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Evolutionary stabilities in multidimensional-traits and several-species models

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ABSTRACT

Questions: Co-evolutionary models with one to multidimensional strategies can result in stable coalitions of many strategies. Are coalition strategies that are evolutionarily stable (ESS) and neighbourhood invader (NIS) also convergence stable? What is the implication for co-evolutionary models?

Mathematical methods: Optimization of the fitness function and dynamical systems based on the selection gradient of the fitness function.

Key assumptions: The fitness of a trait depends on its strategy value and on the environment consisting of strategy values of other traits and their population sizes. Co-evolutionary strategies in a close neighbourhood of a singular point of the canonical equation maintain stable population dynamic equilibria.

Conclusions: In single-species evolutionary games with a multidimensional strategy set, a strategy that is both an ESS and NIS is also a strong convergence stable strategy and thus convergence stable. In co-evolutionary games, this implication is not guaranteed and there can never be a strategy that is strong NIS. Therefore, 'fast evolution', which can occur in single-species evolution when a singular point is both ESS and NIS, may not occur in co-evolutionary models.

Keywords: absolute convergence stability, convergence stability, evolutionary stability, evolutionarily stable strategy, neighbourhood invader strategy, strong convergence stability, strong neighbourhood invader stability.

INTRODUCTION

In survey articles, Lessard (1990) and Eshel (1996) reported that there are several evolutionary stability concepts in the literature, although Eshel and Motro (1981) were the first to point out that there is more than a single concept for evolutionary stability. Two of the concepts have been used extensively in the evolutionary games literature. These are the *evolutionarily stable strategy* (ESS) concept (Maynard Smith and Price, 1973) and the *convergence stable* strategy concept (Eshel and Motro, 1981; see also, for example, Eshel, 1983; Taylor, 1989; Lessard, 1990; Nowak, 1990; Christiansen,

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1991; Leimar, 2001, in press; Meszéna *et al.*, 2001; Cressman *et al.*, 2006). Convergence stability ensures that small deviations of the entire population strategy from the ESS will end up with selection advantage to mutations that render the population strategy back to the ESS. The corresponding dynamics in single species have been demonstrated by Eshel *et al.* (1997).

Leimar (2001, in press) showed that mutation processes play a role in determining the eventual outcome of evolution when a 'Darwinian demon' has power to influence the types of mutations that may occur. This is done through the extension of the convergence stability concept to several-species and/or multidimensional-traits evolutionary models to obtain two concepts called strong convergence stability and absolute convergence stability. It was demonstrated that in models involving several species, these concepts were too restrictive and even more so in the case of absolute convergence stability. It is important to note here that for co-evolutionary models, there is also the concept of convergence stability (Meszéna *et al.*, 2001), which is different from strong convergence stability. In fact, a co-evolutionary strategy that is strong convergence stable is also convergence stable, and an absolute convergence stable strategy is also a strong convergence stable strategy.

An evolutionary stability concept similar in nature to the convergence stability concept is the *neighbourhood invader strategy* (NIS) concept (McKelvey and Apaloo, 1995; Apaloo, 1997b; Geritz *et al.*, 1998). In the case of single species with one-dimensional trait evolutionary models, this concept has been compared with the convergence stability concept and the relationship between them is now quite clear (see, for example, Apaloo, 1997b, 2005; Geritz *et al.*, 1998; Meszéna *et al.*, 2001; Cressman, 2008; Apaloo *et al.*, 2009). The extension of the notion of neighbourhood invader strategy to several-species and/or multidimensional-trait evolutionary models has been considered (Apaloo, 1997a; Apaloo *et al.*, 2005). The two concepts discussed are NIS and strong NIS. It turns out that no strategy can satisfy the conditions for strong NIS (R. Cressman, personal communication). If there is any strategy that satisfies the strong NIS conditions, then such a strategy will also be an NIS. This has a consequence for the speed of evolution that we discuss below, and points to the need for stronger conditions for neighbourhood invasibility. Progress has been made in this direction. Cressman (2008) has developed NIS conditions for two-species models of frequency-dependent behavioural evolution when individuals have traits in continuous strategy spaces. These NIS conditions are stronger than the NIS conditions given in this article. We do not consider the stronger conditions given in Cressman (2008) here because they are for two species, whereas we consider in general a finite number of species.

The relationships between these evolutionary stability concepts are not so clear in the case of several-species and/or multidimensional-trait models. The main goal of this article is to shed some light on the relationships between the NIS concept and the convergence concepts. Lessard (1990) was the first to extend convergence stability to multidimensional-trait models. But the notion of convergence stability has also been addressed more generally in Leimar (2001, in press; see also, for example, Meszéna *et al.*, 2001; Cressman *et al.*, 2006).

In what follows, we will use the notation and definitions of evolutionary stability in multidimensional-traits and several-species evolutionary models as presented by Leimar (in press). We will examine the six stability concepts in a several-species and multidimensional-traits setting: ESS, convergence stability, strong convergence stability, absolute convergence stability, NIS, and strong NIS. More specifically, we compare and contrast the NIS to the strong convergence stability and absolute convergence stability concepts.

