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Evolutionary Optimisation Models and Matrix Games in the Unified Perspective of Adaptive Dynamics

G. MESZÉNA,[1*] É. KISDI,[2,3] U. DIECKMANN,[4] S. A. H. GERITZ[2] and J. A. J. METZ[5,4]

[1]*Department of Biological Physics, Eötvös University, Budapest, Hungary,*
[2]*Department of Mathematics, University of Turku, Turku, Finland,*
[3]*Department of Genetics, Eötvös University, Budapest, Hungary,*
[4]*Adaptive Dynamics Network, International Institute for Applied Systems Analysis, Laxenburg, Austria,*
[5]*Section Theoretical Evolutionary Biology, Institute of Evolutionary and Ecological Sciences (EEW), Leiden University, Leiden, The Netherlands*

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Matrix game theory and optimisation models offer two radically different perspectives on the outcome of evolution. Optimisation models consider frequency-independent selection and envisage evolution as a hill-climbing process on a constant fitness landscape, with the optimal strategy corresponding to the fitness maximum. By contrast, in evolutionary matrix games selection is frequency-dependent and leads to fitness equality among alternative strategies once an evolutionarily stable strategy has been established. In this review we demonstrate that both optimisation models and matrix games represent limiting cases of the general framework of nonlinear frequency-dependent selection. Adaptive dynamics theory considers arbitrary nonlinear frequency and density dependence and envisages evolution as proceeding on an adaptive landscape that changes its shape according to which strategies are present in the population. In adaptive dynamics, evolutionarily stable strategies correspond to conditional fitness maxima: the ESS is characterised by the fact that it has the highest fitness if it is the established strategy. In this framework it can also be shown that dynamical attainability, evolutionary stability, and invading potential of strategies are pairwise independent properties. In optimisation models, on the other hand, these properties become linked such that the optimal strategy is always attracting, evolutionarily stable and can invade any other strategy. In matrix games fitness is a linear function of the potentially invading strategy and can thus never exhibit an interior maximum: Instead, the fitness landscape is a plane that becomes horizontal once the ESS is established. Due to this degeneracy, invading potential is part of the ESS definition for matrix games and dynamical attainability is a dependent property. We conclude that nonlinear frequency-dependent theory provides a unifying framework for overcoming the traditional divide between evolutionary optimisation models and matrix games.

Keywords: Evolution, adaptive dynamics, ESS, fitness landscapes, matrix games, optimisation models, frequency-dependent selection

1. Introduction

Evolutionary optimisation and matrix game theory are two of the main conceptual frameworks in evolutionary ecology. Both have been powerful in shaping research hypotheses for empirical work as well as in analysing theoretical models, and both frameworks are deeply rooted in modern evolutionary biology. Nevertheless, these approaches offer two different, and often conflicting, perspectives on the expected outcomes of evolutionary processes.

Optimisation theory is a straightforward, if narrow, formalisation of Darwin's idea of natural selection as the 'preservation of favourable variations and the rejection of injurious variations' (Darwin, 1859). In optimisation theory, a measure

* Corresponding author: Géza Meszéna, Department of Biological Physics, Eötvös University, H-1117 Budapest, Pázmány Péter sétány 1A, Hungary, E-mail: geza.meszena@elte.hu

of fitness is directly attached to each heritable variant, henceforth called strategy. Strategies with higher fitness outcompete strategies with lower fitness and eventually the strategy with the highest fitness, called the 'optimal' strategy, takes over the population (see e.g. Maynard Smith, 1989). This process of optimisation can be envisaged to take place on some fixed adaptive landscape (Wright, 1931; Lande, 1976), which depicts the fitness measure as a function of the strategy. If mutations cause only small changes in strategy, then the population makes a small step uphill on the adaptive landscape each time an advantageous mutant replaces a less fit resident strategy. At evolutionary equilibrium, the population will therefore attain a local maximum or 'peak' of the adaptive landscape. This view of the adaptive process is compatible with the quantitative genetic theory of phenotypic evolution (Lande, 1976, 1979).

Optimisation theory, is applicable only if selection is frequency-independent, i.e. if the fitness of each strategy is independent of the kind and frequency of other strategies present in the population. The need for incorporating frequency-dependent selection into evolutionary models was first recognised in studies of animal behaviour: Here it was evident that the success of a behavioural strategy in pairwise interactions between animals depends on the strategy of the opponent. Evolutionary game theory and the concept of evolutionary stability was devised in this context by Maynard Smith (Maynard Smith and Price, 1973; Maynard Smith, 1982), building on the notion of 'unbeatable' strategies established by Hamilton (1967). See Heino et al. (1998) for a general definition of frequency dependence.

When the fitness of a strategy depends on the frequency of other strategies, 'optimal' strategies can only be defined in a conditional sense, that is, given the strategies of the resident population. Accordingly, the concept of simple optimality is replaced by that of evolutionary stability. An evolutionarily stable strategy (ESS) is characterised by the condition that if all individuals choose this strategy, then no other strategy can spread in the population (Maynard Smith, 1982). Notice that the ESS essentially is a static concept: There is nothing in the definition of the ESS that ensures that the dynamical process of evolution by small mutational steps converges to an ESS (Eshel, 1983; Taylor, 1989; Nowak, 1990; Christiansen, 1991). Moreover, directional evolution may lead to the establishment of strategies that are not evolutionarily stable (see e.g. Christiansen and Loeschcke, 1980; Hofbauer and Sigmund, 1990; Abrams et al., 1993).

The evolution of strategies adopted in pairwise interactions between animals often leads to mixed strategies that can conveniently be modelled using matrix games (Maynard Smith, 1982). An individual with a mixed strategy uses each of a number of distinct behavioural patterns, called pure strategies, with a certain probability specified by its strategy, irrespectively of the action of its opponent. If fitness is determined by the average payoff gained in independent encounters, then the expected fitness of an individual is linear in both its own strategy and in the population strategy, leading to the matrix formulation. As a consequence, once a mixed ESS is established, each pure strategy that is contained in the mixed ESS must have the same fitness as the mixed ESS itself (Bishop and Cannings, 1978). The reason for this eventual fitness equality is that, if a pure strategy had higher fitness than the mixed ESS, then it could invade the ESS. Conversely, if a pure strategy that is contained in the mixed ESS had lower fitness than the ESS, then a mixed strategy that is similar to the ESS, but does not include this particular pure strategy, could invade. The ESS of a matrix game thus implies fitness equality and thus describes a situation that is very different from a population sitting on a fitness peak, as is the case for optimisation theory.

