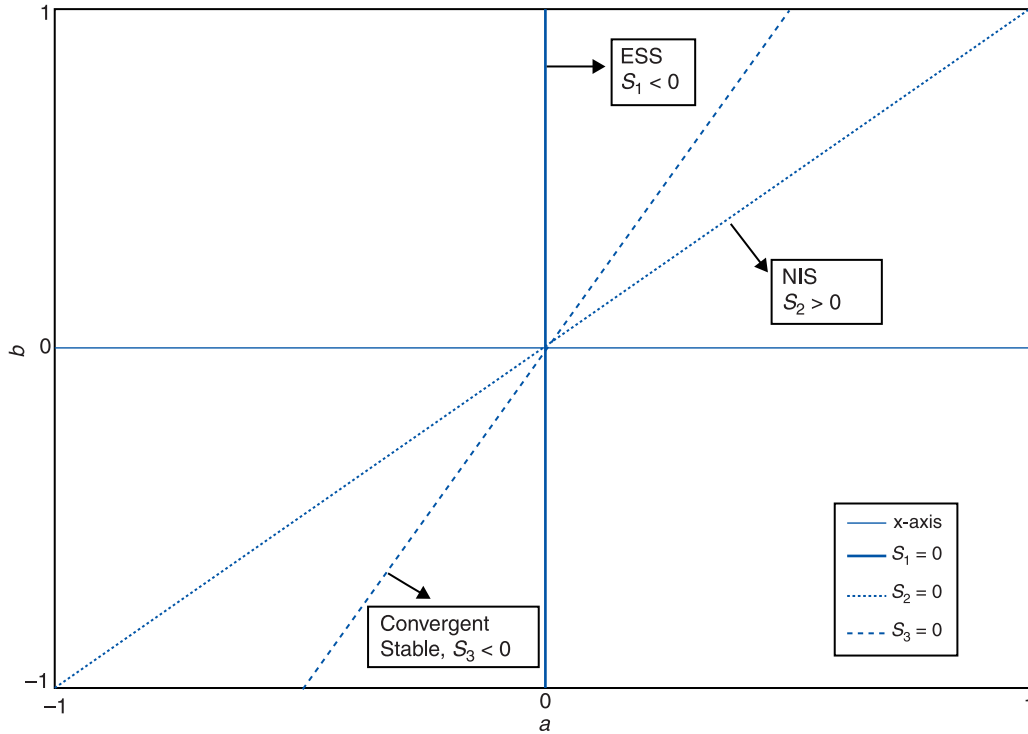


Fig. 1. For the model given by equation (7), the figure illustrates the effect of the parameters a and b on the three aspects of evolutionary stabilities.

ecologically stable equilibrium and therefore all three solutions are ESS. The solutions $u_1 = 1$ and $u_3 = 8$ are convergence stable and the solution $u_2 = 4$ is not convergence stable. Thus being ESS (by any present definition of an ESS) does not imply convergence stability in general. Because solution 4 is an ESS but not convergence stable, it cannot be an NIS. Of the three ESS solutions, $u_1 = 1$ is an NIS whereas $u_2 = 4$ and $u_3 = 8$ are not. The second-order conditions for the evolutionary stabilities can be checked analytically (if the G -function is simple enough), numerically or graphically. An *NIS landscape* (in the case of a single scalar coalition strategy) is the graph of $G(v, [u_c, u_m], [0, x_m^*])|_{v=u}$ plotted against u_m . The *adaptive landscape* is similarly obtained by plotting $G(v, [u_c, u_m], [x_c^*, 0])$ versus v . In what follows, we provide some graphical results in Figures 2–11. These graphs are given in terms of the adaptive landscape, NIS landscapes and Darwinian dynamics. In Fig. 2, we see that the strategy $u_1 = 1$ is an ESS and NIS. It is an ESS because the adaptive landscape with $u_c = u_1 = 1$ achieves a local maximum when $v = u_1 = 1$. Similarly, it is an NIS because the NIS landscape with $v = u_1 = 1$ achieves a local minimum when $u_m = u_1 = 1$. The corresponding results for the strategies $u_2 = 4$ and $u_3 = 8$ are shown in Figs. 3 and 4.

The adaptive landscape provides an additional and complementary graphical tool for viewing these three stability properties that have previously been shown using pairwise invasibility plots (Geritz *et al.*, 1998) or invasion diagrams (Waxman and Gavrillets, 2005). The height of the landscape shows the per capita growth rate of any resident species and any potential species that ‘invades’ at near zero population size. $G(v) = 0$ provides a kind of waterline,

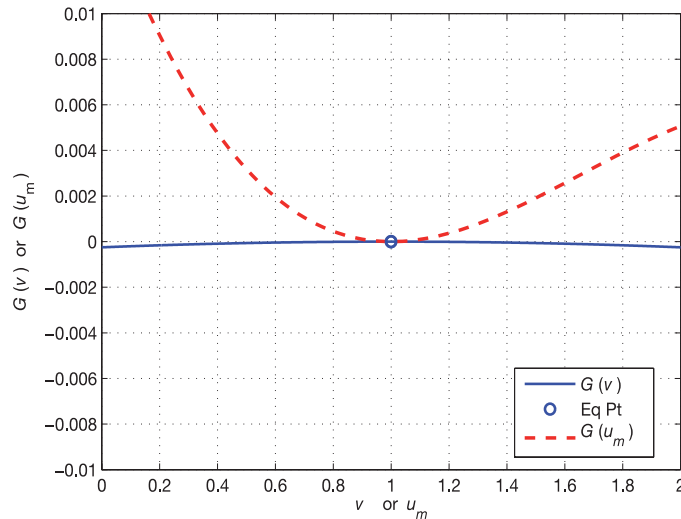


Fig. 2. The strategy $u_1 = 1$ is a local ESS and a NIS.

