

Multidimensional convergence stability

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ABSTRACT

Questions: Are there general stability conditions for the evolution of multidimensional traits, regardless of genetic correlations between traits? Can genetic correlations influence whether evolution converges to a stable trait vector?

Mathematical methods: Adaptive dynamics theory and the weak selection limit of quantitative genetics.

Key assumptions: Evolutionary change is represented as either (i) any gradualistic adaptive path in trait space, consisting of a sequence of small-effect mutant invasions, allowing for pleiotropic mutants, or (ii) a solution to the ‘canonical equation’ of adaptive dynamics with a gradually varying mutational covariance matrix. Assumption (ii) is a special case of (i).

Conclusions: It is possible to formulate robust stability conditions for multidimensional traits, but most evolutionary equilibria will not satisfy these conditions. Under the liberal assumption (i), there will in general be no ‘absolutely convergence stable’ equilibria in multidimensional trait spaces (except for simplified models). Under the more restrictive assumption (ii), a much larger proportion of evolutionary equilibria is ‘strongly convergence stable’, i.e. are stable irrespective of genetic correlations.

Keywords: adaptive dynamics, canonical equation, evolutionary stability, genetic correlations.

INTRODUCTION

An evolutionary analysis of several traits considered together can differ from a set of single-trait analyses in two basic ways. First, there may be fitness interactions between traits, so that the strength and perhaps direction of natural selection on one trait depend on other traits. Fitness interactions may be present both for traits belonging to a single species and for traits of different species (co-evolution). Second, genetic variation may be correlated among traits, for instance through genes acting pleiotropically, causing the response to selection on one trait to be distributed among several traits. Such correlations will mainly occur for traits within a species. My aim here is to bring together various results from the literature (e.g. Leimar, 2001, 2005; Cressman *et al.*, 2006; Dieckmann *et al.*, 2006; Brown *et al.*, 2007; Durinx *et al.*, 2008) to address the question of how fitness interactions and genetic correlations can be taken

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into account when considering evolutionary stability. On the one hand, I will note that it is essentially futile to expect a completely general stability criterion based solely on (invasion) fitness, and this state of affairs is particularly acute for multidimensional trait spaces. On the other hand, I will argue that fitness-based stability criteria can be quite useful, in the sense of providing a classification of evolutionary equilibria into those where evolutionary stability is guaranteed only if genetic variation is of a special kind, for instance if genetic correlations are absent, and those where stability is more robust to genetic details.

Models of adaptive evolution often have the property that change is guided by, but not fully determined by, fitness. In a given situation, many different mutant phenotypes may have a fitness advantage over the residents, and are thus potential invaders, implying that the mutational process plays an important role in deciding which particular invasion will take place (Matessi and Di Pasquale, 1996). Granting that adaptive dynamics contains at least these two parts – a process generating genetic variation and natural selection acting on the variation – one might wonder whether there is much hope of determining attractors of the dynamics by only looking at the natural selection part. In fact, as we will see, this is not possible in general.

However, in certain cases stability is less dependent on the details of genetic variation. The single-trait convergence stability criterion (Eshel and Motro, 1981; Eshel, 1983; Taylor, 1989; Christiansen, 1991; Metz *et al.*, 1996; Eshel *et al.*, 1997; Geritz *et al.*, 1998) has a rather natural fitness-based generalization to situations with several traits. Let us use the convention of calling a matrix, say \mathbf{A} , positive definite if its symmetric part, $(\mathbf{A} + \mathbf{A}^T)/2$, is positive definite, and similarly for negative definiteness, and so on. The multidimensional criterion then states that the Jacobian of the selection gradient should be negative definite (Leimar, 2005). This criterion is sufficient for strong convergence stability, where strong convergence stability is defined as stability for the canonical deterministic adaptive dynamics (Dieckmann and Law, 1996), provided the mutational covariance matrix varies in a sufficiently gradual fashion. For the formally similar weak selection limit of quantitative genetics (Lande, 1979; Iwasa *et al.*, 1991), assuming a gradually varying genetic covariance matrix, a negative definite Jacobian also implies stability. So, if one is faced with a negative definite Jacobian, one need not worry about inter-trait genetic correlations, at least not as long as such correlations vary sufficiently smoothly. This is clearly a valuable piece of information to have about an evolutionary equilibrium – one will often lack any kind of *a priori* information about genetic correlations – thus lending a particular status to strong convergence stability.

The criterion is nevertheless not entirely robust to the properties of mutational genetic variation. For instance, strong stability of an equilibrium (a singular point) does not guarantee that any gradualistic, adaptive path through trait space, consisting of a sequence of successful mutant invasions, must converge to or even remain near the point. On the contrary, unless fitness interactions are absent or have a very special form, an adaptive escape from any small neighbourhood of the point will be possible, although the sequence of mutations generating such invasions must have unlikely properties (Leimar, 2001).

On the whole, there will usually be little reason to expect gradualistic evolution away from strongly convergence stable points. It is possible to formulate more robust criteria, at the expense of having fewer situations where these criteria are satisfied. For instance, one could require that a point should attract any nearby gradualistic, adaptive path, a property that may be called ‘absolute convergence stability’ (Leimar, 2001). In addition, there is the question of whether there is stabilizing selection at a singular point, preventing the appearance of polymorphisms (Christiansen, 1991). For a single trait, the combination of stabilizing selection

and convergence stability is usually referred to as ‘continuous stability’ (Eshel and Motro, 1981; Eshel, 1983).

It is worth noting that maximum robustness obtains when the situation allows an evolutionary optimization principle (Mesz ena *et al.*, 2001; Metz *et al.*, 2008). Such a principle is assumed to hold when one deals with so-called optimality models. In spite of their quite special nature, optimality models have played a very important role in life-history theory.

EXAMPLE OF FISHER’S RUNAWAY PROCESS

One can readily find multidimensional examples where a point in the trait space is an attractor given that certain genetic correlations are absent or small, but ceases to be an attractor for larger correlations. The most well-known such example, although not usually thought of in this manner, is Fisher’s runaway process. Using quantitative genetics, Lande (1981) found that a line of equilibria ceases to attract when the genetic correlation between male ornament and female preference exceeds a certain value. The phenomenon does not depend on there being a line of equilibria instead of a point, but will remain if the model is modified to remove the degeneracy (Fig. 1).