Visualising evolutionary processes based on matrix games in terms of adaptive landscapes is less straightforward than in case of optimisation. The adaptive landscape of a matrix game describes fitness as a function of the mixing probabilities. Since, under conditions of frequency dependence, the fitness of a strategy depends on the resident population's strategy, the adaptive landscape changes as the composition of the population changes during evolution. In particular, when the evolving population has attained an ESS, the adaptive landscape becomes flat. [See Garay (1999) for a relation between fitness advantage and Fisher's Fundamental Theorem.]

Predictions of optimisation models and of matrix games regarding the outcome of evolutionary processes are thus qualitatively incompatible. Op-

timisation models predict that, at evolutionary equilibrium, the strategy widespread in a natural population should maximise fitness; therefore the widespread strategy should have a higher fitness than rare alternative variants, which may arise from mutation, immigration or from artificial manipulation. The state of an adaptive process can thus be assessed by measuring fitness differences in the field. In contrast, matrix game models of evolution suggest that, at an ESS, each strategy observable in a population should have the same fitness: Although the ESS is the result of adaptation, the fitness advantage of the ESS over alternative strategies disappears once the ESS is attained. In matrix game models, the 'fingerprint' of adaptation is fitness equality of all different strategies contained in a mixed ESS. Under the appropriate ecological conditions, the seemingly contradicting expectations derived from optimisation models and matrix games are both supported by empirical evidence; see, for example, Pettifor et al. (1988) for observed fitness maximisation and Gross (1985) for fitness equality under frequency dependence.

Although optimisation models and matrix games are not in direct contradiction (because they require different conditions to be satisfied), their disagreeing outlook on qualitative aspects of the evolutionary process may seem hard to reconcile. In this paper, we demonstrate that the theory of adaptive dynamics offers a unifying framework in which optimisation models and matrix games represent two limiting cases. (Non-linear games, however, correspond to the generic case of adaptive dynamics.) That optimal strategies and evolutionarily stable strategies of matrix games can be regarded as special cases in the context of adaptive dynamics was noticed, for one-dimensional strategies, by Geritz et al. (1998). Here we elaborate on this notion and extend it to multidimensional strategies. By bringing together results from Maynard Smith (1982), Hines (1980, 1987), Eshel (1983), Brown and Vincent (1987a), Hofbauer and Sigmund (1990, 1998), Dieckmann and Law (1996), Metz et al. (1996a, b), Geritz et al. (1997, 1998), Kisdi (1998), Leimar (in press), Mylius and Metz (in press), Dieckmann and Metz (in prep.) and Dieckmann et al. (in prep.), we provide an integrative approach to adaptive dynamics, evolutionary optimisation, and matrix games.

2. Optimisation models and matrix games

In this section, we summarise the basic formalisms of optimisation models and of matrix games in the language of adaptive dynamics. We present this formulation both for vector-valued traits and for one-dimensional traits. The latter description is less general but is easier to visualise, while still capturing the basic idea (Figs 1–3).

2.1. Optimisation models

We consider a vector $\boldsymbol{x}$ containing the continuous variables $x_1,\ldots,x_n$ that characterises a multidimensional strategy and that undergoes simultaneous frequency-independent evolution. The elements of $\boldsymbol{x}$ thus may stand, for example, for body size, fecundity, time spent foraging, etc. In the simplest case, the strategy is only one-dimensional and is given by a single scalar variable, x.

A general measure of fitness can be defined as the long-term per capita population growth rate of a strategy when it appears as a rare mutant in a given resident population. The fitness, therefore, is derived from the underlying population dynamics ("invasion fitness", Metz et al., 1992; Rand et al., 1994; Ferriere and Gatto, 1995). In contrast, optimisation models apply to those ecological settings where the long-term growth rate of a strategy is determined by a fitness measure $W(\boldsymbol{x})$ that is independent of the kind and frequency of other strategies in the population. For example, foraging models often assume that the amount of food collected per unit time unequivocally determines the population growth rate of a strategy and therefore can be used as an indirect measure of fitness (e.g. Charnov, 1976; Stephens and Krebs, 1986). In optimisation models, a mutant with strategy $\boldsymbol{y}$ can spread in a population with established strategy $\boldsymbol{x}$ if its fitness advantage, $s_x(y)$, defined as

$$s_{\mathbf{x}}(\mathbf{y}) = W(\mathbf{y}) - W(\mathbf{x}) \qquad (1)$$

is positive; otherwise the mutant is deleterious and dies out.

The optimal strategy, denoted by $\boldsymbol{x}^*$, maximises $W(\boldsymbol{x})$. If $\boldsymbol{x}^*$ is a local interior optimum, it is char-

