

## Evolutionary Change and Darwinian Demons

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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. By introducing an imaginary 'Darwinian demon' in charge of mutations, one can examine the maximal role that mutation could play in determining evolutionary change. Taking into account pleiotropic mutations and shifting fitness landscapes, it seems likely that a Darwinian demon could exert considerable influence and most likely would be able to produce any viable form of organism. This kind of perspective can be helpful in clarifying concepts of evolutionary stability.

**Keywords:** Mutation, selection, adaptation, evolutionary stability, convergence stability

### 1. Introduction

The idea of spontaneous production of new heritable variants which may differ in reproductive success is fundamental in Darwin's theory of natural selection. Mutations are often thought of as random, primarily in the general sense of being independent of whatever modification of function they may cause, but also in the particular sense of following some distribution. At the same time, there is an emphasis on selection as the process responsible for the appearance of function, so that mutation plays the role of providing raw material for selection to act on. It is common that explanations of evolutionary change are formulated only in terms of selection and that mutation is treated as a relatively uninteresting background process.

New variants arising independently of their function is a feature which distinguishes Darwinism from Lamarckism and which has long been accepted as empirically valid. Even so it is still of

interest to examine, as a matter of principle, what the relative roles of mutation and selection can be in determining evolutionary change. Such an examination can increase our awareness of the role the mutational process might play in directing evolution. It could also help sharpen our concepts of evolutionary stability, which traditionally have been formulated in terms of selection only. In general, the evolutionary stability of some trait combination may depend on the mutational process.

To gain an understanding of the potential role of mutations, it can be illustrative to think in terms of the ability of a 'Darwinian demon' to influence evolutionary change. A Darwinian demon is a hypothetical being with power to decide exactly which mutations appear, but without any influence over the ensuing natural selection. The name is coined in analogy with the famous Maxwell's demon, whose activities of selectively letting fast and slow gas molecules pass between two compartments were aimed at violating the second law of thermodynamics (Maxwell, 1908). A Darwinian demon does not violate any law of nature, but shares with Maxwell's demon an uncanny ability

to be informed about the world together with an inclination towards mischief. One can then ask how much of an influence a Darwinian demon could have over the outcome of evolutionary change. Is it perhaps the case that the demon could, in a somewhat roundabout fashion, produce essentially any forms of organisms in whatever combination, or would the influence of the demon be restricted to relatively minor modifications? My conclusion here will be that the former case, with great influence for the demon, is closer to the truth.

A single mutation often affects several traits of an organism. This phenomenon is called pleiotropy and implies that changes in several traits are selected as a unit. A modification of one trait, which might be disfavoured by selection on its own, could then be pulled along by a favoured modification of another trait. Pleiotropy greatly increases the possibilities for a Darwinian demon. Another factor working in the demon's favour will be fitness interactions among traits. Fitness interactions are present when the strength and possibly also the direction of selection acting on variation in one trait depend on other traits in a population. The importance of fitness interactions is that they correspond to a shifting fitness landscape.

In the following, I will bring up a few points about the importance of pleiotropy and fitness interactions for evolutionary change. The modelling framework I will use is that of mutation-limited adaptive dynamics in large populations (Metz et al., 1996; Geritz et al., 1998), where a succession of mutations either fail to invade or go to fixation, or possibly produce additional polymorphism. Evolution is then a sequence of fixations, each happening by natural selection. This corresponds to a long-term perspective on evolutionary change.

The general idea that an analysis of fitness differences is not enough to understand evolutionary change and stability is not new to my treatment here, but has been explored a number of times (e.g. Lande, 1981; Friedman, 1991; Pomiankowski et al., 1991; Abrams et al., 1993; Motro, 1994; Marrow et al., 1996; Eshel et al., 1997), including the idea that mutation can have a qualitative influence on the outcome of evolution (Matessi and Di Pasquale, 1996). Compared to earlier work, my emphasis will be on considering all changes that are consistent with natural selection, corresponding

to the concept of a Darwinian demon, rather than on the question of which changes are expected given some mutational process. Thus, my intention is not to study which changes are most likely to happen, but rather to study which changes are possible.