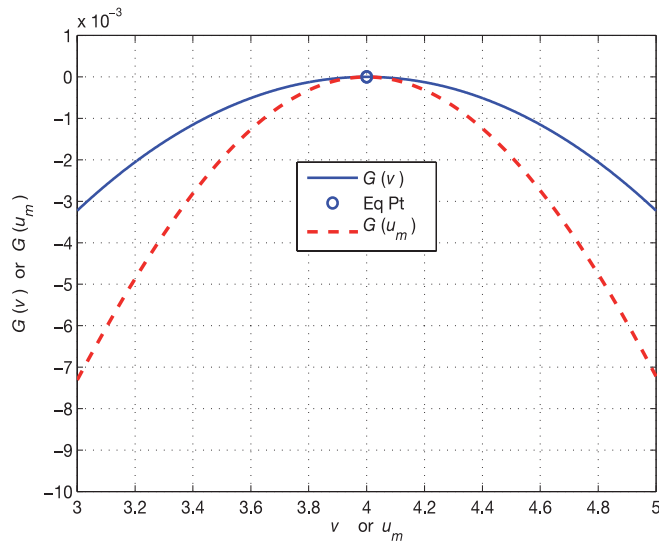


Fig. 3. The strategy $u_2 = 4$ is an ESS but it is not convergence stable or a NIS.

where any strategy with positive growth rate would increase in population size, and any strategy with negative growth rate would decline. A positive slope of the adaptive landscape is in the direction of change a resident species strategy will undergo via strategy dynamics. The relationship between population and strategy dynamics is not so clear with invasibility plots. For example, the lack of explicit consideration of population dynamics in Waxman and Gavrillets (2005) leads to some ‘invasion landscapes’ that are not ecologically reasonable or feasible.

The presence or absence of convergence stability in the strategies $u_1 = 1$, $u_2 = 4$, and $u_3 = 8$ is shown in Figs. 5–7. In these figures, it is important to note that only adaptive landscapes

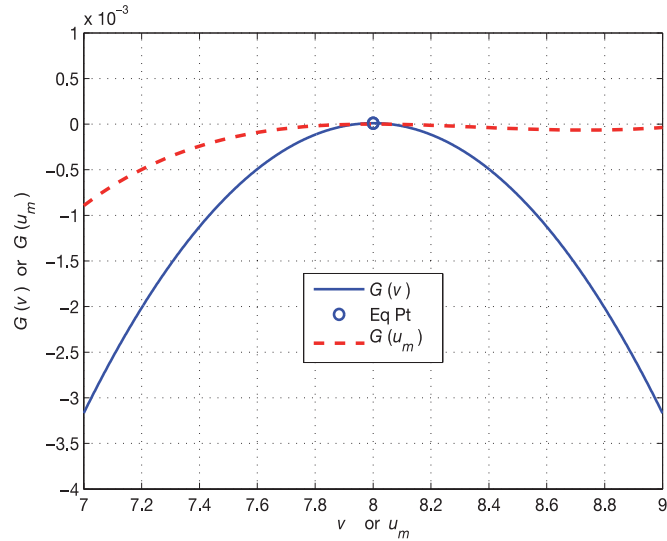


Fig. 4. The strategy $u_3 = 8$ is a local ESS that is convergence stable but is not a NIS.

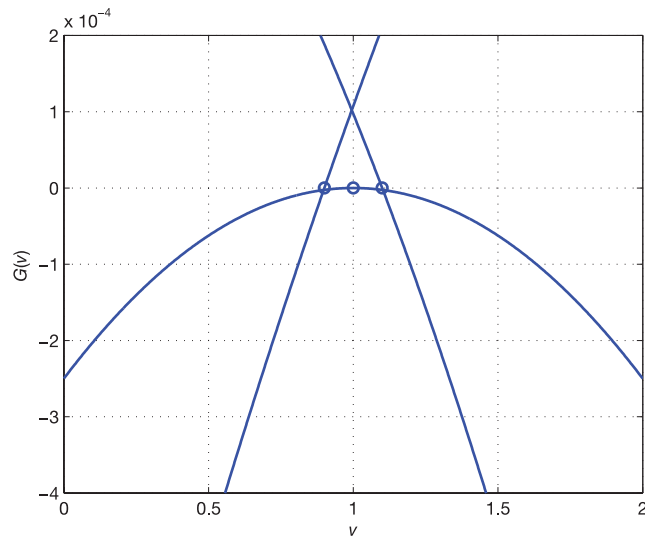


Fig. 5. The strategy $u_1 = 1$ is ESS, NIS, and convergence stable, as illustrated by evaluating the shapes of the three adaptive landscapes resulting from resident populations using the strategies $u_1 - 0.1$, 1 , and $u_1 + 0.1$. The strategy is convergence stable because in a resident population using the strategy $u_1 - 0.1$, strategies $v > u_1 - 0.1$ yield higher fitness, and in a resident population of $u_1 + 0.1$, strategies $v < u_1 + 0.1$ yield higher fitness. The strategy is NIS because in a population using the strategy $u_1 - 0.1$ and in a population using the strategy $u_1 + 0.1$, the strategy $u_1 = 1$ yields higher fitness than the resident strategy. The strategy is ESS because the adaptive landscape takes on a maximum at $v = 1$.

are displayed. For the strategy to be convergence stable, the adaptive landscapes with u fixed at points in the close neighbourhood and on either side of the convergence stable strategy should have slopes that favour strategies in the direction of the convergence stable