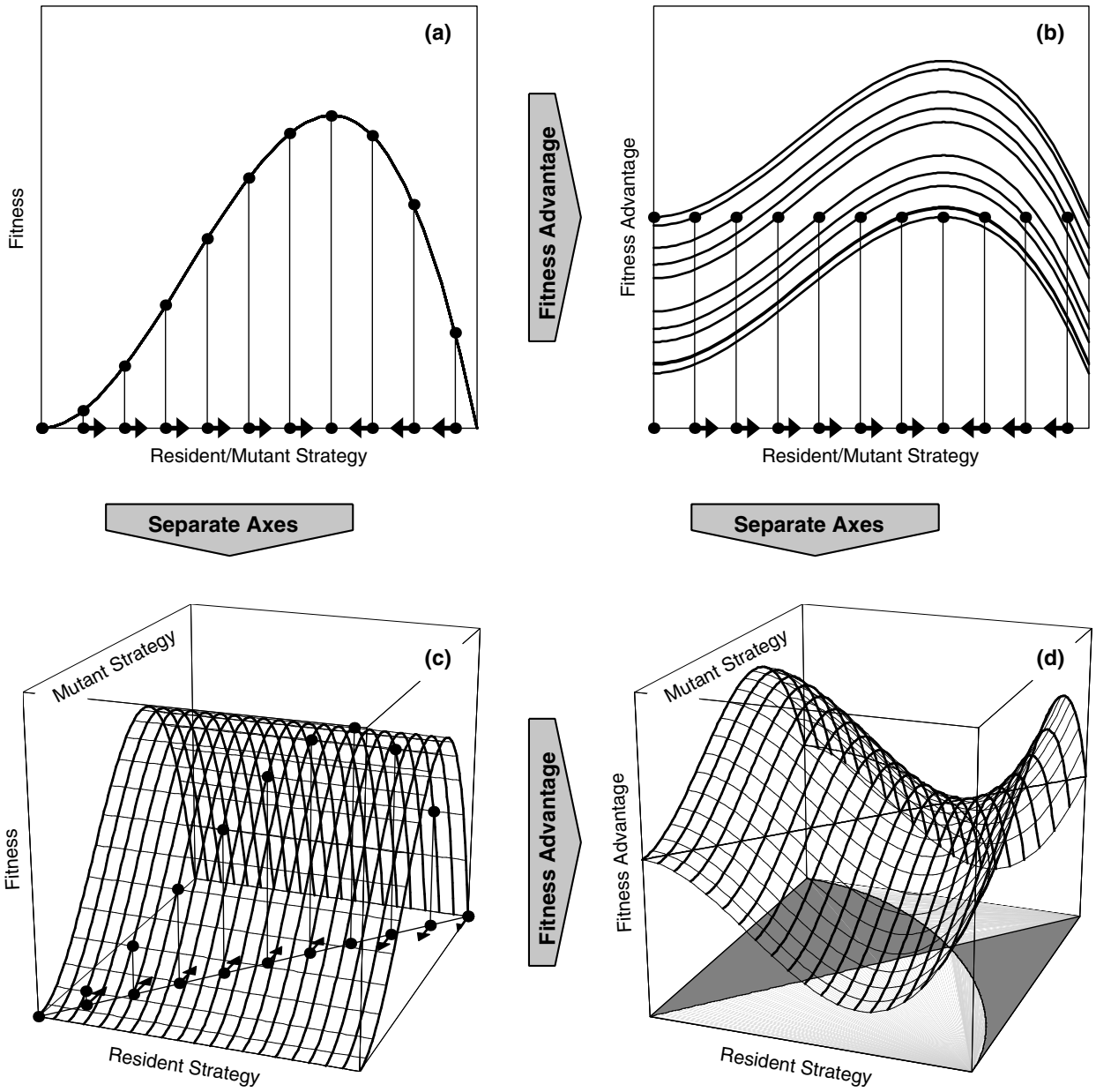

FIG. 1. The adaptive landscape of frequency-independent optimisation, rendered in four ways suitable to compare with the frequency-dependent cases. (a) Fitness function or adaptive landscape. Evolution converges to the fitness maximum as indicated by the arrows. (b) Fitness *advantage*. Curves represent the fitness advantage of the mutant as a function of the mutant strategy for the different resident strategies separately. Vertical lines indicate which curve belongs to which resident strategy. That these curves only differ by their offsets is a characteristic feature of the frequency-independent case. (c) Fitness of the mutant as a function of mutant *and* resident strategy. Thick lines: fitness as a function of the mutant strategy; these are the same curves as shown in (a). Thin lines: fitness as a function of the resident strategy. There is no dependence on the resident strategy in this case. Arrows along the main diagonal of the bottom plane indicate the direction of evolution, i.e. the sign of the fitness gradient. (d) Fitness advantage of the mutant as a function of resident and mutant strategy. Grey areas on the bottom plane indicate combinations of resident and mutant strategies for which the mutant can grow and invade; in contrast, white areas correspond to mutants that are deleterious relative to to the considered resident strategy. The main diagonal naturally is neutral to invasion. The crossing point of the main diagonal and of the second zero contour line corresponds to an ESS attractor that is located at the optimal strategy. The direction and outcome of evolution can be predicted based solely on this 'Pairwise Invasibility Plot' (PIP). The anti-symmetric shape of the PIP is the fingerprint of optimising evolution