For a male with ornament z_m in a population with mean male ornament \bar{z}_m and mean female preference \bar{z}_f , reproductive success is the product of survival and mating success,

$$W_m = e^{-cz_m^2} e^{a(z_m - \bar{z}_m)\bar{z}_f},$$

where the parameters c and a determine the cost of the ornament and the choice efficiency. For a female with preference z_f , her choosiness imposes a survival cost,

$$W_f = e^{-bz_f^2},$$

where b determines the cost of choosiness. The selection gradient S used by Pomiankowski *et al.* (1991) has two components,

$$\begin{aligned} S_m &= \partial \log W_m / \partial z_m \Big|_{z_m = \bar{z}_m} = -2c\bar{z}_m + a\bar{z}_f \\ S_f &= \partial \log W_f / \partial z_f \Big|_{z_f = \bar{z}_f} = -2b\bar{z}_f \end{aligned}$$

and is zero at $\bar{z} = \bar{z}^* = 0$. Applying quantitative genetics, the change in the vector \bar{z} of mean values is given by $d\bar{z}/dt = \frac{1}{2}\mathbf{G}S$, where \mathbf{G} is the additive genetic covariance matrix. Since the selection gradient is linear in \bar{z} , we can write it as $S = \mathbf{J}\bar{z}$, where \mathbf{J} is the Jacobian of the selection gradient. So, we have $d\bar{z}/dt = \frac{1}{2}\mathbf{G}\mathbf{J}\bar{z}$, with

$$\mathbf{G} = \begin{pmatrix} V_m & C \\ C & V_f \end{pmatrix} \quad \mathbf{J} = \begin{pmatrix} -2c & a \\ 0 & -2b \end{pmatrix} \quad \mathbf{G}\mathbf{J} = \begin{pmatrix} -2cV_m & aV_m - 2bC \\ -2cC & aC - 2bV_f \end{pmatrix},$$

where V_m and V_f are the additive genetic variances of z_m and z_f and C is the additive genetic covariance between these traits. The point $\bar{z}^* = 0$ is an asymptotically stable equilibrium when the eigenvalues of $\mathbf{G}\mathbf{J}$ have negative real parts, which happens if and only if the determinant is positive and the trace is negative. Since $\det(\mathbf{G}\mathbf{J}) = \det(\mathbf{G})\det(\mathbf{J})$ is positive, $\bar{z}^* = 0$ is stable if $aC < 2(cV_m + bV_f)$ and unstable if the inequality is reversed (Fig. 1).

In this example of Fisher’s runaway process, the Jacobian happens to be indefinite. In such cases, the issue of evolutionary stability is best dealt with by saying that the point is stable if genetic variation satisfies certain conditions, and otherwise it is not.

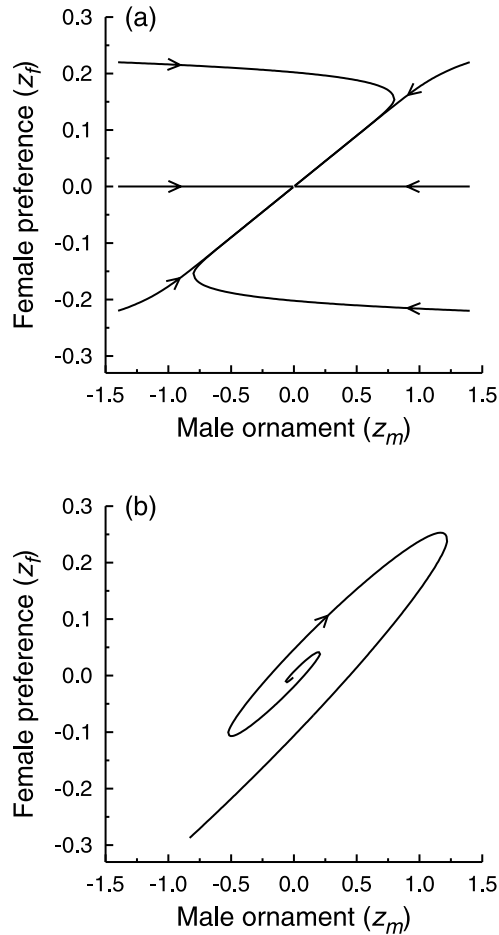


Fig. 1. For Fisher's runaway process, the stability of the point $(z_m, z_f) = (0, 0)$ – no male ornament exaggeration and no female preference – can depend on the genetic correlation between these traits. In (a) the correlation is zero and the point is stable; the trajectories converge to it. In (b) the correlation is 0.25 and the point is unstable, as illustrated by the diverging trajectory. Parameter values are $a = 1$, $b = 0.01$, $c = 0.1$, making the Jacobian \mathbf{J} indefinite. The variances are $V_m = V_f = 0.04$ and the covariance (a) $C = 0$ or (b) $C = 0.01$.

ADAPTIVE DYNAMICS

Let us begin with a fairly general formulation of adaptive dynamics for a co-evolutionary situation with N species (Dieckmann and Law, 1996; Metz *et al.*, 1996). Species k has one or more traits capable of continuous and, in principle, independent variation and x_k is a vector of values of these traits (vectors are regarded as column vectors and transposition indicates row vectors). In accordance with a long-term evolutionary point of view, fitness plays the role of determining if, or with what probability, a mutant trait can invade. A mutant with phenotype x'_k has a chance to invade when its fitness exceeds that of the resident species k phenotype: $F_k(x'_k, x) > F_k(x_k, x)$. The second argument, x , in the fitness function is the

vector of all trait values of all species, $x^T = (x_1^T, \dots, x_N^T)$, and represents the environment generated by a community with these traits. When x_k is multidimensional, the mutant can be pleiotropic, meaning that x'_k can deviate from x_k in more than one trait component. Pleiotropy of mutant genotypes is how genetic correlations appear in the dynamics.