## 2. Gradual change and trait space dimensionality

Many mutations that are fixed during evolution have small effects whereas others have larger effects. The importance of differently sized mutations for evolutionary change has been debated (e.g. Orr, 1998), but here I will limit the presentation to small effects. Allowing also larger effects would of course increase the possibilities for a Darwinian demon. Note first that in a one-dimensional trait space, the direction of gradual change is entirely determined by selection. If  $x$  is a phenotype that is not a local fitness extremum and  $\Delta x$  is a small increment, then either the phenotype  $x + \Delta x$  or the phenotype  $x - \Delta x$ , but not both of them, will be able to replace  $x$ . Thus, mutations cannot influence the direction of gradual change in a one-dimensional trait space; they can only influence the rate at which changes occur. The situation is drastically different when there are two or more traits, corresponding to a multidimensional space. Looking at a fitness landscape in the vicinity of some phenotype vector  $x$ , any small increment vector  $\Delta x$  that points in an uphill direction is a modification that would be favoured by selection. This uphill requirement becomes less of a constraint on change the higher the number of dimensions of the space. If we think of the trait combination that corresponds to the steepest slope of the local landscape as an abstract trait, only this trait is selected for and the rest will change because of pleiotropy. For high numbers of traits, selection thus appears rather weak in directing evolution.

When moving uphill in a fitness landscape of fixed shape, an evolutionary sequence would eventually come to a fitness peak from which no further change is possible. Although the peak could be reached by a multitude of different paths that are uphill every step of the way, the long-term outcome is not influenced by pleiotropy, apart from a possible choice between different peaks to climb.

Thus, it is not so much the local structure of a fitness landscape that constrains evolution but rather the global properties. A fixed landscape contains many regions whose borders can only be crossed by adaptive evolution in the inward direction; all regions defined by fitness being above a given level are of this kind. Some shifting landscapes can in principle also have this property, but it seems reasonable to doubt that most would have it. On the other hand, if there are few or no regions in the trait space from which an adaptive evolutionary sequence cannot escape, adaptive change can range widely over the space.

### 2.1. Invasion fitness and the selection gradient

To shed some light on the properties of fitness landscapes that determine the possible range of gradual adaptive change, we can look at the case of a single large monomorphic population with multidimensional trait space. For a trait vector  $x$  of the resident population, with component traits  $x_i$ , the invasion fitness of a mutant  $x'$  is given by  $F(x', x)$ . Invasion fitness plays the role of determining with what probability a mutant can invade and corresponds to the mean rate of change of the logarithm of the size of the mutant gene subpopulation (Metz et al., 1992; Rand et al., 1994; Ferriere and Gatto, 1995; Dieckmann and Law, 1996). When the mutant is the same as the resident, the rate of change is zero, so that  $F(x, x) = 0$  must hold. A mutant with  $F(x', x) < 0$  has no chance of invading whereas one with  $F(x', x) > 0$  has a positive probability of invasion. If in addition  $F(x, x') < 0$ , the mutant can drive the previous resident to extinction, so that substitution may take place. To study gradual change one can introduce the selection gradient  $\nabla'F$ , whose  $i$ th component is

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

The selection gradient is sometimes called selection derivative (Marrow et al., 1992) or selective pressure (Rand et al., 1994) and indicates the direction of steepest slope of the local fitness landscape. A point in the trait space where the selection gradient is zero is called singular. For a non-singular point  $x$  and a mutant  $x'$  close to  $x$ , Taylor expansion

of  $F(x', x)$  shows that  $x'$  has a chance to invade when the first order increment in fitness

$$\sum \nabla'_i F(x, x)(x'_i - x_i) \quad (2)$$

is positive, whereas the mutant cannot invade when the increment is negative.

For a fitness landscape of fixed shape the selection gradient becomes an ordinary gradient of some function defined on the trait space. For instance, with invasion fitness of the form  $F(x', x) = R(x') - R(x)$  we have  $\nabla'F(x, x) = \nabla R(x)$ , where  $\nabla_i R(x) = \partial R(x) / \partial x_i$ . In this case evolutionary change can only be towards increasing  $R(x)$ . More generally, if the selection gradient is proportional to the gradient of a function  $R(x)$ , so that  $\nabla'F(x, x) = p(x)\nabla R(x)$  for some positive  $p(x)$ , gradual change must increase  $R(x)$ . On the other hand, it is hard to see what could limit the range of possible adaptive change when the selection gradient cannot be expressed as proportional to some  $\nabla R(x)$ . Fitness interactions, where the fitness increments associated with variation in a mutant trait  $x'_i$  depend on a resident trait  $x_j$ , can make it impossible to express  $\nabla'F$  in such a form.