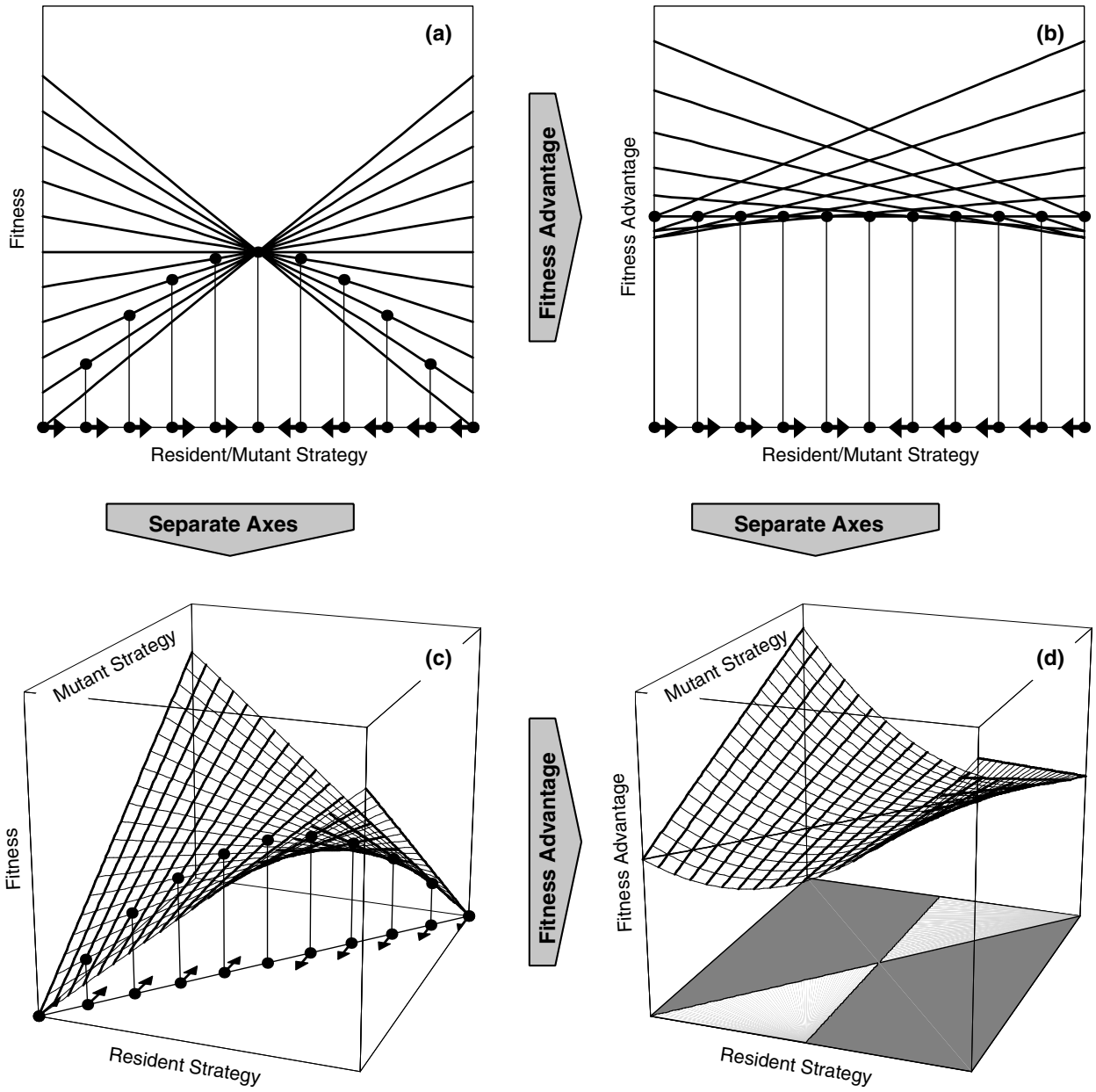

FIG. 2. The adaptive landscape of matrix games. (a) For each resident strategy, fitness is a linear function of the mutant strategy, but the slopes of the lines differ in dependence on the resident strategy. Vertical lines indicate which line belongs to which resident strategy. The central strategy is the ESS; evolution therefore converges towards this strategy. The fitness function or adaptive landscape that corresponds to the ESS as resident is horizontal: once the ESS is established, all mutants are neutral. (b) As a mutant, the ESS strategy has positive fitness advantage and can therefore invade any other resident strategy: at the ESS, all lines other than the horizontal one are above zero. This ensures that the second ESS condition is satisfied. It also implies that the fitness lines are tilted in a way that guarantees convergence towards the ESS. (c) Mutant and resident strategies are now varying along separate axes. The changing slope of the thick lines, which are the same as in (a), shows frequency dependence: the higher the percentage of a pure strategy is in the resident population, the smaller its payoff will be. (d) In the PIP on the bottom plane, the crossing point of the two straight zero contour lines determines the location of the ESS. Notice that the second zero contour line is not only straight but also parallel to the mutant's axis: this feature reflects the fitness equality or mutant neutrality that ensures once the ESS is established and is the fingerprint of evolution under a linear fitness function

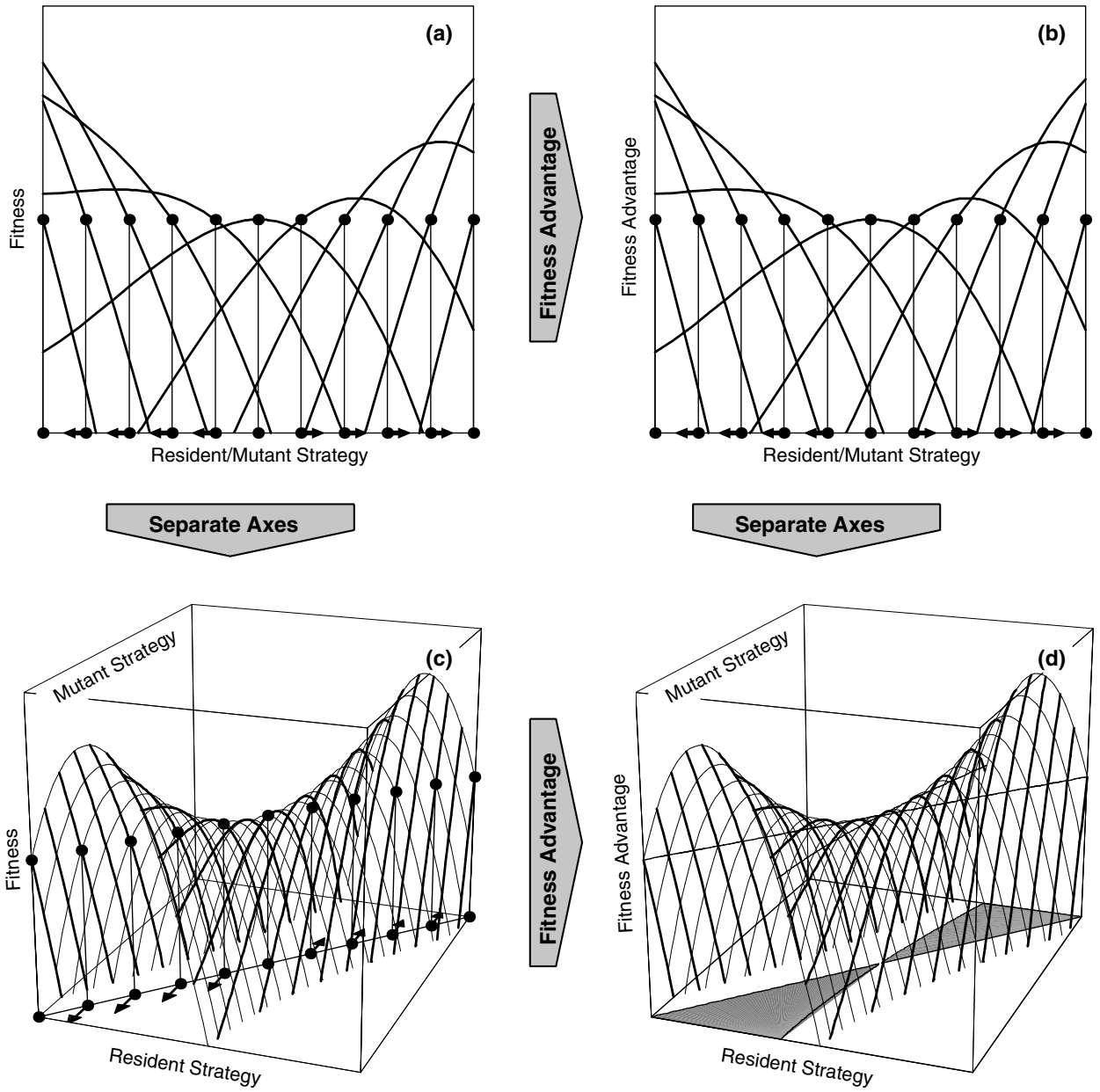

FIG. 3. An adaptive landscape of adaptive dynamics. The example shows a 'Garden of Eden' configuration: an ESS, which nevertheless acts as an evolutionary repellor. (a, b) In adaptive dynamics theory, there is no difference between fitness and fitness advantage because the fitness of an invader that is identical to a given resident is zero according to the definition of invasion fitness. (c, d) The evolutionarily singular strategy can be located in the PIP as the crossing point between the two zero contour lines. This singular strategy corresponds to a local fitness maximum with respect to variations in the mutant strategy; it is therefore an ESS. However, the fitness gradients around the ESS point away from the singular strategy: although the singular strategy would be stable once reached, it cannot be attained by small mutational steps. Notice that both evolutionary stability and the repelling nature of the singular strategy can be deduced just from studying the PIP