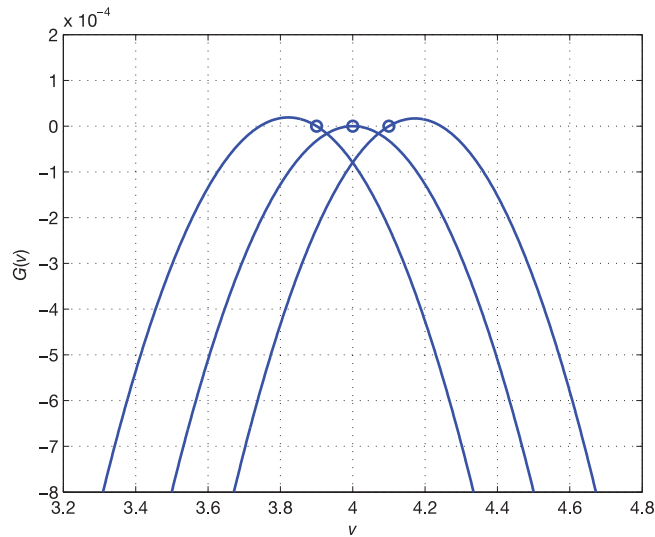


Fig. 6. The strategy $u_2 = 4$ is ESS, not NIS, and not convergence stable, as illustrated by evaluating the shapes of the three adaptive landscapes resulting from resident populations of $u_2 - 0.1$, 4, and $u_2 + 0.1$. The strategy is not convergence stable because in a resident population using the strategy $u_2 - 0.1$, strategies $v < u_2 - 0.1$ yield higher fitness, and in a resident population using the strategy $u_2 + 0.1$, strategies $v > u_2 + 0.1$ yield higher fitness. The strategy is not NIS because in a population using the strategy $u_2 - 0.1$ and in a population using the strategy $u_2 + 0.1$, the strategy $u_2 = 4$ yields lower fitness than the resident strategy. The strategy is ESS because in a population using the resident strategy $u_2 = 4$ the adaptive landscape takes on a maximum at $v = 4$.

strategy. Thus the strategies $u_1 = 1$ and $u_3 = 8$ are convergence stable as seen in Figs. 5 and 7, the strategy $u_2 = 4$ is not convergence stable as seen in Fig. 6

The evolutionary stability of the strategies $u_1 = 1$ and $u_3 = 8$ can be demonstrated using Darwinian dynamics. From Fig. 8 we see that the Darwinian dynamics with an initial strategy just to the left of the strategy $u_2 = 4$ evolves to the convergence stable ESS of 1. Snapshots of the NIS landscapes as the strategy evolves to the strategy 1 are given in Fig. 9. Note how the NIS landscape evolves from a local maximum initially to a local minimum at the convergence stable ESS of 1. Similar graphs are shown for the evolution of the strategy starting with an initial value just to the right of the ESS of 4 in Figs. 10 and 11.

DISCUSSION

The three aspects of evolutionary stability are resistance to invasion (ESS), convergence stability, and neighbourhood invadability (NIS). Geritz *et al.* (1998) showed all three of these through the use of pairwise invasibility plots. In addition, the existence of these evolutionary stabilities can be visualized geometrically through the use of adaptive landscapes and NIS landscapes. Evolutionary stability focuses on which strategies can and cannot invade a resident strategy.

To be resistant to invasion, a strategy must reside at a maximum of the adaptive landscape. All other strategies, when rare, will experience lower fitness in this population and hence will be precluded from invading. To be NIS, the strategy when rare must be able

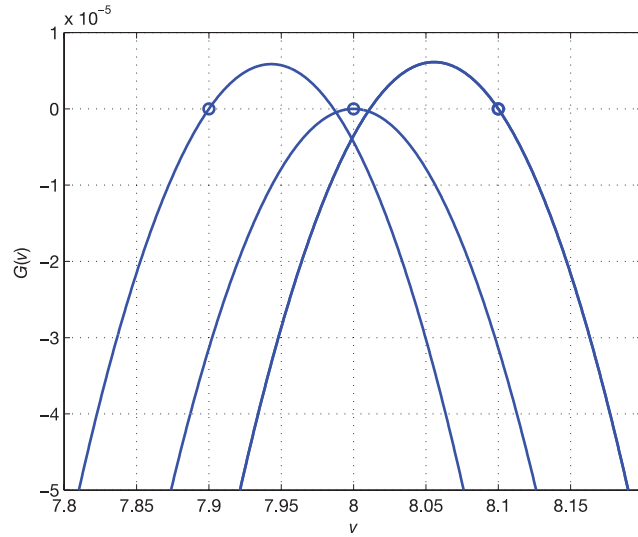


Fig. 7. The strategy $u_3 = 8$ is ESS, not NIS, and convergence stable, as illustrated by evaluating the shapes of the three adaptive landscapes resulting from resident populations using the strategies $u_3 - 0.1$, 8 , and $u_3 + 0.1$. The strategy is convergence stable because in a resident population of $u_3 - 0.1$, strategies $v > u_3 - 0.1$ yield higher fitness, and in a resident population of $u_3 + 0.1$, strategies $v < u_3 + 0.1$ yield higher fitness. The strategy is not NIS because in a population of $u_3 - 0.1$ and in a population of $u_3 + 0.1$, the strategy $v = 8$ yields lower fitness than the resident strategy. The strategy is ESS because in a resident strategy of $u_3 = 8$ the adaptive landscape takes on a maximum at $v = 8$.

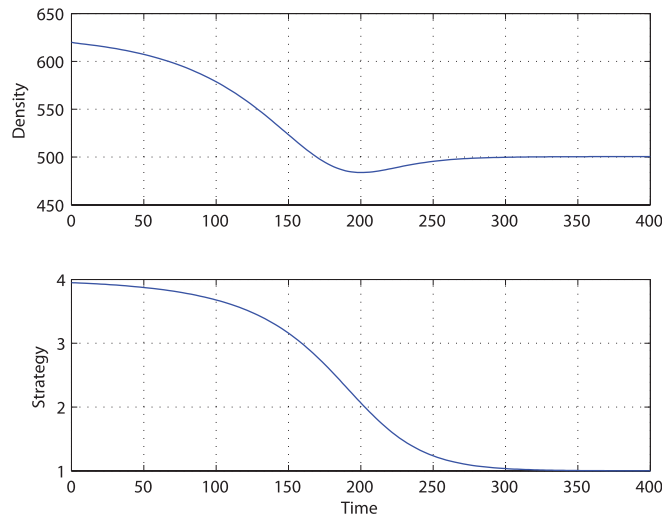


Fig. 8. Strategy and population dynamics for the model when the ESS strategy of $u_1 = 1$ is convergence stable. Starting the population at strategy $u = 4$, the strategy evolves at an accelerating and then decelerating rate towards $u_1 = 1$ (lower figure). Over this time the population density actually declines in going from a population with $u = 4$ to the ESS population of $u_1 = 1$ (upper figure).