### 2.2. Examples of demonic evolution

To give a perspective on the concept of evolutionary stability for matrix games (Maynard Smith, 1982), let  $x = (x_1, x_2, x_3)$  be a mixed strategy for the Rock–Scissors–Paper game in Table 1. There must be at least three pure strategies in a matrix game for a genuinely multidimensional trait space, since the components of  $x$  sum to one. For the RSP game, it is easy to show that the strategy  $x^* = (\frac{1}{3}, \frac{1}{3}, \frac{1}{3})$  is an ESS, provided that the parameter  $a$  is positive. For  $a = 0$ , which corresponds to the ‘original’ game,  $x^*$  is only neutrally stable (Maynard Smith, 1982) and for negative  $a$  the point is unstable. From the payoff function

$$W(x', x) = \sum x'_i u_{ij} x_j,$$

where the  $u_{ij}$  are the payoffs in Table 1, we can construct an invasion fitness of the form

$$F(x', x) = \log(W(x', x)/W(x, x)).$$

TABLE 1

Payoff matrix for a generalised Rock–Scissors–Paper game

	R	S	P
R	1	$2+a$	0
S	0	1	$2+a$
P	$2+a$	0	1

The evolutionary sequences in Figure 1 (where  $a = 2$ ) illustrate that there is convergence to the ESS both when moving along the selection gradient and when mutational increments are randomly directed. Nevertheless, a Darwinian demon could easily arrange an adaptive escape, starting from nearby the ESS, for instance along the bold curve in Figure 1.

The possibility of an adaptive escape depends on the form of the selection gradient. For a matrix game with three pure strategies, one finds that the selection gradient is proportional to the gradient of some function  $R(x)$  when the payoffs satisfy

$$u_{12} + u_{23} + u_{31} = u_{13} + u_{21} + u_{32},$$

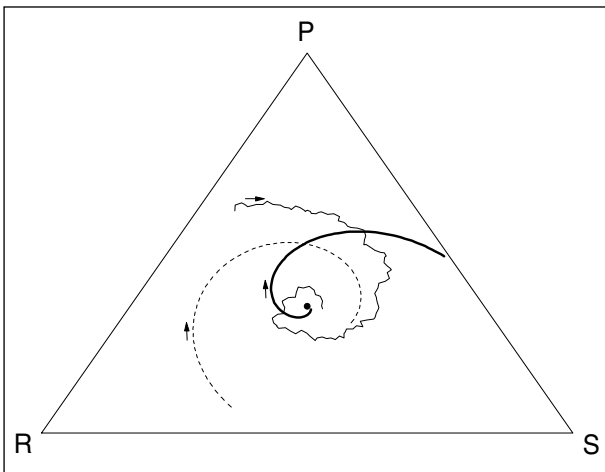


FIG. 1. Trajectories of gradual adaptive change for a Rock–Scissors–Paper game. For the payoff parameters used (Table 1 with  $a = 2$ ) the mixed strategy phenotype  $x^* = (\frac{1}{3}, \frac{1}{3}, \frac{1}{3})$ , shown by the filled dot, is an ESS. The trajectories consist of sequences of small but finite increments, each corresponding to the fixation of a mutant, and the arrows show the direction of change. For the dashed curve, which converges to the ESS, each increment is in the direction of the selection gradient. The thin solid curve also converges to the ESS and is the result of generating randomly directed mutational increments. The thick solid curve illustrates an adaptive escape from the neighbourhood of the ESS

which becomes  $a = -2$  for the payoffs in Table 1. The selection gradient is then proportional to the gradient of  $R(x) = x_1^2 + x_2^2 + x_3^2$ . In this particular case of  $a = -2$ , all gradual change must increase  $R(x)$  and thus be directed away from  $x^*$ . For all other values of  $a$ , the Jacobian of the selection gradient will be non-symmetric at  $x^*$  and one can show that there will be adaptive trajectories both leading away from and leading towards  $x^*$ .