acterised by the standard conditions for the maximum of a multivariate function,

$$\left.\frac{\partial W(\mathbf{x})}{\partial x_i}\right|_{\mathbf{x}=\mathbf{x}^*} = \left.\frac{\partial s_{\mathbf{x}}(\mathbf{y})}{\partial y_i}\right|_{\mathbf{y}=\mathbf{x}^*} = 0 \text{ for all } i \qquad (2a)$$

and

$$\left[\left.\frac{\partial^2 W(\mathbf{x})}{\partial x_i \partial x_j}\right|_{\mathbf{x}=\mathbf{x}^*}\right] = \left[\left.\frac{\partial^2 s_{\mathbf{x}}(\mathbf{y})}{\partial y_i \partial y_j}\right|_{\mathbf{y}=\mathbf{x}^*}\right]$$

is negative definite. (2b)

In this paper we denote a matrix with elements M_{ij} by $\boldsymbol{M} = [M_{ij}]$. For a one-dimensional strategy x, conditions (2) simplify to the familiar form $\left.\frac{dW(x)}{dx}\right|_{x=x^*} = \left.\frac{\partial s_x(y)}{\partial y}\right|_{y=x^*} = 0$ and $\left.\frac{d^2W(x)}{dx^2}\right|_{x=x^*} = \left.\frac{\partial^2 s_x(y)}{\partial y^2}\right|_{y=x^*} < 0$.

The locally optimal strategy obviously cannot be invaded by any nearby mutant ($s_{\mathbf{x}^*}(\mathbf{y}) < 0$ for all $\boldsymbol{y}$ close to $\boldsymbol{x}^*$), and therefore is a (local) ESS. On the other hand, the optimal strategy itself can invade any other nearby strategy ($s_{\mathbf{x}}(\mathbf{x}^*) > 0$ for all $\boldsymbol{x}$ close to $\boldsymbol{x}^*$). The optimal strategy is also the best invader in the sense that for any given resident strategy it is the optimal strategy $\boldsymbol{x}^*$ that has the largest fitness advantage and therefore spreads fastest in a population. In the course of evolution, each time that an advantageous mutant strategy replaces the former resident strategy, the population acquires a higher fitness and therefore successively ascends on the adaptive landscape $W(\boldsymbol{x})$ until the peak is reached and evolution comes to a halt (see Fig. 1).

This notion of optimality can be extended to density-dependent optimisation models (Charlesworth and León, 1976; Michod, 1979; Meszéna and Pásztor, 1990; Hernandez and León, 1995), giving rise to optimisation principles of a different kind. These are applicable if, for example, the environment of a population can be characterised by a one-dimensional quantity, such as the total population density N, to which the growth rate of all possible strategies reacts monotonically (Metz et al., 1996b). In such cases, the fitness $W(\boldsymbol{y},N(\mathbf{x}))$ of a rare mutant with strategy $\boldsymbol{y}$ has to be evaluated at the equilibrium density $N(\mathbf{x})$ of the resident strategy $\boldsymbol{x}$ and is thus dependent on the resident strategy. A strategy $\boldsymbol{x}$ then is optimal if $W(\boldsymbol{y},N(\mathbf{x}))$, as a function of its first variable, is maximal at $\boldsymbol{y}=\boldsymbol{x}$. It is easy to see that this condition of optimality is equivalent to maximising the equilibrium density $N(\mathbf{x})$ as a function of the strategy $\boldsymbol{x}$ (Charlesworth, 1980; Mylius and Diekmann, 1995). Therefore, provided that the mentioned monotonicity condition holds, the optimal strategy is determined, once again, by maximising a fixed strategy-dependent function, $N(\mathbf{x})$, despite the fact that the fitness function W itself changes its shape in the course of the evolutionary process.

2.2. Matrix games

In the context of evolutionary matrix games, the elements of the strategy vector $\boldsymbol{x}$ determine the probabilities for an individual to choose among a n different pure strategies; therefore $x_1+...+x_n=1$. Let $\boldsymbol{A}$ be the payoff matrix of the evolutionary game, i.e. the matrix components A_{ij} denote the amount by which an individual increases its fitness when it plays the ith pure strategy in a contest against an opponent that plays the jth pure strategy. Under the assumption of strategy-independent encounters, the average payoff of a rare mutant strategy $\boldsymbol{y}$ in a resident population playing strategy $\boldsymbol{x}$ is

$$E(\mathbf{y},\mathbf{x}) = \sum_{i,j} y_i A_{ij} x_j = \mathbf{yAx}\,. \qquad (3)$$

Notice that $E(\boldsymbol{y},\boldsymbol{x})$ is bilinear in $\boldsymbol{x}$ and $\boldsymbol{y}$. The mutant can spread if it has a greater average payoff than the resident, that is, if the fitness advantage

$$s_{\mathbf{x}}(\mathbf{y}) = E(\mathbf{y},\mathbf{x}) - E(\mathbf{x},\mathbf{x}) = \mathbf{yAx} - \mathbf{xAx} \qquad (4)$$

is positive; otherwise the mutant dies out. Notice that $s_x(\boldsymbol{y})$ is linear in $\boldsymbol{y}$ but quadratic in $\boldsymbol{x}$.

The well-known conditions for a strategy $\boldsymbol{x}^*$ to be an ESS of a matrix game were given by Maynard Smith (1982, p. 14; Maynard Smith and Price, 1973) and are described by the following two inequalities

$E(\boldsymbol{y},\boldsymbol{x}^*) \le E(\boldsymbol{x}^*,\boldsymbol{x}^*)$ for all $\boldsymbol{y}$ and (5a)

$E(\boldsymbol{x}^*,\boldsymbol{y}) > E(\boldsymbol{y},\boldsymbol{y})$ for $\boldsymbol{y}\neq\boldsymbol{x}^*$ if equality holds in (5a). (5b)

According to Equation (4), these conditions are equivalent to

$s_{x^*}(\boldsymbol{y}) \le s_{x^*}(\boldsymbol{x}^*) = 0$ for all $\boldsymbol{y}$ and (6a)

$s_y(\boldsymbol{x}^*) > s_y(\boldsymbol{y}) = 0$ for $\boldsymbol{y}\neq\boldsymbol{x}^*$ if equality holds in (6a). (6b)

The first ESS condition (6a) means that each possible mutant is either deleterious or neutral when it is infinitesimally rare in a population playing the ESS. This is obviously necessary if the ESS is to be immune against invasion. More significantly, the second ESS condition (6b) states that for all $\boldsymbol{y}$ for which neutrality holds in (6a), the ESS, when employed by a rare mutant, must be able to invade a resident population with strategy $\boldsymbol{y}$.