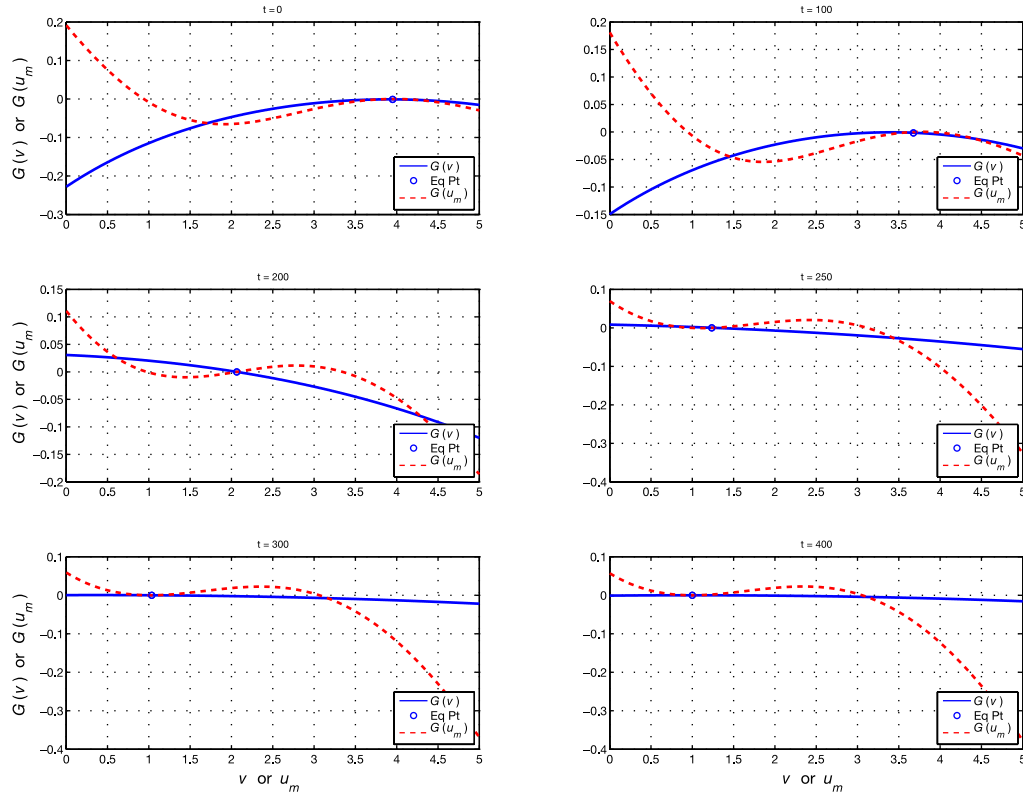


Fig. 9. Changes over time in the adaptive landscape and the NIS landscape as a population starting at $u = 4$ at time $t = 0$ evolves towards the ESS of $u_1 = 1$ by $t = 400$. As a convergence stable point, the adaptive landscape always has negative slope from the resident population $u > 1$, until the population resides on the peak of the adaptive landscape when $u = v = 1$. The NIS landscape changes from a local maximum at $v = 4$ and $u = 4$ at $t = 0$ to a minimum at $t = 400$ when $u = v = 1$.

to invade any nearby resident strategy. The adaptive landscape must yield a higher fitness value at the NIS than the fitness of any nearby strategy that is resident in the population.

To be convergence stable, the slope of the adaptive landscape must change in the opposite direction of a perturbation to the population's strategy. If the population's strategy is shifted towards a larger value than the convergence stable strategy, then the slope of the adaptive landscape at this new strategy must be negative; and vice versa if the perturbation is towards a lower strategy. This concept involves invadability in the sense that a strategy a bit closer to the convergence stable point must be able to invade a strategy slightly farther from the convergence stable point.

All three aspects can have local or global properties. A strategy that is resistant to invasion must be so for all evolutionarily feasible values of the strategy, u . But, to be resistant to invasion, the strategy need only resist rare alternative strategies. However, if the strategy is able to resist invasion from any alternative strategy regardless of its initial population size, then the ESS is global. Because the global ESS can resist invasion even when it is rare, it must also be a global NIS. And an ESS that is NIS must be convergence

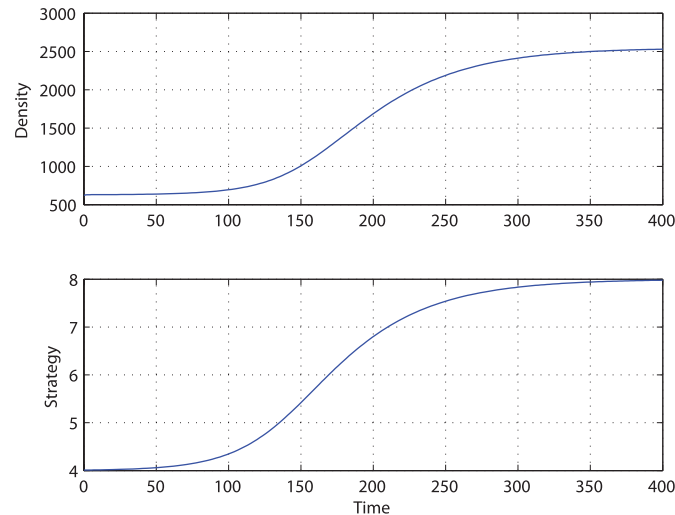


Fig. 10. Strategy and population dynamics for the model when the ESS strategy of $u_3 = 8$ is convergence stable. Starting the population at strategy $u = 4$, the strategy evolves at an accelerating and then decelerating rate towards $u_3 = 8$ (lower figure). Over this time the equilibrium population density increases dramatically from a population of $u = 4$ to the ESS population of $u_3 = 8$ (upper figure).

stable. Hence, when globally resistant to invasion, the strategy possesses globally all three aspects of evolutionary stability.

An NIS need only be able to invade resident strategies within its immediate neighbourhood. However, if the strategy can invade all other evolutionarily feasible strategies, the NIS is global. A global NIS must either be non-ESS and not convergence stable, or as above it must be both a global ESS and globally convergence stable.