The phenomenon of adaptive escape from the neighbourhood of suggested stable points is not limited to the special fitness landscapes of matrix games. In a stylised example of life-history evolution (Fig. 2), the productive trait  $x_1$  could be the size of the crown of a tree and the competitive trait  $x_2$  the height of the trunk. With  $W(x', x) = P(x')Q(x', x)$ , where  $P(x')$  is survival from ger-

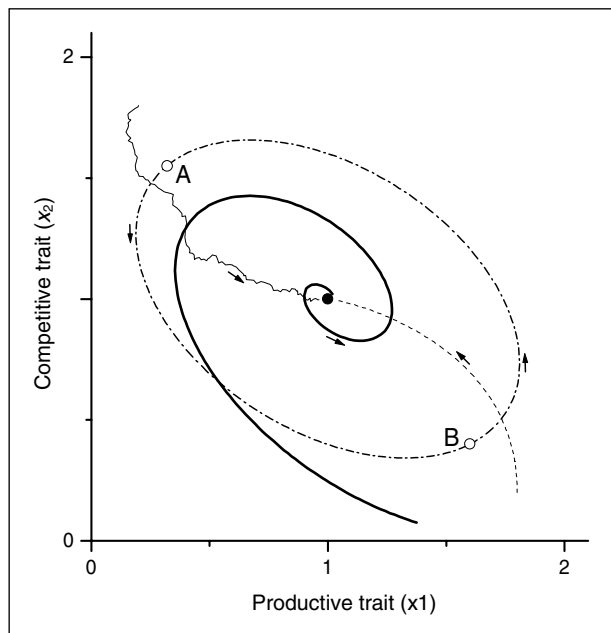


FIG. 2. Trajectories of adaptive change for two life-history traits:  $x_1$  is an investment in productive capacity and  $x_2$  an investment in competitive ability (see text). The point  $x^* = (1,1)$ , shown by the filled dot, is uninvadable and strongly convergence stable. The trajectories consist of sequences of small increments, corresponding to the fixation of mutants, and the arrows show the direction of change. The dashed curve follows the selection gradient and the thin solid curve is produced from randomly directed mutational increments; both these curves converge to  $x^*$ . The thick solid curve is an adaptive escape from the neighbourhood of  $x^*$  and the dash-dotted circuit illustrates that, for arbitrary points A and B, there are adaptive paths leading from A to B and back

minating seed to adult plant and  $Q(x', x)$  the seed production, the fitness  $F(x', x) = \log(W(x', x)/W(x, x))$  corresponds to discrete generations and regulation of the size of the population of germinating seeds. Using

$$P(x') = e^{-\frac{1}{2}(x'_1+x'_2-1)^2} \quad \text{and} \quad Q(x', x) = e^{x'_1(1+x'_2-x_2)},$$

a mutant's seed production depends on its competitive investment in relation to the residents. We then have the fitness gradient  $\nabla'F = (2-x_1-x_2, 1-x_2)$  which is zero at  $x^* = (1, 1)$ . This singular point is clearly uninvadable and also possesses some convergence stability. From the criterion of negative definiteness of the Jacobian matrix of the selection gradient,  $x^*$  is strongly convergence stable (Leimar, 2002), which means that it will attract solutions of the so-called canonical equation (Dieckmann and Law, 1996). Also, performing two separate one-dimensional analyses, one finds that  $x_1 = 2 - x_2$  is a global fitness maximum for  $x_1$  with  $x_2$  held fixed and that  $x_2 = 1$  is a global fitness maximum for  $x_2$  with  $x_1$  held fixed. Although there seems to be little reason to worry about the stability of  $x^*$ , a Darwinian demon could in fact produce an adaptive escape from the neighbourhood of  $x^*$  (Fig. 2; see also appendix). The reason is that the Jacobian matrix of the selection gradient is non-symmetric at  $x^*$ , which means that the selection gradient cannot be approximated as proportional to the gradient of some  $R(x)$  near  $x^*$ .

### 2.3. Invariance under adaptive change

It can be useful to think in terms of subsets of the trait space that are invariant under adaptive change, in the sense that any adaptive sequence starting in such a subset cannot leave it. For the life-history example, the point  $x^*$  is invariant under adaptive change, but there is only one other such set, namely the entire trait space. Barring extinction of the population, there are adaptive trajectories leading from any point except  $x^*$  to any other point in the trait space (see Fig. 2). This situation may be fairly typical, although it is not universal. One important exception would be trait spaces with boundaries forming corners, as in Figure 1. If the

selection gradient points in the general direction of a corner, there may be no adaptive trajectories leading away from it. For the RSP game, this happens for  $a \leq -2$ .