According to a theorem by Bishop and Cannings (1978), all pure strategies contained in a mixed ESS are neutral in a resident population that plays the ESS. Since these pure strategies payoff equally well, so does any combination of them: All mixed strategies that contain the same pure strategies as the ESS are therefore neutral as well, and $s_{x^*}(\boldsymbol{y})=0$ is constant as a function of $\boldsymbol{y}$ in the range of $\boldsymbol{y}$ that has the same non-zero components as $\boldsymbol{x^*}$ (i.e. $y_i > 0$ only if $x_i^* > 0$). The proof of the Bishop–Cannings theorem relies only on the assumption of fitness advantages being a linear function of mutant strategies $\boldsymbol{y}$. The invariance of fitness over such subsets of strategies implies that mixed ESSs are never fully defined by the first ESS condition (6a) alone, but always rely on the second ESS condition (6b) as well. The mixed ESS must therefore always be able to invade a resident population of individuals that use the same pure strategies in a different mixture.

The fitness equality resulting from the Bishop–Cannings theorem can be conveniently illustrated in case of two pure strategies played with probabilities x and $1–x$, respectively. Relative to a mixed ESS ($0<x^*<1$) both pure strategies and any mixture of them are neutral, i.e. $s_{x^*}(y)=0$ for all $0\le y\le 1$ (see Fig. 2). This behaviour is not unexpected because the function $s_{x^*}(y)$, being linear in y, cannot have an interior maximum with respect to y. Since $s_{x^*}(x^*)$ is zero (Equation (4)), it follows that if $s_{x^*}(y)$ were not zero everywhere then it would be positive for some y, which is impossible if x^* is to be an ESS. When the resident strategy x is different from the ESS, $s_x(y)$ is described by a tilted line such that $s_x(x)$ is zero and $s_x(x^*)$ is positive. This follows directly from the fact that, according to (6b), the ESS must be able to invade any other resident strategy. Obviously, any mutant strategy that lies between the resident strategy and the ESS is then able to invade (see Fig. 2b). If the mutants differ only slightly from the resident, then mutants nearer to the ESS take over so that the population gradually evolves towards the ESS. As evolution converges towards the ESS, the slope of the adaptive landscape decreases to zero (Hines, 1987; see also Fig. 2). Cressman (1996) discusses density-dependent matrix games.

3. Adaptive dynamics

In this section we briefly introduce the basic concepts of adaptive dynamics theory. The framework outlined here was developed by Metz et al. (1996a), Geritz et al. (1997, 1998) and Dieckmann and Law (1996) for one-dimensional strategies and has been summarised in Dieckmann (1997). The multidimensional extension is based on Dieckmann and Law (1996), Metz et al. (1996a), Leimar (in press) and Dieckmann et al. (in prep.).

3.1. Invasion fitness

In order to study the generic patterns of evolution driven by frequency-dependent selection, the fitness of a mutant strategy $\boldsymbol{y}$ in a resident population with strategy $\boldsymbol{x}$, $s_{\boldsymbol{x}}(\boldsymbol{y})$, must not be constrained to any particular form. What $s_{\boldsymbol{x}}(\boldsymbol{y})$ looks like depends on the biological problem at hand; we merely assume that $s_{\boldsymbol{x}}(\boldsymbol{y})$ is known, twice continuously differentiable, and defined in such a manner that mutants with positive values of $s_{\boldsymbol{x}}(\boldsymbol{y})$ can grow and invade, whereas mutants with negative values of $s_{\boldsymbol{x}}(\boldsymbol{y})$ die out in a resident population of strategy $\boldsymbol{x}$. Notice that by this definition $s_{\boldsymbol{x}}(\boldsymbol{x})=0$ holds for any $\boldsymbol{x}$ because the resident strategy itself is neither growing nor declining in its own established population. Optimisation models and matrix games are specific cases of this general definition in which $s_{\boldsymbol{x}}(\boldsymbol{y})$ is given by Equation (1) or by Equations (3) and (4), respectively.

For a resident strategy $\boldsymbol{x^*}$ to be evolutionarily stable it is necessary that $s_{\boldsymbol{x}^*}(\boldsymbol{y})\le 0$ for all $\boldsymbol{y}$, i.e. that no mutant has a fitness advantage when it interacts with the resident only. The relation $s_{\boldsymbol{x}^*}(\boldsymbol{y})<0$ for all $y \neq x^*$ is stricter and guarantees that the mutant dies out if its initial frequency is sufficiently low. When $s_{\boldsymbol{x}^*}(\boldsymbol{y})$ is a nonlinear function of $\boldsymbol{y}$, fitness equality, $s_{\boldsymbol{x}^*}(\boldsymbol{y})=0$, occurs only in very special and degenerate cases. The generic condition of evolu-

tionary stability is $s_{x^*}(\mathbf{y}) < s_{x^*}(\mathbf{x}^*)=0$ for all $\mathbf{y} \neq \mathbf{x}^*$. In other words, fitness as a function of the mutant strategy must attain a maximum at the ESS, provided that the ESS is the established resident (Maynard Smith, 1982). The ESS can therefore be regarded as a *conditionally* optimal strategy, i.e. it is optimal in its own established population (see Fig. 3). Obviously, this conditional optimality does not impart any information about the outcome of selection when the ESS has not yet been established. Unlike an optimal strategy in frequency-independent selection, the ESS is not necessarily the best invader against an arbitrary resident and in fact may not be capable at all of invading such an arbitrary resident. The ESS also does not necessarily coincide with the attractor of directional evolution (see, for example, Eshel, 1983; Abrams et al., 1993).