A convergence stable point need only be local with respect to nearby strategies. However, if the point is convergence stable with respect to all evolutionarily feasible strategies, it is global. A global convergence stable point need not be resistant to invasion – it may be a minimum of the adaptive landscape. And, it need not be NIS. But a globally convergence stable maximum of the adaptive landscape must be a global ESS.

The ESS remains the single most important concept in evolutionary game theory. An ESS cannot be invaded by mutant strategies, and hence once established remains fixed. Furthermore, the ESS represents an adaptation in the sense that it occupies peaks of the adaptive landscape.

However, the ESS concept does not address the evolutionary process that leads a population to evolve to an evolutionary equilibrium. The ESS concept does not answer the question of whether an ESS can be reached if evolution begins with a strategy that is not already at an ESS. It does not address the dynamic stability of an ESS. This gives the stability concept of convergence stability a central role. In nature, it may be that most of the time species' traits occur at or close to convergence stable points. The endpoint of natural selection in both theoretical models and in nature may be strategies that are ESS and convergence stable. When the convergence stable point is not ESS and is instead a minimum of the adaptive landscape, this may permit evolutionary branching, adaptive speciation, or diversification through the invasion of a species with a strategy somewhat different than the

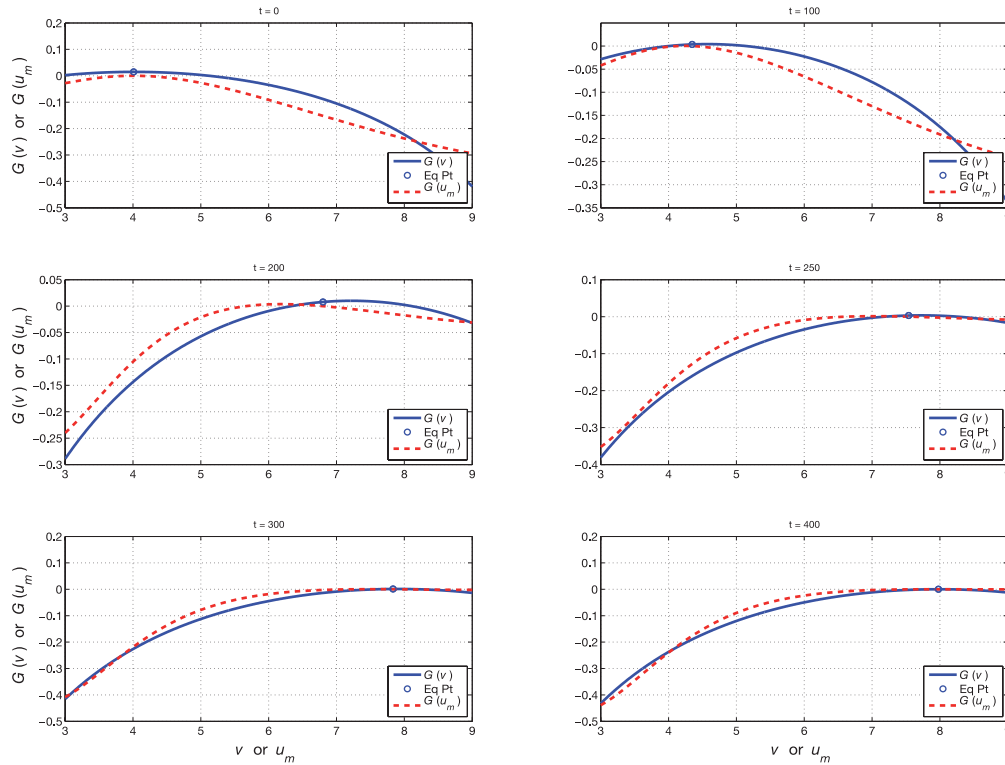


Fig. 11. Changes over time in the adaptive landscape and the NIS landscape as a population starting at $u = 4$ at time $t = 0$ evolves towards the non-NIS, convergence stable ESS of $u_3 = 8$ by $t = 400$. As a convergence stable point, the adaptive landscape always has a positive slope from the resident population $u > 4$, until the population resides on the peak of the adaptive landscape when $u = v = 8$. The NIS landscape remains a local maximum at $v = 4$ and $u = 4$ and at $v = 8$, showing that the ESS is not NIS.

convergence stable point. It remains an exciting and important empirical question whether actual species reside for long at such minima, and whether these convergence minima explain actual speciation events.

At first glance, the NIS appears to be a stronger form of convergence stability rather than a distinct solution concept. But, as a distinct solution concept, the NIS has significance for modelling, and perhaps greater significance for evolution in nature. From a modelling perspective, identifying a strategy as both ESS and NIS will ensure convergence stability, and for some modelling exercises it may be easier to apply the NIS minimum principle than the conditions for convergence stability. In seeking the solution to an evolutionary game, if a strategy is ESS and NIS then one need not look any further. A striking number of convergence stable ESSs in the modelling literature also possess the NIS property. When an ESS is convergence stable but not an NIS, the precise value of the ESS will not be attained if evolution begins with a strategy that is different from the ESS and mutants are rare. When an ESS is also NIS, then the precise value of the ESS can be attained. This becomes important in nature, if an adaptation has resulted from a non-NIS convergence stable ESS, then the strategy may never achieve the ESS and we may expect to see considerable drift or

variation in the actual strategy possessed by the individuals of a species, or by the species over time. When NIS, we can expect to see less variation among individuals within a species, and a species' actual strategy should be very close to or at its ESS value.

The three evolutionary concepts are all important for both modelling evolutionary game theory and for understanding the actual traits of organisms as shaped by natural selection. Each sheds different light on an evolutionary process. From Table 1, a strategy can simply be an ESS in the absence of convergence stability or NIS. Evolution cannot progress towards such an ESS, such an endpoint should not occur in nature. In fact, evolution can actually move a species' strategy away from the ESS.