The fitness $F_k(x'_k, x)$ has the interpretation of a dominant Lyapunov exponent (Metz *et al.*, 1992; Ferriere and Gatto, 1995) corresponding to the mean rate of change of the logarithm of the size of the mutant gene subpopulation. Consequently, whenever the mutant is the same as the resident, $F_k(x_k, x) = 0$ must hold.

Whether a particular mutant x'_k invades depends on the sign of $F_k(x'_k, x)$. A mutant with $F_k < 0$ has no chance of invading in a large population, whereas one with $F_k > 0$ has a positive probability of invasion. Taking into account the risk of extinction during an initial phase of low mutant copy number, one finds that this probability is proportional to F_k , to lowest order in F_k (Dieckmann and Law, 1996). Even if the phenotype x'_k invades, it could still fail to drive the previous resident x_k to extinction and instead produces additional polymorphism in the community (Metz *et al.*, 1996; Geritz *et al.*, 1998), but such phenomena would occur only at exceptional points in the trait space.

GRADUALISTIC, ADAPTIVE PATHS IN TRAIT SPACE

If only mutations where x'_k is close to x_k occur, evolutionary change will be gradual. Such change can be regarded as guided by the selection gradient. The species k selection gradient, $\nabla'_k F_k(x_k, x)$, is a vector whose i th component is

$$(\nabla'_k F_k(x_k, x))_i = \left. \frac{\partial F_k}{\partial x'_{ki}} \right|_{x'_k = x_k} . \quad (1)$$

At a point where the selection gradient is non-zero, and with x'_k close to x_k , Taylor expansion of F_k shows that the mutant x'_k has a chance to invade if the scalar product of the mutational increment with the selection gradient is positive,

$$(x'_k - x_k)^T \nabla'_k F_k(x_k, x) > 0, \quad (2)$$

whereas the mutant cannot invade when the scalar product is negative. So, if a mutant x'_k satisfies (2) and thus can invade a resident x_k , the reverse invasion, where a mutant x_k invades a resident x'_k , cannot happen, at least if the selection gradient is a continuous function. One can then usually assume that x'_k drives x_k to extinction (Metz *et al.*, 1996; Geritz *et al.*, 1998, 2002; Geritz, 2005; Dercole and Rinaldi, 2008). We see that any path through trait space where each successive change consists of a small mutational increment satisfying (2), with only one species changing at a time, is a possible trait substitution sequence.

When considering the stability of a point in trait space, one alternative is to take all paths of this kind into account and to require that any such path starting near to the point should converge to it. The main benefit of such absolute convergence stability would be that it guards against a destabilizing influence from any conceivable sequence of mutations with small increments, although it has the drawback of posing very strict requirements on the fitness function.

CANONICAL EQUATION

With gradual change guided by the selection gradient and a given distribution of mutational increments, the law of large numbers ensures that all but a small proportion of sample paths will be close to an average path, or trajectory. Dieckmann and Law (1996) derived an equation of the form

$$\frac{d}{dt}x_k = m_k(x)\mathbf{C}_k(x_k)\nabla'_k F_k(x_k, x) \quad (3)$$

for the trajectory in the so-called deterministic limit of small mutational increments, and referred to it as the canonical equation. In this equation, the real-valued, positive function m_k accounts for variation in the rate of occurrence of mutations, for instance because of variation in population size, and the distribution of increments is point symmetric about the origin with covariance matrix \mathbf{C}_k .

A covariance matrix is symmetric and positive definite or, for a degenerate distribution, positive semidefinite. Assuming positive definiteness, we see that inequality (2) will hold for a small increment in x_k along a trajectory produced by the canonical equation.

To correctly apply the canonical equation, it is important to note that it represents an idealization of a situation with small but finite mutational increments. In particular, near to where the selection gradient is zero, the equation might provide an inaccurate picture of the adaptive dynamics, for instance because we can no longer assume that an invading phenotype will drive the previous resident to extinction (Durinx *et al.*, 2008). It will be convenient to write the canonical equation as

$$\frac{d}{dt}x = \mathbf{B}(x)\nabla'F(x, x), \quad (4)$$

where \mathbf{B} is a block diagonal, symmetric, positive definite matrix with blocks $\mathbf{B}_{kk} = m_k\mathbf{C}_k$, and $\nabla'F(x, x)$ is the vector of selection gradients of all species. These express the two parts of the canonical adaptive dynamics: the process generating genetic variation is described by the mutational matrix \mathbf{B} and natural selection by the selection gradient $\nabla'F(x, x)$.

In addition to providing a useful approximation of gradual adaptive change through a sequence of mutant invasions, the canonical equation has the same form as the equation for the vector of average breeding values used in quantitative genetics, assuming weak selection or, equivalently, small genetic variances (Lande, 1979; Iwasa *et al.*, 1991). Thus, it is quite reasonable to take the canonical equation as a starting point for considerations of evolutionary stability.

SINGULAR POINTS

A point x^* in trait space where the selection gradients of all species are zero is called 'singular',

$$\nabla'F(x^*, x^*) = 0, \quad (5)$$

and it is among such points that one should look for stable equilibria of the adaptive dynamics. When no nearby phenotype of any species can invade a singular point, it is said to be locally uninvadable. Uninvadable singular points are commonly referred to as ESSs. This terminology is somewhat unfortunate, and will not be used here, since it deviates from

what is usually understood by stability for dynamical systems; from the term ‘evolutionarily stable strategy’ one might have expected that the point would be an attractor of some evolutionary dynamics, but uninvadability does not have this interpretation in general.

Around a singular point x^* , mutant fitness has the Taylor expansion

$$F_k(x'_k, x^*) = \frac{1}{2} (x'_k - x_k^*)^T \mathbf{H}_{kk} (x'_k - x_k^*) + \dots \quad (6)$$

where the matrix \mathbf{H}_{kk} , referred to as the selection Hessian, has elements

$$(\mathbf{H}_{kk})_{ij} = \frac{\partial^2 F_k}{\partial x'_{ki} \partial x'_{kj}} \Big|_{x'_k = x_k^*, x = x^*}. \quad (7)$$

We see that for the point to be locally uninvadable, it is sufficient that the selection Hessians of all species are negative definite and necessary that they are negative semidefinite.