If an evolutionary process is such that any resident coalition strategy that is distinct from the ESS coalition can be invaded by mutant strategies consisting of the ESS or any strategy in an arbitrarily close neighbourhood of it, then we classify the evolution as being fast; otherwise, we will say that evolution is slow. We note here that slow evolution has been discussed in the literature (e.g. Dieckmann and Law, 1996). We will then show that in several-species and multidimensional-traits evolutionary models, fast evolution may not occur even if the ESS is also an NIS. This is contrary to the case of evolution in single species with one-dimensional traits where fast evolution can always occur when the singular point is an ESS and NIS (Apaloo, 2003). This state of affairs is due to the fact that co-evolutionary models cannot have a strategy that is a strong NIS. Also in single-species and one-dimensional traits models, an ESS is convergence stable if it is a NIS (Apaloo, 1997b). We will explore this result in the multidimensional-traits and several-species models.

This article is organized as follows. In the next section, we provide definitions of the various evolutionary stability concepts and compare and contrast them. Next, we provide some numerical examples of these evolutionary stabilities in the case of single-species evolution with two-dimensional trait values. We then consider a co-evolutionary game that involves two species each with two-dimensional traits. All of the calculations for the two numerical examples were carried out in MAPLE version 10. All files containing the MAPLE commands will be provided upon request from the first author. We conclude with some remarks.

EVOLUTIONARY STABILITIES

We consider in general multidimensional-traits and several-species evolutionary models in which there are n species in the population, and individuals of the kth species are characterized by z_k-dimensional trait space. Let x_k denote a vector of values of the kth species traits (vectors are regarded as column vectors and transposition indicates row vectors), and x_{ki} denote the ith element of the vector x_k. We denote by $F_k(x'_k, x)$ the fitness of a mutant with strategy x'_k in an environment that is generated by all given trait values of all species given by the row vector $x^T = (x_1^T, \ldots, x_n^T)$. We will generally use the subscripts or superscripts k, l, and s as indices for species, and i and j as indices for components of vectors or matrices.

Leimar (in press) defines strong convergence stability and absolute convergence stability in the framework of adaptive dynamics. The pertinent model for this is the canonical equation (Dieckmann and Law, 1996), which is given by

$$\frac{d}{dt} x_k = m_k(x)\, C_k(x_k)\, \nabla'_k F_k(x_k, x)$$

where m_k is a measure of rate of occurrence of mutations, C_k is the variance–covariance matrix for the distribution of mutational increments, and $\nabla'_k F_k(x_k, x)$ is a vector whose ith component is given by

$$(\nabla'_k F_k(x_k, x))_i = \left. \frac{\partial F_k(x'_k, x)}{\partial x'_{ki}} \right|_{x'_k = x_k}$$

The study of the eventual outcome of evolution is commonly based on there being a point of equilibrium x^* of the canonical equation. Such points are commonly called *singular points* and they are obtained by solving the following system of equations simultaneously:

$$(\nabla'_k F_k(x_k^*, x^*))_i = (\nabla'_k F_k(x_k, x))_i \Big|_{x_k = x_k^*,\ x = x^*} = 0$$

for each i and each k. Indeed, this system of equations is also a necessary condition for all of the evolutionary stability concepts that are discussed in this article. We now define the evolutionary stabilities. For further details on the concepts we use or mention in this article in the context of multi-species and multidimensional traits, the reader may review references as follows: strong convergence stability and absolute convergence stability (Leimar, in press); ESS (Apaloo, 1997a; Leimar, 2008); convergence stability (Meszéna *et al.*, 2001); NIS and strong NIS (Apaloo, 1997a).

Definition 1. (*ESS*) *The coalition strategy* x^* *is an ESS if it cannot be invaded by any mutant strategy that is arbitrarily close to any of the strategies that form the ESS coalition* (*i.e.* $F_k(x_k, x^*) < 0$ *for any* $x_k \neq x_k^*$ *and in a close neighbourhood of* x_k^* *for each* $k = 1, 2, \ldots, n$).

The canonical equation can be written more conveniently as

$$\frac{d}{dt} x = B(x)\, \nabla' F(x, x)$$

where $B(x)$ is a block diagonal, symmetric, positive definite matrix with blocks $B_{kk}(x) = m_k(x) C_k(x_k)$, and $\nabla' F(x, x)$ is a vector of selection gradients of all species (Leimar, in press). The canonical equation provides the context in which the convergence concepts are defined. It is important to note that the neighbourhood invader concepts are static concepts but they shed light on evolutionary dynamics.

Definition 2. (*Convergence stability*) *The coalition strategy* x^* *is a convergence stable strategy if it is a locally asymptotically stable equilibrium point of* **an** *adaptive* (*strategy*) *dynamics.*

Definition 3. (*Strong convergence stability*) *The coalition strategy* x^* *is strong convergence stable if it is an asymptotically stable equilibrium of the canonical adaptive dynamics for* **any** *smoothly varying, symmetric, positive definite mutational matrix* $B(x)$.