From Table 1, a convergence stable strategy cannot be simultaneously non-ESS and non-NIS. When a strategy is a convergent stable minimum (non-ESS, convergence stable), it must be NIS. For a minimum of the adaptive landscape to be convergence stable requires that the slope of the landscape change in the opposite direction as a perturbation of the population's strategy. Since the gradient of the fitness landscape 'points' upward in the direction of the convergence stable minimum, individuals with the strategy of the convergence stable point would be able to invade the population with the perturbed strategy value. From Table 1, a strategy that is both NIS and ESS must also be convergence stable. To be ESS, the strategy occupies a peak of the adaptive landscape. To be NIS means that this strategy can invade any population that has a strategy that is slightly perturbed from the ESS. To do so means that the gradient of the fitness landscape of the perturbed population must point back towards the ESS, and hence the ESS must also be convergence stable. Thus, convergence stability both in models and in nature must occur in concert with at least one of ESS or NIS.

Two configurations from Table 1 may contribute to species diversification in real systems. A strategy that is convergence stable leads to the well-known theoretical phenomena of evolutionary branching and adaptive speciation. Less studied theoretically are strategies that are NIS but neither an ESS nor convergence stable. While unattainable through incremental steps of natural selection, the existence of such points may point to ESSs that contain additional species. In nature, the diversification from such a point to a more diverse ESS may require the invasion of species with quite different strategies to those of the resident species.

Evolutionary stabilities' Tower of Babel

Starting with Hamilton's (1967) concept of an unbeatable strategy up until the present, there has been a proliferation of terms associated with evolutionary stability. Most of these can be understood and categorized based on three properties: resistance to invasion, neighbourhood invadability, and convergence stability. Many of these terms identify one or a combination of these properties. These definitions can be quite specific in terms of games such as matrix games or sex-ratio games. A few are couched in terms of some specific underlying genetics. Others are quite general in terms of continuous strategies and/or vector-valued strategies. To see these relationships, we present a glossary of concepts, terms, and definitions, roughly in their chronological order of appearance. In this subsection we relate these to the three primary stability concepts.

The following terms often differ in notation, sometimes in the scope of their evolutionary games (matrix vs. continuous games, for instance), or assumptions regarding the source and nature of the strategies and their associated payoffs (genetic models, vector-valued

strategies, monomorphisms, polymorphisms). We do not claim to have listed all of the evolutionary stability concepts that have been published in the literature. It is our intent to update this list from time to time. Comments are welcome and may be sent to the first author via e-mail. The latest listing may be found on the URL

<http://people.stfx.ca/japaloo/publications/evolutionarystabilities.pdf>.

Seeking both commonality and differences between the definitions, there are five primary properties that we identify with each of the definitions:

1. *Resistance to invasion*: this is the property that ensures that a focal strategy is proof against invasion by rare alternative strategies.
2. *Convergence stable*: this property ensures that a focal strategy is approached through a sequence of strategy substitutions when evolution begins with a strategy in its close neighbourhood.
3. *Neighbourhood invader*: this property requires a focal strategy to have ability to invade any strategy in its close neighbourhood
4. *Continuous game*: this designation will be associated with games in which the set of pure strategies is drawn from a continuous set.
5. *Population dynamics*: this designation applies to games that explicitly include population size(s) and/or density dynamics, or population frequencies provided that the frequency dynamics and total population size and/or density dynamics are also included.

Table 2 lists these properties with an associated symbol. If a definition has one or more of these properties, the appropriate symbol(s) is(are) attached.

Table 2. Symbols associated with a given property

★	Resistance to invasion
✱	Convergence stable
♠	Neighbourhood invader
◆	Continuous (non-matrix) game
♣	Population dynamics

Because of the great variety of notations used, all of the definitions are given as word definitions. As a consequence, there is a loss of mathematical precision, but we have provided a reference in each case so that the interested reader can go to the original source.

1. *Unbeatable strategy* ★♠ (Hamilton, 1967). An ‘unbeatable’ sex ratio is a sex ratio such that ‘the Y chromosome that produces it has selective advantage over any other, whatever the current gene frequency’ (Hamilton, 1967, p. 481). See the use of this terminology also in Bomze and Weibull (1995, p. 178).
2. *Evolutionarily stable strategy (ESS)* ★ (Maynard-Smith and Price, 1973). ‘An ESS is a strategy such that, if most members of a population adopt it, there is no “mutant” strategy that would give a higher reproductive fitness’ (Maynard-Smith and Price, 1973, p. 15). See reformulation and generalization of this concept, for example, in Taylor and Jonker (1978, p. 147). Here distinction between monomorphic ESS and polymorphic ESS is made.