The adaptive dynamics near a singular point can be investigated using Taylor expansion of the selection gradient (see Appendix):

$$\nabla' F(x, x) = \mathbf{J}(x - x^*) + \dots \quad (8)$$

The matrix \mathbf{J} is the Jacobian of the selection gradient and it is given by

$$\mathbf{J} = \mathbf{H} + \mathbf{Q}, \quad (9)$$

where \mathbf{H} is a symmetric, block diagonal matrix with the selection Hessians \mathbf{H}_{kk} as blocks, and \mathbf{Q} is a matrix with blocks \mathbf{Q}_{kl} , with elements

$$(\mathbf{Q}_{kl})_{ij} = \frac{\partial^2 F_k}{\partial x'_{ki} \partial x_{lj}} \Big|_{x'_k = x_k^*, x = x^*}. \quad (10)$$

If the mutational matrix $\mathbf{B}(x)$ in (4) varies smoothly with x around the singular point, and with $\mathbf{A} = \mathbf{B}(x^*)$, the linearized canonical equation becomes

$$\frac{d}{dt} (x - x^*) = \mathbf{A}\mathbf{J}(x - x^*). \quad (11)$$

The mutational matrix \mathbf{A} is symmetric, positive definite, and, with more than one species, block diagonal, whereas nothing can in general be assumed about the Jacobian \mathbf{J} . Note finally that it is meaningful to linearize the canonical equation only if the mutational increments are considerably smaller than the range around a singular point where (11) is an acceptable approximation of (4).

CRITERIA FOR EVOLUTIONARY STABILITY

Taking the canonical equation (4) as a starting point, a natural fitness-based stability criterion would be a requirement on the fitness function that implies stability for a whole class of mutational processes. In the case of a single species, where mutational genetic variation in any two traits conceivably could be correlated, let us define strong convergence stability of a singular point to mean that the point is an asymptotically stable equilibrium of the canonical adaptive dynamics for any smoothly varying, symmetric, positive definite mutational matrix $\mathbf{B}(x)$. For a situation with several species, one would instead require

stability only for a subset of these mutational matrices, namely those with an appropriate block diagonal structure, corresponding to the absence of interspecific genetic correlations.

A singular point x^* will be asymptotically stable if all eigenvalues of the matrix \mathbf{AJ} in the linearized canonical equation (11) have negative real parts and unstable if at least one eigenvalue has a positive real part (this is Lyapunov's criterion). One can then formulate stability criteria as requirements on the Jacobian \mathbf{J} of the selection gradient, ensuring that the eigenvalues of \mathbf{AJ} have negative real parts for any symmetric, positive definite \mathbf{A} with an appropriate block diagonal structure.

Strong convergence stability for a single species

For a single species, a result by Hines (1980) and Cressman and Hines (1984), which appears as matrix algebra result 1 in the Appendix, provides an explicit formulation of the requirements on the Jacobian of the selection gradient (Leimar, 2005):

- For strong convergence stability of a singular point, it is sufficient that the Jacobian of the selection gradient is negative definite at the point, whereas if the Jacobian is not negative semidefinite, there is some mutational matrix for which the point is an unstable equilibrium of the canonical equation.

Conversely, with a positive definite Jacobian, instability is guaranteed, since a variant of result 1 in the Appendix would state that all eigenvalues of \mathbf{AJ} in (11) have positive real parts for any symmetric, positive definite \mathbf{A} . There is also an intermediate scenario, when the Jacobian is indefinite at a singular point, and one might then want to characterize the set of mutational matrices \mathbf{A} yielding stability in (11) for the particular matrix \mathbf{J} in question. Except for two-by-two matrices, where the calculations are easy (see Appendix), an explicit characterization appears not to be available.

Note that uninvasibility of a singular point plays no role in the stability criterion for the canonical equation (although one sees from (9) that negative definiteness of the selection Hessian \mathbf{H} 'helps' to make the Jacobian \mathbf{J} negative definite). However, as noted above, the validity of the canonical equation near a singular point cannot be taken for granted, and this is where uninvasibility enters the picture. From (6), when the selection Hessian is indefinite or positive definite, there will be disruptive selection along some direction in trait space, which might result in an accumulation of genetic variation along that direction (Christiansen, 1991; Eshel *et al.*, 1997). An especially interesting type of accumulation of genetic variation is a branching of the evolutionary trajectory, which could be induced by disruptive selection at a singular point (Christiansen, 1991; Metz *et al.*, 1996; Geritz *et al.*, 1998). Clearly, a build-up of genetic variation invalidates both the idea of invading mutations replacing the residents and the assumption of small genetic variances needed for the quantitative genetics version of the canonical equation. In summary:

- At a locally uninvadable singular point, mutant phenotypes are not exposed to disruptive selection that could lead to an accumulation of genetic variation.

The vagueness of the statement is a reflection of our currently rather limited knowledge, for instance about how the nature of the mutational process influences the build-up of genetic variation (see also Durinx *et al.*, 2008).

Nevertheless, it is reasonable to define a continuously stable strategy (CSS) as a locally uninventable, strongly convergence stable singular point (Leimar, 2005). We then have the following stability criterion:

- For a singular point to be a CSS, it is sufficient that the selection Hessian and the Jacobian of the selection gradient are negative definite at the point and necessary that they are negative semidefinite.

This criterion agrees with the formulation of multidimensional continuous stability by Lessard (1990). In general terms, the idea behind multidimensional continuous stability is that, when it applies, one need not fear that the particularities of genetic variation could compromise stability, at least not within a quite reasonable class of mutational processes.

In connection with the criteria above, involving second-order derivatives of a fitness function $F(x',x)$ at a singular point $x' = x = x^*$, it is worth noting that the identity $F(x,x) = 0$ implies certain relationships between derivatives, making it possible to formulate the criteria in different but equivalent ways. For instance, for a one-dimensional trait space, one can eliminate the mixed derivative and instead use the second-order partial derivatives with respect to x' and x , as was done by Metz *et al.* (1996) and Durinx *et al.* (2008).