Definition 4. (*Absolute convergence stable*) *The coalition strategy* x^* *is an absolute convergence stable strategy if* **all conceivable** *gradualistic adaptive paths starting near* x^* *obeying an adaptive* (*strategy*) *dynamics will converge to it.*

Let $x^{*,k} = [x_1^{*T}, x_2^{*T}, \ldots, x_{k-1}^{*T}, x_k^T, x_{k+1}^{*T}, \ldots, x_n^{*T}]^T$.

Definition 5. (*NIS*) *The coalition strategy* x^* *is a NIS if any of the strategies that form the NIS coalition can invade any coalition strategy that has all its strategy values fixed at the corresponding NIS values, except the component corresponding to the candidate invader takes values that are in an arbitrarily close neighbourhood of it* (*i.e.* $F_k(x_k^*, x^{*,k}) > 0$ *for any* $x_k \neq x_k^*$ *and in a close neighbourhood of* x_k^* *for each* $k = 1, 2, \ldots, n$).

Definition 6. (*Strong NIS*) *The coalition strategy* x^* *is a strong NIS if any of the strategies that form the strong NIS coalition can invade any coalition strategy that is in an arbitrarily close neighbourhood of it* (*i.e.* $F_k(x_k^*, x) > 0$ *for any* $x \neq x^*$ *and in a close neighbourhood of* x^* *for each* $k = 1, 2, \ldots, n$).

First, we note that a co-evolutionary strategy that is absolute convergence stable is also strong convergence stable, and a strategy that is strong convergence stable is also convergence stable. Note that the converses of the preceding implications need not be true. Let $F(x, x)$ be the vector whose kth row is $F_k(x_k, x)$. A common assumption in evolutionary game theory is that $F(x, x) \equiv 0$, which arises from the requirement that any co-evolutionary strategy in a close neighbourhood of the singular point can maintain a stable equilibrium. We refer to this assumption as the ecological equilibrium assumption. Apaloo (1997a) showed that a strong NIS cannot exist in any two-species co-evolutionary model each with one-dimensional strategy space when the assumption of ecological equilibrium is in force. But this indeed is a general result in the sense that there is never a co-evolutionary strategy that satisfies the definition for strong NIS (R. Cressman, personal communication). In the context of the above evolutionary stability definitions, this general result occurs because of the ecological equilibrium assumption. To see this, suppose that $x^* = [0^T, 0^T, \ldots, 0^T, 0^T, 0^T, \ldots, 0^T]^T$ is a strong NIS by the above definition. Consider, for example, a resident strategy $x^{*,k} = [0^T, 0^T, \ldots, 0^T, \varepsilon_k^T, 0^T, \ldots, 0^T]^T$ with the components of the vector ε_k sufficiently small. Then $F_l(x_l^*, x^{*,k}) > 0$ is false for each $l \neq k$ since in these cases $F_l(x_l^*, x^{*,k}) = 0$, which contradicts the assumption that x^* is a strong NIS (R. Cressman, personal communication). Despite this, we will still give sufficient conditions for this concept as it does help to shed light on the speed at which co-evolution may occur. This will be discussed further below.

Leimar (in press) does not provide sufficient conditions for absolute convergence stability for co-evolutionary models, or sharp sufficient conditions for co-evolutionary strong convergence stability. Despite all the shortcomings listed above, we will consider all these stabilities for completeness, although some will be considered only to a limited extent. For this reason, we provide sufficient conditions for all the stability concepts below.

The ESS, NIS, and strong NIS definitions can be stated in terms of maximization or minimization of the corresponding fitness functions (see, for example, Apaloo, 1997a). Several matrices are needed in the statement of sufficient conditions for the above stabilities. For the ESS we need the selection Hessian H_{kk} whose ijth component is given by:

$$(H_{kk})_{ij}\,(x_k^*, x^*) = \left.\frac{\partial^2 F_k(x_k', x)}{\partial x_{ki}' \partial x_{kj}'}\right|_{x_k' = x_k^*,\ x = x^*}$$

We denote the symmetric block diagonal matrix with the selection Hessian's H_{kk} as the blocks by H.

For the convergence concepts we require the matrix Q whose block matrices are Q_{kl} with its ijth component given by

$$(Q_{kl})_{ij}(x_k^*, x^*) = \left.\frac{\partial^2 F_k(x_k', x)}{\partial x_{ki}' \partial x_{lj}}\right|_{x_k' = x_k^*,\ x = x^*}$$

In the case of the NIS concept we require the matrix R whose symmetric block diagonals are given by R_{kk}. The ijth component for the block matrix R_{kk} is given by:

$$(R_{kk})_{ij}(x_k^*, x^*) = \left.\frac{\partial^2 F_k(x_k', x)}{\partial x_{ki} \partial x_{kj}}\right|_{x_k' = x_k^*,\ x = x^*}$$

Finally, for strong NIS we need the matrix T^k whose block matrices are T_{sl}^k with its ijth component given by

$$(T^k_{sl})_{ij}(x^*_k, x^*) = \left.\frac{\partial^2 F_k(x'_k, x)}{\partial x_{si}\partial x_{lj}}\right|_{x'_k = x^*_k,\ x = x^*}$$