3.2. Directional evolution

In order to model the evolutionary process in the framework of adaptive dynamics, we assume that mutations are of small phenotypic effect so that a mutant $\mathbf{y}$ is always similar to its ancestor $\mathbf{x}$; $|\mathbf{y}-\mathbf{x}|$, therefore, is small. The population makes a small evolutionary step each time a mutant successfully invades and replaces the former resident (see Metz et al., 1992; Dieckmann, 1994; Dieckmann et al., 1995; Metz et al., 1996a; Dieckmann and Law, 1996; Geritz et al., 1997, 1998; see Jacobs et al., in prep.; Geritz et al., in prep.; Geritz and Kisdi, in prep.; for proofs that an invader replaces the resident in case of small evolutionary step and non-zero fitness gradient.). A sequence of these small steps constitutes a stochastic evolutionary path that can be approximated by the deterministic trajectory described by the so-called canonical equation of adaptive dynamics,

$$\frac{d\mathbf{x}}{dt} = \frac{1}{2}\alpha u(\mathbf{x})N(\mathbf{x})\mathbf{C}(\mathbf{x})\left.\frac{\partial s_{\mathbf{x}}(\mathbf{y})}{\partial \mathbf{y}}\right|_{\mathbf{y}=\mathbf{x}} \qquad (7)$$

(Dieckmann and Law, 1996; Dieckmann and Metz, in press). Here u denotes the probability of a mutation per birth event and $N(\mathbf{x})$ is the equilibrium size of the resident population for strategy $\mathbf{x}$. The factor ½ reflects the fact that one half of the nearby mutants of a strategy are deleterious and thus cannot contribute to the evolutionary change described by (7). The constant α depends on details of the individual-based demography of the evolving population and equals 1 for the continuous-time birth-and-death processes considered in Dieckmann and Law (1996). The variance-covariance matrix of the mutation distribution is given by $\mathbf{C}$, which therefore characterises the expected size of mutational steps in different components of $\mathbf{x}$ as well as their potential correlations. The equilibrium density, $N(\mathbf{x})$, may depend on the resident strategy $\mathbf{x}$, while u and $\mathbf{C}$ may depend on $\mathbf{x}$ but in the simplest case are just constants. Finally, the fitness gradient $\left.\frac{\partial s_{\mathbf{x}}(\mathbf{y})}{\partial \mathbf{y}}\right|_{\mathbf{y}=\mathbf{x}}$ describes the force of selection: Given the adaptive landscape for a resident strategy $\mathbf{x}$, this gradient points into the direction of the steepest ascent on the adaptive landscape and therefore determines the direction as well as scales the speed of evolutionary change. For one-dimensional strategies, $\mathbf{C}$ is simply the variance of mutational changes in x and evolution proceeds towards smaller or larger values of x depending on the sign of the fitness gradient, i.e. depending on whether smaller or larger mutants are advantageous and thus capable of replacing the resident. For multi-dimensional strategies, however, the variance-covariance matrix $\mathbf{C}$ can also affect direction and outcome of the evolutionary process.

3.3. Evolutionary singularities

Evolutionarily singular strategies are the fixed points of adaptive dynamics as described by the canonical equation (7). A strategy $\mathbf{x}^*$ therefore is singular if its fitness gradient $\left.\frac{\partial s_{\mathbf{x}}(\mathbf{y})}{\partial \mathbf{y}}\right|_{\mathbf{y}=\mathbf{x}=\mathbf{x}^*}$ vanishes. For simplicity we do not consider boundary fixed points of Equation (7) where the fitness gradient need not be zero (Dieckmann and Law, 1996). Singular strategies are the only candidates for ESSs: an interior strategy with a non-zero fitness gradient always has potential invaders. Singular strategies can be fully characterised in terms of four properties (Geritz et al., 1998). For the purposes of this paper, however, we shall consider only the following three properties.

(i) A singular strategy is *convergence stable* (Christiansen, 1991), if it is an asymptotically sta-

ble fixed point of the canonical adaptive dynamics given by Equation (7) (Dieckmann and Law, 1996; Marrow et al., 1996). The stability of a fixed point depends not only on the fitness function $s_x(\mathbf{y})$ but also on the variance-covariance matrix $\boldsymbol{C}$. However, the evolutionarily singular strategy $\boldsymbol{x^*}$ is asymptotically stable for *any* choice of the variance-covariance matrix if the matrix

$$\left[\left.\frac{\partial^2 s_{\mathbf{x}}(\mathbf{y})}{\partial y_i \partial y_j}\right|_{\mathbf{y}=\mathbf{x}=\mathbf{x}^*}\right] + \frac{1}{2}\left[\left.\frac{\partial^2 s_{\mathbf{x}}(\mathbf{y})}{\partial y_i \partial x_j}\right|_{\mathbf{y}=\mathbf{x}=\mathbf{x}^*} + \left.\frac{\partial^2 s_{\mathbf{x}}(\mathbf{y})}{\partial x_i \partial y_j}\right|_{\mathbf{y}=\mathbf{x}=\mathbf{x}^*}\right]$$

is negative definite (8)

(Leimar, in press).

For one-dimensional strategies this condition for convergence simplifies to $\left.\frac{\partial^2 s_x(y)}{\partial y^2}\right|_{y=x=x^*} + \left.\frac{\partial^2 s_x(y)}{\partial x \partial y}\right|_{y=x=x^*} < 0$ (Eshel, 1983). To see this, notice that the local fitness gradient has to be positive for $x<x^*$ and negative for $x>x^*$ to ensure convergence stability. That is, the derivative of the fitness gradient $\frac{d}{dx}\left(\left.\frac{\partial s}{\partial y}\right|_{y=x}\right)$ must be negative, which leads to the previous expression.

(ii) A singular strategy $\boldsymbol{x^*}$ is *locally evolutionarily stable* if no nearby mutant can invade the resident population of $\boldsymbol{x^*}$. As we have seen in the previous section, the generic (and sufficient) condition for evolutionary stability is that $s_{x^*}(\boldsymbol{y})$ attains a maximum at $\boldsymbol{y}=\boldsymbol{x^*}$, i.e. that the matrix

$$\left[\left.\frac{\partial^2 s_{\mathbf{x}}(\mathbf{y})}{\partial y_i \partial y_j}\right|_{\mathbf{y}=\mathbf{x}=\mathbf{x}^*}\right] \text{ is negative definite.} \quad (9)$$

For one-dimensional strategies, $\left.\frac{\partial^2 s_x(y)}{\partial y^2}\right|_{y=x=x^*} < 0$ is the analogous condition for a fitness maximum (Maynard Smith, 1982; Brown and Vincent, 1987a).