Absolute convergence stability

It is possible to go further in the direction of stability being robust to the nature of mutational genetic variation (Leimar, 2001). Let us define absolute convergence stability of a point to mean that all conceivable gradualistic, adaptive paths starting near the point will converge to it. Again considering a single species, suppose the fitness function has the property that, at least in the vicinity of a singular point x^* , the selection gradient points in the same direction as the gradient of some function $U(x)$ with a single (local) maximum at x^* . The selection gradient can then be expressed as

$$\nabla'F(x,x) = \alpha(x)\nabla U(x), \quad (12)$$

where α is a positive function. In such a case, any gradualistic, adaptive path, with small increments satisfying inequality (2), will proceed to higher and higher values of U , and thus approach the singular point x^* .

Note that the Jacobian of a selection gradient of this form must be symmetric at the singular point (since $\nabla U(x^*) = 0$ holds). On the other hand, in cases where the Jacobian is not symmetric, at least some gradualistic, adaptive paths will diverge from the singular point. To see this, consider an entirely hypothetical sequence of mutations where the (small) mutational increments happen to be in a direction that is a linear function of the direction of the selection gradient; for instance, assume that only mutations in the direction $\mathbf{A}\nabla'F(x,x)$ occur, where \mathbf{A} is some as yet unspecified matrix. As long as this matrix \mathbf{A} is positive definite, these mutations satisfy inequality (2) and have a chance to invade. Linearizing around a singular point x^* , we get an equation like (11), where the matrix \mathbf{A} is positive definite but not necessarily symmetric. If \mathbf{J} is not symmetric, matrix algebra result 2 in the Appendix then tells us that one can find an \mathbf{A} that makes the point unstable. We then have the following criterion:

- For absolute convergence stability of a singular point, it is sufficient that the selection gradient in the vicinity of the point can be expressed in the form (12), whereas it is

necessary that the Jacobian of the selection gradient is symmetric and negative semidefinite at the point.

For a one-dimensional trait space, the selection gradient of any smooth fitness function can be expressed in the form (12) around a convergence stable point [for instance, by choosing $\alpha = 1$, $U(x^*) = 0$ and solving (12) as a differential equation for $U(x)$ in the vicinity of x^* ; because the selection gradient changes sign from positive to negative at a convergence stable point, U has a maximum at x^*]. However, with multidimensional trait spaces, there is in general no reason to expect the matrix \mathbf{Q} in (10) to be symmetric, and (9) then shows that there is no reason to expect \mathbf{J} to be symmetric. Thus, apart from the single-trait case, absolute convergence stability is a very restrictive requirement that in general is fairly unlikely to hold.

Perhaps the most important point to note is that the hypothetical sequence of mutations described above is quite unrealistic: the direction of increments must differ for nearby points, with a discontinuity at the singular point. Since the sequence is representative of what is needed for an adaptive escape from a strongly stable point, it is justifiable to have faith in strong convergence stability.

Co-evolutionary stability

For co-evolutionary fitness interactions, let us define strong convergence stability of a singular point as asymptotic stability of the canonical adaptive dynamics for any smoothly varying, symmetric, positive definite, block diagonal mutational matrix, where the blocks correspond to the absence of interspecific genetic correlations. Since mutational matrices where only one species mutates are a limiting case of the set of matrices considered, we immediately have the following criterion, where the matrices \mathbf{H}_{kk} and \mathbf{Q}_{kk} are from (7) and (10) above:

- For co-evolutionary strong convergence stability of a singular point, it is necessary that for each species k in the community, the Jacobian $\mathbf{J}_{kk} = \mathbf{H}_{kk} + \mathbf{Q}_{kk}$ is negative semidefinite at the point.

The criterion is not the sharpest possible – some condition involving the off-diagonal blocks \mathbf{J}_{kl} of the total Jacobian ought to be added. Just as for the single-species case, negative definiteness of \mathbf{J} is sufficient for strong stability; however, negative definiteness of \mathbf{J} is unduly restrictive when interspecific genetic correlations are absent. Presumably, negative definiteness of the \mathbf{J}_{kk} forms part of a sharper sufficient condition.

In the case of two species, each with a single trait (see Abrams *et al.*, 1993; Motro, 1994; Marrow *et al.*, 1996a; Matessi and Di Pasquale, 1996), it is straightforward to work out this sharper condition (see Appendix). In the criterion, note that the blocks of \mathbf{J} are one-by-one matrices, i.e. numbers.

- Consider two species, each with a single trait. For strong convergence stability of a singular point, it is sufficient that the Jacobian at the point satisfies $\det(\mathbf{J}) > 0$, $\mathbf{J}_{11} < 0$, $\mathbf{J}_{22} < 0$ and necessary that the corresponding weak inequalities hold.

As pointed out by Marrow *et al.* (1996a), a singular point that fails the necessary condition cannot be regarded as unstable without further qualification. So, if the condition on the

Jacobian fails, all one knows is that there are some (diagonal) mutational matrices making the point unstable. In such a case, one might want to characterize the set of mutational matrices yielding stability (see Appendix).

Returning to general co-evolutionary interactions we can, in analogy with the single species case, define a CSS as a locally uninvable, strongly convergence stable singular point. As pointed out in connection with equations (6) and (7) above:

- For a singular point to be locally uninvable, it is sufficient that the selection Hessians \mathbf{H}_{kk} of all species are negative definite at the point and necessary that they are negative semidefinite.

ILLUSTRATION OF STABILITY CRITERIA

The weak selection limit of quantitative genetics (Iwasa *et al.*, 1991), used for the example of Fisher's runaway process (see above; Fig. 1), has the same form as the canonical equation. For the runaway process, the primary reason for an ornament-preference genetic correlation would be assortative mating in a genetically variable population (Lande, 1981), making quantitative genetics a natural modelling approach, but pleiotropic mutations could in principle lead to runaway. Whatever the cause of genetic correlations, we can conclude that the singular point $\bar{z}^* = 0$ in the example is not strongly convergence stable for parameter values where the Jacobian of the selection gradient is indefinite. For the example, efficient choice (large a) at low cost (small b) and an ornament that can be exaggerated fairly cheaply (small c) tend to make the Jacobian indefinite.