The first-order conditions for NIS and strong NIS are given in terms of the gradient vector whose ith component is given by

$$(\nabla_k F_k(x_k, x))_i = \left.\frac{\partial F_k(x'_k, x)}{\partial x_{ki}}\right|_{x'_k = x_k}$$

In addition,

$$(\nabla_k F_k(x^*_k, x^*))_i = (\nabla_k F_k(x_k, x))_i\Big|_{x_k = x^*_k,\ x = x^*}$$

Let $\nabla' F(x^*, x^*)$ and $\nabla F(x^*, x^*)$ denote the vectors whose kth block vectors are $\nabla'_k F_k(x^*_k, x^*)$ and $\nabla_k F_k(x^*_k, x^*)$ respectively. Leimar (in press) showed that a linearization of the canonical equation about x^* results in the equation:

$$\frac{d}{dt}(x - x^*) = AJ(x - x^*)$$

where $J = H + Q$ and A is the mutational matrix that is symmetric and positive definite. For several species each with multidimensional traits, we have the following sufficient conditions for the various evolutionary stabilities:

Theorem 7. (*ESS*) *The coalition strategy x^* is an ESS if $\nabla' F(x^*, x^*) = 0$ and H_{kk} is a negative definite matrix for each $k = 1, 2, \ldots, n$ or that H is a negative definite matrix.*

Theorem 8. (*Convergence stability*) *The coalition strategy x^* is convergence stable if $\nabla' F(x^*, x^*) = 0$ and all eigenvalues of the matrix AJ have negative real parts.*

Theorem 9. (*Strong convergence stability*) *The coalition strategy x^* is strong convergence stable if $\nabla' F(x^*, x^*) = 0$ and J is a negative definite matrix.*

Theorem 10. (*Absolute convergence stability*) *The strategy x^* is absolute convergence stable if $\nabla' F(x^*, x^*) = 0$ and J is a symmetric and negative definite matrix.*

Theorem 11. (*NIS*) *The coalition strategy x^* is a NIS if $\nabla F(x^*, x^*) = 0$ (or equivalently $\nabla' F(x^*, x^*) = 0$) and the resident variation selection Hessian R_{kk} is a positive definite matrix for each $k = 1, 2, \ldots, n$.*

Theorem 12. (*Strong NIS*) *A coalition strategy $x^*$is a strong NIS if*

$$\nabla F(x^*, x^*) = 0$$

and the matrix T^k is positive definite for each $k = 1, 2, \ldots, n$.

At this juncture, several remarks will be useful. Leimar (in press) noted that the absolute convergence stable concept is unduly restrictive and has very limited practical use. In fact, only a necessary condition and a sufficient condition are given for strong convergence stability and no sharper conditions for strong convergence stability were given. In addition, no conditions are explicitly given for absolute convergence stability in the several-species and multidimensional-traits models.

From the ecological equilibrium assumption identity, the first-order total derivatives give rise to the following identity:

$$\nabla' F(x, x) + \nabla F(x, x) \equiv 0$$

This is the reason why the equality conditions in the theorems above for ESS and NIS are equivalent. In addition, the equality conditions in the NIS and strong NIS theorems are equivalent because of the identities

$$\left.\frac{\partial F_k(x'_k, x)}{\partial x_{li}}\right|_{x'_k = x_k} \equiv 0 \text{ if } k \neq l$$

Recall that an ESS that is convergence stable is called a CSS and a strategy that is an ESS and NIS is called an ESNIS. In the case of single-species and single-trait models, it has been shown that an ESNIS is also a CSS (Apaloo, 1997b). We explore this result for the models involving multidimensional-traits and/or several-species interactions in the following two sections. However, in this instance we will use strong convergence stability rather than convergence stability, since NIS and strong convergence stability have sufficient conditions given in terms of only Hessians of the selection gradient. In addition, we provide numerical examples for the stabilities discussed above.

SINGLE-SPECIES EVOLUTION

In the preceding section, it can be seen that the evolutionary stability concepts are generally independent of each other when considered alone except for the implications noted above. We provide some numerical examples here. We do this through an example given in Leimar (2001). This is an example of life-history evolution where x_1 denotes a productive trait such as the size of the crown of the tree and x_2 denotes a competitive trait such as the height of the trunk of the tree. The fitness function used was:

$$F(x', x) = \log\left(\frac{W(x', x)}{W(x, x)}\right)$$

where $W(x', x) = P(x')\,M(x', x)$, $P(x') = e^{-\frac{1}{2}(x'_1 + x'_2 - 1)^2}$ and $M(x', x) = e^{x'_1(1 + x'_1 - x_2)}$. Note that we have dropped the subscript k since we are now dealing with single-species (monomorphic) evolution. In the examples we provide, we use a variant of the functional form of M as follows:

$$M(x', x) = e^{x'_1(1 + ax'_2 + bx_1 - cx_2)}$$

where a, b, and c are constants to account for different singular points with different combinations (though not exhaustive) of the above evolutionary stabilities. The classifications of some singular points are given in Table 1.