3. *Regular ESS* ★ (Taylor and Jonker, 1978). An equilibrium strategy p is a regular ESS if the fitness of any pure strategy that is not in the support of p is strictly less than the fitness of the equilibrium point, and for any other strategy q distinct from p with the support of q contained in the support of p , the payoff of $q - p$ playing against itself is strictly less than zero (Taylor and Jonker, 1978, p. 148).
4. *Continuously stable strategy (CSS)* ★✱◆ (Eshel and Motro, 1981). ‘An ESS will be called a *continuously stable strategy* (CSS) if, whenever the entire population has a strategy which is close enough to it, there will be a selective advantage to some individual strategies which are closer to the CSS’ (Eshel and Motro, 1981, p. 427).
5. *Evolutionary genetic stability (EGS)* ✱ (Eshel and Feldman, 1982; Eshel, 1985). ‘The concept of EGS applies to a phenotype strategy \mathbf{x} (mixed or pure) within a given genetic system, if, within this system, a new mutant is favored if and only if it renders the population strategy closer to \mathbf{x} ’ (Eshel and Feldman, 1984, p. 638). A *partial* EGS property is m -stability at viability-analogous Hardy-Weinberg (VAHW) equilibria (Feldman and Liberman, 1986; see Lessard, 1990, p. 167).
6. *Strong ESS* ★ (Uyenoyama and Bengtsson, 1982; Uyenoyama, 1984). A mean strategy adopted by an infinite resident population has r^* -stability if a rare mutant population with any mean strategy (distinct from and close to the resident mean strategy) has a mean payoff per individual that is strictly less than the mean payoff per individual for the resident mean strategy. A strong ESS is a resident strategy r^* satisfying r^* -stability (see Lessard, 1990, p. 164).
7. *Weak ESS* ★ (Uyenoyama and Bengtsson, 1982; Uyenoyama, 1984). A weak ESS is a resident strategy \mathbf{r}^* satisfying \mathbf{r} -stability defined in Lessard (1990, p. 164), which is a multidimensional version of the ESS concept.
8. *Anti-ESS* (Uyenoyama and Bengtsson, 1982; Uyenoyama, 1984). An *anti-ESS* is a resident strategy \mathbf{r}^* that does not satisfy the \mathbf{r} -stability property with equality precluded (see Lessard, 1990, p. 164). Also see *genetic anti-ESS* in, for example, Liberman (1976), Lessard (1985, 1987).
9. *Evolutionarily stable strategy (ESS)* ★◆♣ (Vincent and Brown, 1984, 2005). A local ESS is a strategy (a) that is not invadable by any strategy or strategies in the entire strategy set, (b) and such that the population equilibrium point when it is present alone is locally stable in any augmented population dynamics which includes any arbitrary collection of rare mutants. If in addition the population equilibrium is globally stable, the strategy is a global ESS (Vincent and Brown, 2005, p. 164).
10. *Evolutionarily stable set (ES set)* ★ (Thomas, 1985). An evolutionarily stable set in a matrix game is a set of strategies such that, if most members of a population adopt any strategy in the set, no mutant strategy would give a higher fitness (Cressman, 1992, p. 97).
11. *Uninvadability* ★◆ (Vickers and Cannings, 1987). ‘A strategy is uninvadable if it is protected by a positive *global* invasion barrier, i.e. if immunity against mutants is uniform’ (Bomze, 1990, p. 192). The mathematical description of this concept is given in Vickers and Cannings (1987) but the name was given in Bomze and Potscher (1989). The terms uninvadable and evolutionarily stable have been used synonymously (see, for example, Maynard-Smith, 1982, p. 205; Thomas, 1985).
12. *m -stability* ✱◆ (Taylor, 1989). A strategy m^* possesses m -stability if, for any strategy m in the close neighbourhood of m^* , local mutants on the m^* -side of m in a population adopting the strategy m will be more fit than those on the other side (Taylor, 1989, p. 127). Note that this condition is the condition required of an ESS for it to be classified as a CSS (Eshel and Motro, 1981). Also see a multidimensional version of this concept in Lessard (1990).

13. δ -stability $\star\blacklozenge$ (Taylor, 1989). This is identical to the ESS (Maynard-Smith and Price, 1973) concept (Taylor, 1989, p. 127).
14. r -stability $\star\blacklozenge$ (Lessard, 1990). This is a multidimensional version of the ESS (Maynard-Smith and Price, 1973) concept (Lessard, 1990, p. 164).
15. \mathbf{r}^* -stability \star (Lessard, 1990). A mean strategy adopted by an infinite resident population has \mathbf{r}^* -stability if a rare mutant population with any mean strategy (distinct from and close to the resident mean strategy) has a mean payoff per individual that is strictly less than the mean payoff per individual for the resident mean strategy (Lessard, 1990, p. 164).
16. \mathbf{m}^* -stability \spadesuit (Lessard, 1990). A mutant mean strategy that is rare in an infinite resident population with any resident mean strategy (distinct from and close to the mutant mean strategy) is said to have \mathbf{m}^* -stability if the rare mutant mean strategy has mean payoff per individual that is strictly greater than the mean payoff per individual of the resident mean strategy (Lessard, 1990, p. 164).
17. *Evolutionarily attractive* population strategy \blackstar (Lessard, 1990). ‘In general two-sex one-locus multi-allele viability models, there may be small fluctuations over successive equilibria before an EGS population strategy is reached, which maximizes the product of the male and female mean viabilities (Lessard, 1998a). In such a case, we have an EGS property *over sequences of equilibria*. When there is convergence according to this scheme, we say that we have an *evolutionarily attractive* population strategy (Lessard 1984)’ (Lessard, 1990, p. 167).
18. *Evolutionarily stable state* \star (Lessard, 1990). ‘Is an ESS, as a mean strategy, at a population equilibrium restored following small perturbations on the equilibrium frequencies of individual strategies? If the answer is yes, we have an *evolutionarily stable (ES) state*’ (Lessard, 1990, p. 167). Also see the notions of *internal stability* and *external stability*. Eshel (1996) also considers internal stability and external stability among other notions: *short-term evolution, long-term evolution, limited external stability*. The notion of internal stability is similar to that of *ecologically stable equilibrium* (Vincent and Brown, 2005).
19. *Strong uninvadability* $\star\blacklozenge$ (Bomze, 1990). A state is said to be strongly uninvadable if for any distinct strategy sufficiently close to it, the mean payoff per individual of the state in an infinite resident population that adopts the strategy is strictly greater than the mean payoff per individual with the strategy (Bomze, 1990, p. 193). This is a stricter version of the ESS concept (Maynard-Smith and Price, 1973)
20. *Convergence stability* $\blackstar\blacklozenge$ (Christiansen, 1991). This is the same as the m -stability concept (Christiansen, 1991, p. 40).
21. *Evolutionary stability Type I (ES I)* $\star\blacklozenge\clubsuit$ (McKelvey and Apaloo, 1995, p. 420). This is the same as ESS (Maynard-Smith and Price, 1973).
22. *Evolutionary stability Type II (ES II)* $\spadesuit\blacklozenge\clubsuit$ (McKelvey and Apaloo, 1995, p. 420). This is the same as the *neighbourhood invader stability* concept defined below.
23. *Neighbourhood invader stability (NIS)* $\spadesuit\blacklozenge\clubsuit$ (Apaloo, 1997). A NIS is a strategy that can invade any population with a strategy in the neighbourhood of the NIS (Apaloo, 1997, p. 72). NIS may be local or global. A strategy that is an ESS and an NIS is referred to as an *evolutionarily stable neighbourhood invader strategy (ESNIS)*.
24. *Branching point or evolutionary branching point* $\blackstar\blacklozenge\clubsuit$ (Geritz *et al.*, 1997; Geritz *et al.*, 1998, p. 42). This is a strategy that is convergence stable but is not an ESS.
25. *Mutual invasibility or nearby dimorphisms* $\blacklozenge\clubsuit$ (Geritz *et al.*, 1997; Geritz *et al.*, 1998, p. 41). This terminology is used when there are pairs of strategies in the neighbourhood of the candidate ESS (singular point) that can invade each other when one of them is rare.