The fitness interactions described in this example could in principle occur between species (say, some sort of pollination interaction). In such a case, one would no longer expect the traits to be correlated, and the conclusion about the stability of the singular point changes. It is straightforward to see that the point satisfies the two-species, single-trait strong convergence stability criterion above. Since the point is also uninvable, it is in fact a co-evolutionary CSS.

The circumstance that strong and absolute convergence stability are equivalent for one-dimensional trait spaces has sometimes been used as a technical device to locate stable equilibria. A well-known instance is the so-called MacArthur product rule for sex allocation (Charnov, 1982), which is illustrated in Fig. 2 (using a special case of the hermaphrodite life-history example worked out in the Appendix). In one dimension, it is always possible to find some function $U(x)$ that has a (local or global) maximum at a convergence stable point x^* .

In multidimensional trait spaces, strong convergence stability is less restrictive than absolute convergence stability. A joint analysis of the traits of sex allocation and reproductive effort, which usually are dealt with separately, can serve as an illustration. With the fitness function assumed for the hermaphrodite life-history example (see Appendix), a separate analysis of sex allocation finds a continuously stable allocation (Fig. 2) and a separate analysis of reproductive effort similarly finds a globally optimal, and thus continuously stable, effort. It would be disturbing, and quite a blow to sex allocation theory and life-history theory, if a joint analysis of the two traits invalidated these conclusions. Instead, to the extent that the canonical equation, or the corresponding quantitative genetics equation, provides an acceptable approximation of evolutionary change, the uninvolvability and strong convergence stability, and thus multidimensional continuous stability, of the singular point x^* confirm the separate analyses (see Appendix).

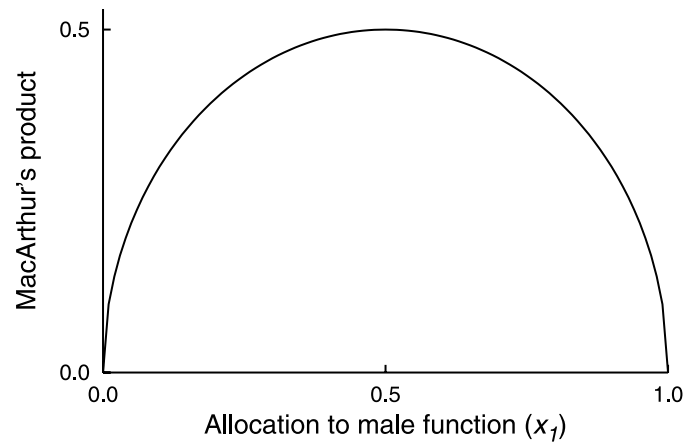


Fig. 2. Strong convergence stability in a one-dimensional trait space, as illustrated by MacArthur's product rule (Charnov, 1982). For fixed reproductive effort x_2 , the stable sex allocation x_1 in the hermaphrodite life-history example (for simplicity, fix effort at semelparity: $x_2 = 1$) can be found by maximizing MacArthur's product $U(x_1) = (x_1)^a(1 - x_1)^b$. For the case illustrated, with $a = b = 0.5$, gradual adaptive change must be towards $x_1^* = 0.5$, increasing the value of U , showing that the form (12) applies.

Nevertheless, as Fig. 3 illustrates (see also Appendix), an adaptive escape from any small neighbourhood of x^* is possible, showing that x^* lacks absolute convergence stability. One could then imagine a 'Darwinian demon', judiciously supplying suitable mutations, creating havoc for, among other things, sex allocation theory and life-history theory (Leimar, 2001). In practice, there is probably no need to worry about such 'Darwinian demons', but the example makes it clear that the issue of evolutionary stability cannot be dealt with effectively without making assumptions about the mutational process.

DISCUSSION

Using the canonical adaptive dynamics, or the weak selection limit of quantitative genetics, as a starting point for considerations of evolutionary change and stability has the advantage of taking into account the basic phenomena of fitness interactions and genetic correlations in a way that is both amenable to analysis and acceptably realistic. In fact, there seems to be no other competing approach delivering a similarly pleasing combination of transparency and relevance. Certainly, a canonical adaptive dynamics can only provide an approximation of real evolutionary processes, and there may well be situations where other formulations are desirable (Dieckmann and Law, 1996). At the present time, however, a really general dynamical treatment of evolutionary stability is only available for the canonical adaptive dynamics and other formally similar dynamical formulations, like the weak selection limit of quantitative genetics.

In any case, a search for the Holy Grail of a universal fitness-based stability criterion, with the power to unambiguously separate stable from unstable, is bound to fail. Such a state of affairs should, however, not cause us to give up using fitness-based stability criteria. Instead, it would be wiser to make use of the kind of classification of singular points in trait space that after all can be achieved. A good reason for such a practice would be if there are

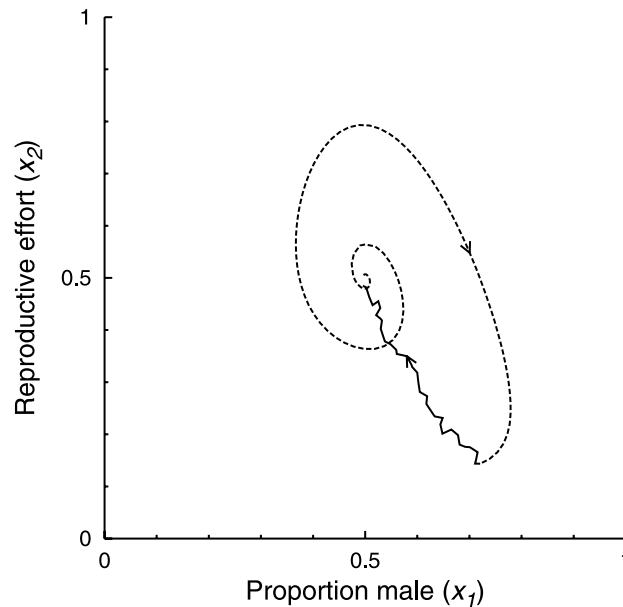


Fig. 3. Gradualistic, adaptive paths in the trait space of an iteroparous hermaphrodite. The point $x^* = (0.5, 0.5)$, with equal allocation to male and female function and 50% yearly survival, is strongly convergence stable and uninvadable, and thus a CSS. Nevertheless, for very special mutational distributions, an adaptive escape starting from nearby the point is possible, as exemplified by the dashed path. By instead letting mutational increments in any direction be equally likely, there is prompt convergence to x^* , as illustrated by the solid path.