Another example may be obtained using the functions:

$$P(x') = e^{-10x'^2_1 - 10x'^2_2 + 2x'_1 + 2x'_2}$$

$$M(x', x) = e^{\{11x'^2_1 + 11x'^2_2 - 1.5x'_1x_1 - x'_1x_2 - 1.6x'_2x_2 + 6x'_1x_2 - 10(x'_1 + x'_2 + x_1 + x_2)\}}$$

Table 1. Examples of singular points with different combinations of the evolutionary stabilities. A check mark in a column indicates that the singular point has the stability that appears in the column

Parameter values	Singular point	Matrices classifications	ESS	CS	ACS	NIS
$a = 1, b = -1, c = 0$	(1, 1)	H, J are negative definite and J is symmetric. R is positive definite	✓	✓	✓	✓
$a = 2, b = 0, c = -1$	(2, 3)	H is negative semidefinite and J is negative definite. R is positive definite and J is not symmetric		✓		✓
$a = 1, b = \frac{1}{1.5}, c = 0$	(6, 1)	H, J are negative definite and J is symmetric. R is indefinite	✓	✓	✓	

For this the relevant matrices have the following properties: H is positive definite, J is positive definite, and R is positive definite. The singular point is (56, 20), which is classified as NIS but not ESS, and not absolute convergence stable or strong convergence stable. The results in Table 1 and the preceding one are only a few of the possible types of singular points in models with single species and multidimensional trait space. Two of these are of interest here. In the last example above, the strategy (56, 20) is a NIS, but does not have any of the other stabilities, and this is consistent with the general result that an NIS need not have any of the other three stabilities.

Another interesting example is the last one in Table 1. Here the singular point (6, 1) has three of the evolutionary stabilities but is not an NIS. Two remarks are necessary here. First, the precise value of this singular point may not be the outcome of ecological competition between itself and a strategy in its close neighbourhood. This observation follows from the fact that the singular point is an ESS and so it is not invadable, and since it is not an NIS it cannot invade some strategies in its close neighbourhood. Thus initial population sizes of the singular point and other strategy will determine the outcome of such ecological interactions. Apaloo (2003, 2005) gives details of the evolutionary dynamics in the neighbourhood of such a singular point.

The second remark is seen from the results in Apaloo (1997a) and Apaloo *et al.* (2005). Since a singular point is not an NIS, there is at least one non-positive eigenvalue of the incumbent variation selection Hessian R. If a Darwinian demon (Leimar, 2001) is capable of supplying a large number of mutations along vector(s) associated with the non-positive eigenvalue(s), then evolution will be slow. The slow evolution arises since there is always a barrier in the neighbourhood of the singular point along the eigenvector into which evolution cannot jump. Indeed, the size of this barrier will tend to zero in the course of evolution. However, along eigenvector(s) corresponding to positive eigenvalue(s), evolution can be fast in the sense that there are no barriers in the neighbourhood of the singular point along the eigenvector(s) into which evolution cannot jump. We have argued therefore that the NIS concept plays an important role in identifying the speed with which evolution will proceed and whether the precise value of the singular point is attainable or not.

Recall that in single species with one-dimensional-trait evolutionary models, a strategy that is an ESNIS is also a CSS. It turns out that this result extends to single species with multidimensional-trait evolutionary models. To see this, note that in general

$$H_{kk} + Q_{kk} + Q_{kk}^T + R_{kk} \equiv 0 \text{ for each } k = 1, 2, \ldots, n$$

due to the ecological equilibrium identity. Therefore, in single-species evolution (i.e. $n = 1$ and so we can drop the subscript), if the singular point is an NIS, then $H + Q + Q^T$ will be a negative definite matrix. Now, if in addition the singular point is an ESS, then it follows that $H + \frac{1}{2}(Q + Q^T)$ is also negative definite and thus the singular point is also strong convergence stable. Thus in single-species evolution with multidimensional traits, a singular point is a CSS if it is an ESNIS. Note that in the preceding result we are using strong convergence stability. However, recall that a strategy that is strong convergence stable is also convergence stable.

CO-EVOLUTION

In co-evolution, two or more species each with one-dimensional or multidimensional trait values interact in an evolutionary fashion. If singular points exist, they can be tested for the evolutionary stabilities defined above. We note here that several authors have specifically considered the situations where there are only two species each with a single trait (Abrams *et al.*, 1993; Motro, 1994; Marrow *et al.*, 1996; Matessi and Di Pasquale, 1996; Apaloo, 1997a; Cohen *et al.*, 1999; Apaloo *et al.*, 2005). Brown *et al.* (2007) provide four examples of two-species co-evolutionary models in which each species uses two-dimensional trait values. We consider one of the examples (called the Lotka-Volterra big bully game) below and test the singular point for the stabilities discussed above and this will be done using their fitness-generating function approach. One difference between the fitness function we have used above and the fitness-generating function is that the fitness-generating function explicitly includes the population sizes of the strategies in the game.