## 3. Absolute convergence stability

An absolutely convergence stable point is a local attractor for all gradual adaptive change. For fitness landscapes of fixed shape, the local fitness maxima are absolutely convergence stable. For shifting fitness landscapes, we wish to find conditions on the fitness function ensuring that any gradualistic adaptive sequence starting near to the point will converge to it. From our previous reasoning, it is clear that if the selection gradient can be expressed as

$$\nabla'F(x, x) = p(x)\nabla R(x), \quad (3)$$

where  $p(x)$  is positive and  $R(x)$  has a local maximum at  $x^*$ , then this point is absolutely convergence stable. To search for a condition expressed in fitness derivatives, we can look at the Taylor expansion of the selection gradient around  $x^*$ . We can write the expansion as

$$\nabla'_i F(x, x) \approx \sum J_{ij}(x_j - x_j^*), \quad (4)$$

where the  $J_{ij}$  are the elements of the so-called Jacobian matrix. For selection gradients of the form (3), it is easy to see that the Jacobian at  $x^*$  will be a symmetric matrix. More generally, if the Jacobian is symmetric and negative definite we can use the quadratic form

$$\sum J_{ij}(x_i - x_i^*)(x_j - x_j^*)$$

as  $R(x)$ , so that (3) holds to first order. On the other hand, a singular point for which the Jacobian of the selection gradient is non-symmetric cannot be absolutely convergence stable, which follows from a simple matrix algebra result (see appendix).

### 3.1. Stability criterion

We can then formulate a stability criterion: For the singular point  $x^*$  to be absolutely convergence

stable, it is necessary that the Jacobian of the selection gradient at  $x^*$  is symmetric and sufficient that it is symmetric and negative definite. Note that the argument for the sufficient condition is that there is an  $R(x)$  such that (3) holds to first order near  $x^*$ , which means that the criterion is approximate in this sense.

For one-dimensional trait spaces, absolute convergence stability is the same as traditional convergence stability (Eshel and Motro, 1981; Eshel, 1983; Taylor, 1989; Christiansen, 1991). However, with two or more traits the Jacobian will not be symmetric unless fitness interactions are absent or have a very special form. Thus, absolute convergence stability is a very strict requirement and is of limited practical use for adaptive dynamics modelling. The main importance of the concept lies in clarifying how we would need to define convergence stability if we wanted to avoid assumptions about the mutational process.

Absolute convergence stability does not guarantee complete evolutionary stability. Apart from the possibility of invasion by large effect mutants, there can also be evolutionary branching at such a point (Christiansen, 1991; Geritz et al., 1998). Since one-dimensional convergence stability implies absolute convergence stability, any branching in a one-dimensional trait space is an example of this.

### 3.2. Product rules

There are special classes of simple fitness functions that are used in modelling and for which absolute convergence stability is a natural stability criterion. The most well-known such case is the application of product rules in sex allocation theory. This approach was initiated by MacArthur (1965) and has since been widely used (e.g. Charnov, 1982; Pen and Weissing, 2002). With an expression for reproductive success of a mutant  $x'$  in the Shaw and Mohler (1953) form

$$W(x', x) \propto \frac{m(x')}{m(x)} + \frac{f(x')}{f(x)},$$

where  $m$  and  $f$  are reproductive success through male and female function, the fitness gradient can be written in the form (3) using the product  $m(x)f(x)$ , or the logarithm of this product, as  $R(x)$ . The product rule is to find stable sex alloca-

tion equilibria as maxima of  $m(x)f(x)$  and these points will then be absolutely convergence stable. In general, with an expression for reproductive success of the form

$$W(x', x) \propto \sum_k \frac{w_k(x')}{w_k(x)}$$

there is a product rule, which will locate absolutely convergence stable equilibria. Such expressions for fitness can be useful when a modeller wants to simplify a phenomenon as much as possible.

## 4. Discussion

The combination of pleiotropic mutations and shifting fitness landscapes can evidently have a strong impact on the range of possible adaptive change. For the technical issue of which criteria for evolutionary stability will be most useful, it is clear that concepts of convergence stability need to involve genetic correlations in some way. Absolute convergence stability is extreme in this regard, allowing for any kind of changing pattern of correlations. A probably more useful concept is strong convergence stability (Leimar, 2002), which entails convergence for any constant or slowly varying correlation structure. A sufficient condition for strong convergence stability is that the symmetric part of the Jacobian matrix of the selection gradient is negative definite, but the Jacobian matrix need not be symmetric (Leimar, 2002). This condition is a summary and generalisation of previous work on stability criteria (e.g. Lessard, 1990; Abrams et al., 1993; Marrow et al., 1996; Matessi and Di Pasquale, 1996). Depending on the kind of adaptive dynamics one studies, there are of course a great number of stability issues and dynamical phenomena to consider, and this field is now quite advanced (Hofbauer and Sigmund, 1998).