stability criteria that define a fairly large expanse of middle ground, between being restrictive enough to ensure stability for more than some very special types of mutational genetic variation and being lenient enough to have a chance to be satisfied in the kinds of situations one wants to analyse. I suggest that strong convergence stability is such a valuable middle-ground criterion. Absolute convergence stability, on the other hand, is so demanding for multidimensional trait spaces that it will often not apply. Nevertheless, for the analysis of many models of simple structure, absolute convergence stability can still be a very useful tool (e.g. Van Dooren and Leimar, 2003; Leimar *et al.*, 2004).

It is worth noting the difference between the perspective presented here and the so-called ‘streetcar theory of evolution’ (Hammerstein and Selten, 1994; Hammerstein 1996; Marrow *et al.*, 1996b). A main aim of the streetcar theory is to show that purely phenotypic, fitness-based criteria can be used to determine ‘final stops’ of an evolutionary process, valid for quite general underlying genetic mechanisms. The streetcar theory succeeds in this aim by limiting consideration to the uninvadability of points in trait space.

However, convergence stability would appear to be of equal, if not greater, relevance to the long-term outcomes of evolutionary processes. A natural question, then, is whether there are purely phenotypic criteria determining final stops also with regard to convergence stability (Weissing, 1996). Taking into account the quite realistic scenario of multidimensional trait spaces with general fitness interactions, my analysis of absolute convergence stability shows that any purely fitness-based convergence stability criterion must be so restrictive that

there will often be no final stops of this kind. With general fitness interactions, one should not expect the Jacobian of the selection gradient to be symmetric at a singular point, from which follows that an adaptive escape from a neighbourhood of the point will be possible (cf. Fig. 3).

In fact, the typical situation for general fitness interactions may well be that for any two points in trait space, there will be gradualistic, adaptive paths starting nearby the first and passing nearby the second, and similarly from the second to the first (Leimar, 2001). Since some of these adaptive paths would be realized only if ‘Darwinian demons’ were to supply precisely the required pleiotropic mutations, whereas for naturally occurring mutational processes such paths are extremely unlikely, it is clear that one needs to include some genetics in phenotypic modelling.

In particular, one needs to take into account the effects of inter-trait genetic correlations on evolutionary stability. The value of the concept of strong convergence stability is that it guarantees stability for arguably the most important situation, where such genetic correlations vary in a gradual fashion. This makes it the main criterion of convergence stability in multidimensional trait spaces.

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APPENDIX

Taylor expansion of the selection gradient

To derive the expansion (8, 9), first note that around a singular point $x = x^*$ the component (1) of the selection gradient has the Taylor expansion

$$(\nabla'_k F_k(x_k, x))_i = \sum_l \sum_j \frac{\partial}{\partial x_{lj}} \left(\frac{\partial F_k}{\partial x'_{ki}} \Big|_{x'_k = x_k} \right) \Big|_{x = x^*} (x_{lj} - x^*_{lj}) + \dots$$

Evaluating the derivative with respect to x_{lj} , and using notation from (7) and (10), we can write this as

$$\nabla'_k F_k(x_k, x) = \mathbf{H}_{kk}(x_k - x^*_k) + \sum_l \mathbf{Q}_{kl}(x_l - x^*_l) + \dots$$

Thus, the Taylor expansion of the selection gradient around x^* is

$$\nabla' F(x, x) = (\mathbf{H} + \mathbf{Q})(x - x^*) + \dots$$

Matrix algebra results

For a linearized adaptive dynamics of the form

$$\frac{d}{dt} z = \mathbf{A}\mathbf{J}z,$$

it is of interest to characterize the set of matrices \mathbf{J} having the property that the eigenvalues of $\mathbf{A}\mathbf{J}$ have negative real parts for any matrix \mathbf{A} from some subset of the positive definite matrices. The following two results are relevant for the case of a single species:

1. For \mathbf{J} negative definite and \mathbf{A} symmetric and positive definite, all eigenvalues of $\mathbf{A}\mathbf{J}$ have negative real parts, whereas if \mathbf{J} is not negative semidefinite, there is some symmetric, positive definite \mathbf{A} such that some eigenvalue of $\mathbf{A}\mathbf{J}$ has positive real part.
2. For \mathbf{J} symmetric and negative definite and \mathbf{A} positive definite, all eigenvalues of $\mathbf{A}\mathbf{J}$ have negative real parts, whereas if \mathbf{J} is not symmetric, there is some positive definite \mathbf{A} such that some eigenvalue of $\mathbf{A}\mathbf{J}$ has positive real part.

The first result is due to Hines (1980) and Cressman and Hines (1984). For the second result, here is a quick sketch of a proof. The first implication follows by noting that $-z^T \mathbf{J} z$ is a Lyapunov function for the linearized dynamics. For the second implication, to any non-symmetric matrix \mathbf{J} one can readily construct a positive definite \mathbf{A} , by adding a suitable antisymmetric part to the identity matrix (which has no effect on positive definiteness), such

that the trace of \mathbf{AJ} becomes positive, implying that some eigenvalue of \mathbf{AJ} must have positive real part.