It is important to note that Brown *et al.* (2007) use Darwinian dynamics instead of the canonical adaptive dynamics. The Darwinian dynamics consists of strategy dynamics and population dynamics which are defined in terms of the so-called fitness-generating function $G_k(x'_k, x, p)$, where p is the vector of population sizes of the resident strategies. The population dynamics equations can be used to solve for equilibrium population sizes, p^*, which will depend on the strategies resident in the population. Thus $G_k(x'_k, x, p^*)$ can be rewritten as $F_k(x'_k, x) = G_k(x'_k, x, p^*(x))$, which will then be in the familiar form used in the definitions given above. With this notation the Darwinian dynamics may be written out as shown below. The strategy dynamics is given by

$$\dot{x}_k = D_k \nabla'_k G_k(x_k, x, p) \text{ for } k = 1, 2$$

where the overdot denotes time derivative and the population dynamics is

$$\dot{p}_k = p_k G_k(x'_k, x, p)\,|_{x'_k = x_k} \text{ for } k = 1, 2$$

(Brown *et al.*, 2007). Recall that m_k is a measure of the rate of occurrence of mutations and C_k is the variance–covariance matrix for the distribution of mutational increments. If we let $D_k = m_k(x)C(x_k)$ and let $G_k = F_k$ in the above strategy dynamics, then the strategy dynamics equation becomes consistent with the canonical equation given in the 'Evolutionary

Stabilities' section. For more details on the connection between the strategy dynamics given above and the canonical equation, the reader is referred to Brown *et al.* (2007).

For the two-species example (Brown *et al.*, 2007; Vincent and Brown, 2005, pp. 208–210) we consider, $G_1 = G_2 = G$ and the common fitness-generating function is

$$G(x'_k, x, p) = \frac{r}{K(x'_k)}\left[K(x'_k) - \sum_{l=1}^{2} \alpha(x'_k, x_l)p_l\right]$$

The functions K and α were defined as:

$$K(x'_k) = (1 - x'^{2}_{k2})K_{\max}\exp\left(-\frac{(x'_{k1})^2}{2\sigma_K^2}\right)$$

$$\alpha(x'_k, x_l) = 1 + E(x'_k, x_l)\exp\left(-\frac{(x'_{k1} - x_{l1} + \beta)^2}{2\sigma_\alpha^2}\right) - \exp\left(-\frac{\beta^2}{2\sigma_\alpha^2}\right)$$

where

$$E(x'_k, x_l) = 1 + E_{\max}(x_{l2} - x'_{k2})$$

The constants in the model were set as follows: $K_{\max} = 100$; $\sigma_K = \sqrt{8}$; $\beta = 2$; $\sigma_\alpha = 2$; $E_{\max} = 1$; $r = 0.25$ (see Brown *et al.*, 2007, Examples 1 and 2). Brown *et al.* (2007) assumed that the covariance terms in the variance–covariance matrix D_k are negligible and thus could be ignored. We do not make this assumption here but rather assume that $D_1 = D_2 = D$ with the common phenotypic variance–covariance matrix given by

$$D = \begin{pmatrix} 0.5 & 0.1 \\ 0.1 & 0.5 \end{pmatrix}$$

(Vincent and Brown, 2005, pp. 139–140). It is important to note that in all the stability concepts we have considered in this article, only convergence stability involves the matrix D.

Using the above model, one can set up the system of six equations that in principle can be solved to obtain the singular coalition strategy vectors along with the corresponding equilibrium population sizes. It turns out that this large system of equations is not easy to solve. Vincent and Brown (2005, p. 206) solve for these singular points by iterating the corresponding Darwinian dynamics until equilibrium is reached. The equilibrium point is then checked to satisfy the system of necessary conditions for singular points. Using this approach, Brown *et al.* (2007) found the singular point:

$$x^*_1 = [-1.204, 0.3025]^T, \quad x^*_2 = [2.275, 0.2609], \quad p^* = [13.69, 61.72]$$

The above singular point can then be tested to ascertain the kinds of evolutionary stabilities it exhibits, if any. This can be done graphically (in the case of ESS and NIS) or numerically through the sufficient conditions given in the theorems. Using the theorems we show that the singular point is an ESS (all the eigenvalues of H are negative), a NIS (all eigenvalues of R are positive), convergence stable (all the eigenvalues of AJ have negative real parts), but not strong convergence stable and thus not absolute convergence stable (J is not negative definite). The nature of ESS and NIS is also evident in the invader variation and the resident variation fitness graphs (Fig. 1) (Apaloo, 2005). These are called adaptive landscape and NIS landscape respectively (Apaloo *et al.*, 2009). Note that the NIS landscapes are minimized at the