In thinking about evolutionary stability, the concept of uninvadability has traditionally played a greater role than convergence stability. For instance, the arguments used by Maynard Smith to motivate the definition of an ESS for a matrix game were formulated in terms of uninvadability (Maynard Smith, 1982), although such an ESS also possesses convergence stability (it is in fact strongly convergence stable; cf. Fig. 1). The so-called streetcar theory of evolution (Hammerstein

and Selten, 1994; Hammerstein, 1996; Marrow et al., 1996) also focuses on uninvasibility. A main aim of this 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. While it is certainly correct that uninvasible points in trait space are invariant under adaptive change, a possible problem with this perspective is that unavoidable perturbations would prevent populations from staying precisely at any particular point in trait space. As long as the trait space is fairly fine grained it seems that convergence stability must be an essential component of evolutionary stability.

Concerning the possible influence of a Darwinian demon, the conclusion seems to be that such a creature could transform the earth’s biota at will, bringing about an arbitrary collection of strange organisms. The mutations used by the demon for this purpose would of course not be random, but they need not be directed in the sense of having a non-zero average effect. By employing pairs of mutational increments, of equal magnitude but in opposite directions, only one of which would have a chance to invade, a demon could work without exerting an average mutation pressure. This demonstrates that the important effect of mutations in directing evolution derive from genetic correlations between traits.

The image of a Darwinian demon controlling the long-term outcome of evolution shows that it is logically possible to relegate natural selection to the position of a relatively uninteresting background process. For real evolution it would certainly be wrong to do so, but it is worthwhile to realise that the role played by mutations in determining large scale evolutionary change can in principle be anything from very small to very big.

## APPENDIX

Use the terminology that a non-symmetric matrix  $\mathbf{A}$  is positive definite if its symmetric part  $\frac{1}{2}(\mathbf{A} + \mathbf{A}^T)$  is positive definite. We have the following result: For any non-symmetric  $n \times n$  matrix  $\mathbf{J}$  there is a positive definite  $n \times n$  matrix  $\mathbf{A}$  such that at least one eigenvalue of  $\mathbf{AJ}$  has positive real part.

The idea for the proof is to find an  $\mathbf{A}$  which makes the trace of  $\mathbf{AJ}$  positive. Since the trace of a matrix equals the sum of its eigenvalues, a positive trace means that some eigenvalue must have positive real part. Since  $\mathbf{J}$  is not symmetric, there must be some  $k$  and  $l$  with  $k \neq l$  such that  $J_{kl} < J_{lk}$ . Consider  $\mathbf{A}$  of the form  $\mathbf{A} = \mathbf{I} + \mathbf{G}$ , where  $\mathbf{I}$  is the identity matrix and all elements of  $\mathbf{G}$  are zero except  $G_{kl} = -G_{lk} = g$ . Clearly,  $\mathbf{A}$  is positive definite. One readily verifies that the trace of  $\mathbf{AJ}$  becomes positive if  $g$  is chosen large enough.

To come to the issue of convergence stability, note from (2) that the mutational increments  $\Delta x = x' - x$  constructed as

$$\Delta x_i = \varepsilon \sum A_{ij} \nabla'_j F$$

have a positive probability of invasion when  $\mathbf{A}$  is positive definite and  $\varepsilon > 0$  is small. Close to a singular point, where the approximation (4) is valid, we then have the dynamics

$$\Delta x_i = \varepsilon \sum A_{ij} J_{jk} (x_k - x_k^*).$$

For small enough  $\varepsilon$ , the stability of  $x^*$  for this dynamics is determined by the signs of the real parts of the eigenvalues of  $\mathbf{AJ}$ . If  $\mathbf{J}$  is non-symmetric, the result above thus shows that we can choose an  $\mathbf{A}$  that makes  $x^*$  unstable.

The ‘demonic trajectories’ in the examples (Figs 1 and 2) were in fact constructed using this kind of matrix  $\mathbf{A}$ . For instance, to construct the adaptive escape (bold curve) in Figure 2, the positive definite matrix

$$\mathbf{A} = \begin{pmatrix} 1 & 4 \\ -4 & 1 \end{pmatrix}$$

was used to generate mutational increments.

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