Two-dimensional trait spaces

For two-dimensional trait spaces, corresponding to either a single species with two traits or a co-evolutionary case of two species, each with a single trait, detailed stability criteria for the canonical equation are easy to derive. For the linearized canonical equation (11), with \mathbf{A} and \mathbf{J} two-by-two matrices, both eigenvalues of \mathbf{AJ} have negative real parts if and only if $\det(\mathbf{AJ}) = \det(\mathbf{A})\det(\mathbf{J}) > 0$ and $\text{tr}(\mathbf{AJ}) < 0$. Since $\det(\mathbf{A}) > 0$ for a symmetric, positive definite \mathbf{A} , we have

$$\det(\mathbf{J}) > 0 \quad (\text{A1})$$

as the first part of a criterion for negative real parts of the eigenvalues of \mathbf{AJ} . Let $\mathbf{J}^s = (\mathbf{J} + \mathbf{J}^T)/2$ denote the symmetric part of \mathbf{J} . Since \mathbf{A} is symmetric, $\text{tr}(\mathbf{AJ}) = \text{tr}(\mathbf{AJ}^s)$, and we have

$$\text{tr}(\mathbf{AJ}^s) = \mathbf{A}_{11}\mathbf{J}_{11} + \mathbf{A}_{22}\mathbf{J}_{22} + \mathbf{A}_{12}(\mathbf{J}_{12} + \mathbf{J}_{21}) < 0 \quad (\text{A2})$$

as the second part of the criterion. Let us look more closely at (A2).

A single species: The mutational matrix \mathbf{A} can be any symmetric, positive definite matrix. By noting that the symmetric matrix \mathbf{J}^s can be diagonalized by an orthogonal transformation, and that $\text{tr}(\mathbf{AJ}^s)$ is invariant under the transformation, we arrive at three cases. First, for a negative definite \mathbf{J} , i.e. when both (real) eigenvalues of \mathbf{J}^s are negative, (A2) holds for all these \mathbf{A} . Second, when only one eigenvalue of \mathbf{J}^s is negative, (A2) holds for some but, if the other eigenvalue is positive, not all of these \mathbf{A} . Third, when neither of the eigenvalues of \mathbf{J}^s is negative, none of these \mathbf{A} satisfy (A2). Note that the first of the cases implies strong convergence stability: for a negative definite \mathbf{J} , both (A1) and (A2) must hold.

Two species: The mutational matrix \mathbf{A} can be any diagonal matrix with positive diagonal elements. For such \mathbf{A} , (A2) becomes

$$\mathbf{A}_{11}\mathbf{J}_{11} + \mathbf{A}_{22}\mathbf{J}_{22} < 0. \quad (\text{A3})$$

First, if both \mathbf{J}_{11} and \mathbf{J}_{22} are negative, (A3) holds for all these \mathbf{A} . Second, if only one of \mathbf{J}_{11} and \mathbf{J}_{22} is negative, (A3) holds for some but, if the other \mathbf{J}_{kk} is positive, not all of these \mathbf{A} . Third, if neither \mathbf{J}_{11} nor \mathbf{J}_{22} is negative, none of these \mathbf{A} satisfy (A3). Note that the first of the cases, together with (A1), implies co-evolutionary strong convergence stability.

Example: Hermaphrodite sex allocation and reproductive effort

Consider an iteroparous hermaphrodite with two traits: allocation to male function ($0 \leq x_1 \leq 1$) and reproductive effort ($0 \leq x_2 \leq 1$). For a mutant x' in a population with x , reproductive success is proportional to

$$W(x', x) = \frac{(x'_1 x'_2)^a}{(x_1 x_2)^a} ((1 - x_1)x_2)^b + ((1 - x'_1)x'_2)^b + (1 - x'_2),$$

where the three terms are success as male, success as female, and survival to next year (the expression is a combination of the standard division of the current-year reproduction R

into male and female function and the form, $W = R + S$, where S is survival to next year, often used to study iteroparity vs. semelparity). The parameters a and b allow for non-linear relations between investment in male and female function and reproductive success, describing phenomena such as diminishing returns on investment and the degree to which success as one sex is obtained at the expense of success as the other sex. With $a, b < 1$, hermaphroditism is usually regarded as stable (Charnov, 1982). Taking fitness to be $F(x', x) = \log W(x', x) - \log W(x, x)$, the selection gradient is $\nabla' F(x, x) = \nabla' W(x, x) / W(x, x)$. With $a = b = 0.5$, there is a singular point at $x^* = (0.5, 0.5)$. Performing two separate one-dimensional analyses, one can see that, for any fixed reproductive effort, the allocation $x_1^* = 0.5$ is continuously stable and, regarding this allocation as fixed, the reproductive effort $x_2^* = 0.5$ is continuously stable (actually, a global optimum). For a two-dimensional analysis, the selection Hessian (7), the matrix \mathbf{Q} in (10), and the Jacobian (9) of the selection gradient are easily computed at x^* :

$$\mathbf{H} = \frac{2}{3} \begin{pmatrix} -1 & 0 \\ 0 & -1 \end{pmatrix} \quad \mathbf{Q} = \frac{2}{3} \begin{pmatrix} -1 & 0 \\ -1 & 0 \end{pmatrix} \quad \mathbf{J} = \mathbf{H} + \mathbf{Q} = \frac{2}{3} \begin{pmatrix} -2 & 0 \\ -1 & -1 \end{pmatrix}.$$

Since \mathbf{H} and \mathbf{J} are negative definite, we conclude that the point is locally uninvadable and strongly convergence stable, and thus a (multidimensional) CSS.

However, the Jacobian is not symmetric, which implies that there is some positive definite \mathbf{A} such that \mathbf{AJ} has some eigenvalue with positive real part (matrix algebra result 2 above). For instance, with

$$\mathbf{A} = \begin{pmatrix} 1 & -5 \\ 5 & 1 \end{pmatrix} \quad \mathbf{AJ} = \frac{2}{3} \begin{pmatrix} 3 & 5 \\ -11 & -1 \end{pmatrix},$$

the eigenvalues of \mathbf{AJ} are $\lambda = \frac{2}{3}(1 \pm i\sqrt{51})$, which means that if mutations in the direction $\mathbf{AJ}(x - x^*)$ predominate, an adaptive escape from x^* occurs (Fig. 3).