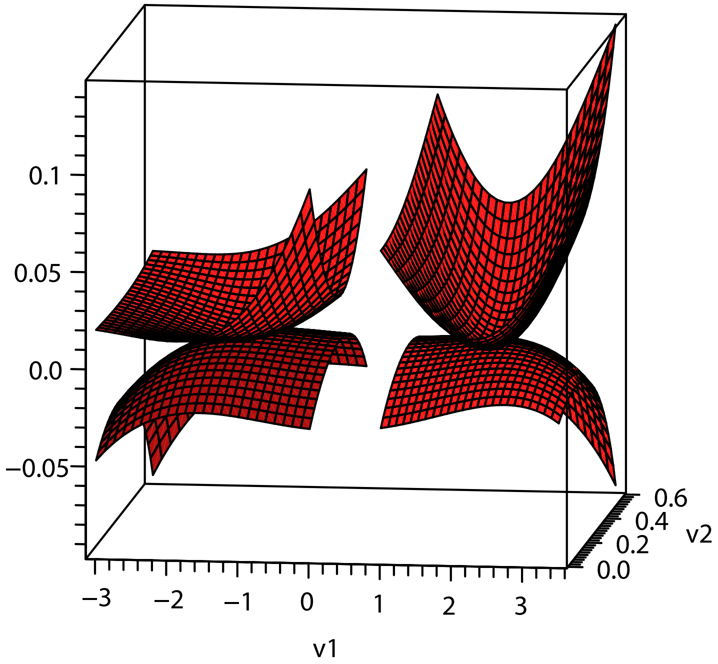

Fig. 1. Adaptive and NIS landscapes showing that the singular point is an ESS and NIS. The upper surfaces are the NIS landscapes, which take on minimum values of 0 at the strategies that form the NIS coalition. The lower surfaces are the adaptive landscapes, which take on maximum values of 0 at the strategies that form the ESS coalition. Note that v_1 and v_2 are dummy variables representing strategies for the invader in the case of adaptive landscapes and strategies for the residents in the case of NIS landscapes.

components of the singular points and the adaptive landscapes are maximized at the components of the singular points.

Recall that no co-evolutionary strategy can be a strong NIS. In fact, in this example the singular point is not a strong NIS as the matrices T^1 and T^2 each have two positive and two negative eigenvalues. This means that there are strategies x in the neighbourhood of x^* that cannot be invaded by some strategies x_k^m which are closer to x_k^* than x_k, since x^* is not a strong NIS. This is a consequence of the fact that there are coalition strategies in an arbitrarily close neighbourhood of x^* that cannot be invaded by a member of the ESNIS coalition. Therefore, certain mutations that are closer to the ESNIS may not successfully invade, which may lead to the phenomenon of slow evolution as described earlier.

Recall that for single-species evolution with multidimensional traits, an ESNIS is also strong convergence stable and thus convergence stable. We see from the above example that this result does not extend to several species with one-dimensional- and/or multidimensional-traits evolutionary models. This can be seen in general from the fact that if x^* is an ESNIS, then H_{kk} and R_{kk} are negative and positive definite respectively for each $k = 1, 2, \ldots, n$. This implies first that $H_{kk} + Q_{kk} + Q_{kk}^T$ is negative definite and, second, that $H_{kk} + \frac{1}{2}(Q_{kk} + Q_{kk}^T)$ (i.e. J_{kk}) is negative definite for each $k = 1, 2, \ldots, n$. Therefore, if x^* is an ESNIS, then the necessary conditions for strong convergence stability of x^* in several-species evolution are satisfied. It is clear, then, that the existence of an ESNIS may not imply the sufficient conditions for strong convergence stability, which would involve off-block diagonal matrices as well as the block diagonal matrices of J. An example to this conclusion is provided above. Note that H and R are block diagonal matrices. In the instance where all the off-diagonal block matrices are zero, then an ESNIS will also be strong convergence stable, in the corresponding co-evolutionary model.

CONCLUSION

In this article, we have briefly reviewed six co-evolutionary stability concepts, including one that cannot be satisfied by any singular point. These stabilities are evolutionarily stable strategy (ESS), convergence stability, strong convergence stability, absolute convergence stability, neighbourhood invader strategy (NIS), and strong NIS. We have shown that no two of them are equivalent in multidimensional-traits and several-species evolutionary models. Each of these concepts plays an important role in determining the eventual outcome of evolution. Among all these stabilities one implication holds in general: a singular strategy that is absolute convergence stable is also strong convergence stable and a strong convergence stable strategy is also a convergence stable strategy.

We have stated above that if an evolutionary process is such that any resident coalition strategy that is distinct from the ESS coalition can be invaded by mutant strategies consisting of the ESS or any strategy in an arbitrarily close neighbourhood of it, then we classify the evolution as being fast. Otherwise, we say that evolution is slow.

We have shown that the ESNIS property may be used to provide insight into the speed of evolution in single species with one-dimensional trait space evolutionary models. In particular, if the singular point is an ESNIS, then evolution can be fast in the sense that mutations that can achieve successful invasion are not confined to only a small neighbourhood of the resident trait but rather to a neighbourhood that always includes the singular point (Apaloo, 2003). We have shown that this result extends to single species with multidimensional traits if approach to an ESS is characterized by the strong convergence stable concept. In the case of several species each with multidimensional traits or several species each with one-dimensional traits, we know that in general the existence of an ESNIS does not imply strong convergence stability. It is not clear here whether an ESNIS will imply convergence stability in general.

Apaloo (1997a) showed that in two species each with one-dimensional trait models, strong NIS is not obtainable. In this article, we have also provided a numerical example involving two species each with two-dimensional trait values that does not possess a strong NIS. This is a general result in that co-evolutionary models can never have a strong NIS. Thus we face the general phenomenon that slow evolution can always occur in several-species evolution. The reason for this phenomenon is because in these models there are strategies closer to the ESS coalition that cannot invade an existing resident co-evolutionary strategy.