26. *Single-mutant-ESS or Matrix(T)-ESS* ★ (Vincent and Cressman, 2000). Traditional ESS as defined by Maynard Smith for matrix games (Vincent and Cressman, 2000, p. 174).
27. *Matrix-ESS or Matrix(G)-ESS* ★ (Vincent and Cressman, 2000). Same as definition 9 above when specifically applied to matrix games in terms of population frequencies (Vincent and Cressman, 2000, p. 174).
28. *Invading potential* ♠♦♣ (Meszina *et al.*, 2001). This is the same as the NIS concept defined above (Meszina *et al.*, 2001, p. 202).
29. *Evolutionary robustness (ER)* ★♦ (Oechssler and Riedel, 2002). A population is said to be evolutionarily robust if for any distinct strategy sufficiently close to it, the mean payoff per individual of the population in an infinite resident population that adopts the strategy is strictly greater than the mean payoff per individual with the strategy (Oechssler and Riedel, 2002 p. 234). This is a similar notion to the concept of strong uninvasibility (Bomze, 1990).
30. *Continuously replicator stable strategy (CRSS)* ★✠♦ (Eshel and Sansone, 2003). A pure strategy is said to be a CRSS if for any initial population strategy whose support is in a sufficiently small neighbourhood of the pure strategy, a replicator dynamic converges in the second moment to the fixation on the pure strategy (Eshel and Sansone, 2003, p. 450).
31. *Strong convergence stable* ✠♦ (Leimar, 2001, in press). This is an extension of the convergence stability property to evolutionary games involving multidimensional traits in monomorphic or polymorphic population evolution. In the case of polymorphisms, no sufficient conditions are given (Leimar, 2001, p. 70).
32. *Absolute convergence stable* ✠♦ (Leimar, 2001, in press). This is the general extension of the convergence stability property to evolutionary games involving multidimensional traits in monomorphic or polymorphic population evolution to preclude any escape from the neighbourhood of the absolute convergence stable strategy (Leimar, 2001, p. 69). In the case of polymorphisms, no sufficient conditions are given.

Resolving the terminology

Evolutionarily stable strategy, as a term, definition or concept, has received the most attention and has spread farthest into the mainstream of evolutionists, animal behaviourists, and evolutionary ecologists. As generally defined it focuses primarily on resistance to invasion. Here, we reserve this aspect of evolutionary stability for the definition of the ESS. Much of the terminology above relates to an ESS as a strategy, which, when common, cannot be invaded by rare alternative strategies. This is evident in the prevalence of the symbol ★, which is used to denote the ESS property in the preceding subsection. While he did not explicitly define an *unbeatable strategy*, Hamilton (1967) seemed to have an ESS-like concept in mind when he considered optimal sex ratios.

Convergence stability is required for the strategy to be the outcome of natural selection and definitions with this property are designated by the symbol ✠. Of course, this convergence stable point may be either a maximum or minimum of the adaptive landscape. At a maximum the strategy is ESS, at a minimum the strategy (also called a branching point) provides the opportunity for adaptive speciation.

We view resistance to invasion as being global with respect to all evolutionarily feasible strategies. Thus, an ESS must be at a global maximum of the adaptive landscape. However, there may be strategies, which, when common, only take on local maxima of the adaptive

landscape. While such strategies can be invaded by some strategies sufficiently far from the neighbourhood of the local maxima, such a strategy may be convergence stable and evolve through strategy dynamics. Some of the above definitions view resistance to invasion as local with respect to strategy rather than global.

Several of the definitions are notable for considering broad classes of evolutionary games with continuous strategy values. These definitions provide resistance to invasion in a very robust sense. Strategies satisfying these definitions will resist invasion from any number of sufficiently rare alternative strategies (the coalition of mutant strategies can have a large number of elements), and these alternative strategies can come from anywhere in the set of evolutionarily feasible strategies. However, while very robust in terms of persisting and resisting invasions, strategies satisfying these definitions will not necessarily be convergence stable. In fact, it appeared until now that the definition of ESS (Vincent and Brown, 2005) also implied convergence stability. But an example that is considered above in the examples section reveals that this implication is not generally true, as it is well known to be the case also for the original ESS definition (Maynard-Smith and Price, 1973)

All of these ESS definitions of resistance to invasion can be identified by applying the ESS maximum principle and analysing, simulating or inspecting the adaptive landscape. Furthermore, under some circumstances, it is possible for two strategies to co-exist when they occur in the neighbourhood of the ESS and on opposite sides of the ESS. Such pairs may exhibit mutual invasibility.

The concept of *continuously stable strategy* (\star and \blackstar) is noteworthy for recognizing and combining the stability properties of resistance to invasion and convergence stability. This is important because as a useful concept the ESS must not only be resistant to invasion but a likely outcome of evolution by natural selection.

The *neighbourhood invader strategy* recognizes the ability of a strategy to invade any nearby resident strategy. Definitions that possess this property have been identified with the symbol \spadesuit . At first glance, it appears that the NIS should simply provide a stronger form of convergence stability – if a strategy can invade its neighbours, then shouldn't it emerge as the winning strategy? Interestingly, this is indeed true for strategies that are also ESS. If a strategy is both a maximum on the adaptive landscape and a minimum on the NIS landscape, it must be convergence stable. Curiously though, the concepts of NIS and convergence stability are quite distinct when the strategy in question is not ESS and is at a minimum of the adaptive landscape. Such a strategy can be NIS but not convergence stable. And, if the minimum of the adaptive landscape is convergence stable, it must be a NIS.

From the discussion and the evolutionary stabilities' Tower of Babel, it is quite clear that the backdrop of the evolutionary stabilities are formed by the concepts of ESS, convergence stability, and NIS. In fact, at least one of these three stabilities appears in all of the evolutionary stabilities' Tower of Babel except for two of the definitions. By far, the ESS property appears the most, followed by the convergence stability property and then the NIS property. We conclude that these three properties of evolutionary stability form the cornerstones for the study of evolution by natural selection.

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