We have noted that co-evolutionary models cannot have strong NIS. This suggests the need for strong conditions for neighbourhood invasibility.

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REFERENCES

Abrams, P.A., Matsuda, H. and Harada, Y. 1993. Evolutionarily unstable fitness maxima and stable fitness minima of continuous traits. *Evol. Ecol.*, **7**: 465–487.

Apaloo, J. 1997a. Ecological species coevolution. *J. Biol. Syst.*, **5**: 17–34.

Apaloo, J. 1997b. Revisiting strategic models of evolution: the concept of neighborhood invader strategies. *Theor. Pop. Biol.*, **52**: 71–77.

Apaloo, J. 2003. Single species evolutionary dynamics. *Evol. Ecol.*, **17**: 33–49.

Apaloo, J. 2005. Inaccessible continuously stable strategies. *Natur. Resource Model.*, **19**: 521–535.

Apaloo, J., Muir, P.W. and Hearne, J.W. 2005. Multi-species evolutionary dynamics. *Evol. Ecol.*, **19**: 55–77.

Apaloo, J., Brown, J.S. and Vincent, T.L. 2009. Evolutionary game theory: ESS, convergence stability, and NIS. *Evol. Ecol. Res.*, **11**: 489–515.

Brown, J.S., Cohen, Y. and Vincent, T.L. 2007. Adaptive dynamics with vector-valued strategies. *Evol. Ecol. Res.*, **9**: 719–756.

Christiansen, F.B. 1991. On conditions for evolutionary stability for a continuously varying character. *Am. Nat.*, **138**: 37–50.

Cohen, Y., Vincent, T.L. and Brown, J.S. 1999. A *G*-function approach to fitness minima, fitness maxima, evolutionarily stable strategies and adaptive landscapes. *Evol. Ecol. Res.*, **1**: 923–942.

Cressman, R. 2008. Neighborhood invader strategies, continuously stable strategies and dynamic stability for two-species behavioral models with continuous trait spaces. *mimeo*.

Cressman, R., Hofbauer, J. and Riedel, F. 2006. Stability of the replicator equation for a single species with a multi-dimensional continuous trait space. *J. Theor. Biol.*, **239**: 273–288.

Dieckmann, U. and Law, R. 1996. The dynamical theory of coevolution: a derivation from stochastic ecological processes. *J. Math. Biol.*, **34**: 579–612.

Eshel, I. 1983. Evolutionary and continuous stability. *J. Theor. Biol.*, **103**: 99–111.

Eshel, I. 1996. On the changing concept of evolutionary population stability as a reflection of a changing point of view in the quantitative theory of evolution. *J. Math. Biol.*, **34**: 485–510.

Eshel, I. and Motro, U. 1981. Kin selection and strong evolutionary stability of mutual help. *Theor. Pop. Biol.*, **19**: 420–433.

Eshel, I., Motro, U. and Sansone, E. 1997. Continuous stability and evolutionary convergence. *J. Theor. Biol.*, **185**: 333–343.

Geritz, S.A.H., Kisdi, É., Meszéna, G. and Metz, J.A.J. 1998. Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evol. Ecol.*, **12**: 35–57.

Leimar, O. 2001. Evolutionary change and Darwinian demons. *Selection*, **2**: 65–72.

Leimar, O. in press. Multidimensional convergence stability and the canonical adaptive dynamics. In *Elements of Adaptive Dynamics* (U. Dieckmann and J.A.J. Metz, eds.). Cambridge: Cambridge University Press.

Lessard, S. 1990. Evolutionary stability: one concept, several meanings. *Theor. Pop. Biol.*, **37**: 159–170.

Marrow, P., Dieckmann, U. and Law, R. 1996. Evolutionary dynamics of predator–prey systems: an ecological perspective. *J. Math. Biol.*, **34**: 556–578.

Matessi, C. and Di Pasquale, C. 1996. Long-term evolution of multilocus traits. *J. Math. Biol.*, **34**: 613–653.

Maynard Smith, J. and Price, J.G.R. 1973. The logic of animal conflict. *Nature*, **246**: 15–18.

McKelvey, R. and Apaloo, J. 1995. The structure and evolution of competition-organized ecological communities. *Rocky Mt. J. Math.*, **25**: 417–436.

Meszéna, G., Kisdi, É., Dieckmann, U., Geritz, S.A.H. and Metz, J.A.J. 2001. Evolutionary optimisation models and matrix games in the unified perspective of adaptive dynamics. *Selection*, **2**: 193–210.

Motro, U. 1994. Evolutionary and continuous stability in asymmetric games with continuous strategy sets: the parental investment conflict as an example. *Am. Nat.*, **144**: 229–241.

Nowak, M. 1990. An evolutionarily stable strategy may be inaccessible. *J. Theor. Biol.*, **142**: 237–241.

Taylor, P.D. 1989. Evolutionary stability in one-parameter models under weak selection. *Theor. Pop. Biol.*, **36**: 125–143.

Vincent, T.L. and Brown, J.S. 2005. *Evolutionary Game Theory, Natural Selection, and Darwinian Dynamics*. Cambridge: Cambridge University Press.