(iii) A third property of the singular strategy x^* determines whether, as a rare mutant, it can spread in the resident population of a nearby strategy. (Notice that this requirement differs from convergence stability: A convergence stable singular strategy may not be able to invade, and vice versa.) Locally, the singular strategy has *invading potential* with respect to the resident population of any other strategy that is similar to itself if $s_x(\boldsymbol{x^*}) > s_x(\boldsymbol{x}) = 0$, i.e. if $s_x(\boldsymbol{x^*})$ attains a local minimum at $\boldsymbol{x^*}$ as a function of $\boldsymbol{x}$. Generically this is the case if

$$\left[\left.\frac{\partial^2 s_{\mathbf{x}}(\boldsymbol{y})}{\partial x_i \partial x_j}\right|_{\mathbf{y}=\mathbf{x}=\mathbf{x}^*}\right] \text{ is positive definite} \quad (10)$$

or, for one-dimensional strategies, if $\left.\frac{\partial^2 s_x(\boldsymbol{y})}{\partial x^2}\right|_{y=x=x^*} > 0$ (Kisdi and Meszéna, 1993, 1995; Apaloo, 1997; Geritz et al., 1997, 1998).

A fourth property of evolutionary singularities (determining whether there exists protected dimorphisms in the singularity's neighbourhood) is important for resolving the full scope of generic evolutionary patterns near evolutionary singularities (Metz et al., 1996a; Geritz et al., 1997, 1998). It is, however, not relevant for our present purposes and therefore we shall not discuss it.

The three properties given by Conditions (8), (9) and (10) are not fully independent. In particular, a strategy that is evolutionarily stable and that is able to invade other nearby strategies is also necessarily convergence stable. In order to see this, we need the following relationship between the second derivatives of $s_x(\boldsymbol{y})$, obtained by replacing $s_x(\boldsymbol{y})$ by its Taylor-expansion in the equation $s_x(\boldsymbol{x})=0$ (Metz et al., 1996a):

$$\left[\left.\frac{\partial^2 s_{\mathbf{x}}(\mathbf{y})}{\partial x_i \partial x_j}\right|_{\mathbf{y}=\mathbf{x}} + \left.\frac{\partial^2 s_{\mathbf{x}}(\mathbf{y})}{\partial y_i \partial x_j}\right|_{\mathbf{y}=\mathbf{x}} + \left.\frac{\partial^2 s_{\mathbf{x}}(\mathbf{y})}{\partial x_i \partial y_j}\right|_{\mathbf{y}=\mathbf{x}} + \left.\frac{\partial^2 s_{\mathbf{x}}(\mathbf{y})}{\partial y_i \partial y_j}\right|_{\mathbf{y}=\mathbf{x}}\right] = 0 \quad (11a)$$

or, for one-dimensional strategies,

$$\left.\frac{\partial^2 s_x(y)}{\partial x^2}\right|_{y=x} + 2\left.\frac{\partial^2 s_x(y)}{\partial x \partial y}\right|_{y=x} + \left.\frac{\partial^2 s_x(y)}{\partial y^2}\right|_{y=x} = 0 \,. \quad (11b)$$

Using Equation (11a), Condition (8) can be rewritten such that the singularity is convergence stable for any choice of the variance-covariance if $\left[\left.\frac{\partial^2 s_{\mathbf{x}}(\mathbf{y})}{\partial y_i \partial y_j}\right|_{\mathbf{y}=\mathbf{x}=\mathbf{x}^*}\right] - \left[\left.\frac{\partial^2 s_{\mathbf{x}}(\mathbf{y})}{\partial x_i \partial x_j}\right|_{\mathbf{y}=\mathbf{x}=\mathbf{x}^*}\right]$ is negative definite (or, for one-dimensional strategies, if $\left.\frac{\partial^2 s_x(y)}{\partial y^2}\right|_{y=x=x^*} - \left.\frac{\partial^2 s_x(y)}{\partial x^2}\right|_{y=x=x^*} < 0$). It now becomes evident that this condition is always satisfied if the singular strategy is both evolutionarily stable (the first matrix is negative definite according to Condition (9)) and has invasion potential (the second matrix is positive definite according to Condition (10)).

4. Optimisation models and matrix games as special cases of adaptive dynamics

Optimal strategies as well as matrix game ESSs must be evolutionarily singular strategies. At non-singular strategies there is directional evolution according to Equation (7), resulting from the invasion of nearby advantageous mutants. In optimisation models this invading mutant must have higher fitness, therefore the original non-singular resident cannot have been optimal. Similarly, invasion cannot occur at an ESS of a matrix game.

4.1. Optimisation models

In optimisation models, $s_x(\boldsymbol{y})$ takes the form given in Equation (1); therefore all mixed partial derivatives are zero, $\left[\frac{\partial^2 s_{\mathbf{x}}(\mathbf{y})}{\partial x_i \partial y_j}\right] = \left[\frac{\partial^2 s_{\mathbf{x}}(\mathbf{y})}{\partial y_i \partial x_j}\right] = \mathbf{0}$. According to Condition (2b), $\left[\left.\frac{\partial^2 s_{\mathbf{x}}(\mathbf{y})}{\partial y_i \partial y_j}\right|_{\mathbf{y}=\mathbf{x}=\mathbf{x}^*}\right]$ is negative definite at the optimal strategy $\boldsymbol{x}^*$. Three properties of the optimal strategy then follow immediately (Metz et al., 1996b; Kisdi, 1998; Mylius and Metz, in press): (i) The optimal strategy is convergence stable because the first term in Condition (8) is negative definite according to Condition (2b) and the remaining terms are zero.
(ii) The optimal strategy is an ESS since Condition (9) is immediately satisfied by Condition (2b). (iii) The optimal strategy can invade all other strategies. To see this, notice that the second and third terms in equation (11a) vanish and that the last term is negative definite. Consequently, the first term must be positive definite, and this is equivalent to Condition (10).

In the simpler case of one-dimensional strategies we can conclude that the mixed partial derivative $\frac{\partial^2 s_x(y)}{\partial x \partial y}$ is zero because $s_x(y)$ is of the form given by Equation (1), and that $\left.\frac{\partial^2 s_x(y)}{\partial y^2}\right|_{y=x^*}$ is negative because the optimal strategy x^* maximises $s_x(y)$. The latter condition is equivalent to evolutionary stability. Moreover, x^* is an attractor since $\left.\frac{\partial^2 s_x(y)}{\partial y^2}\right|_{y=x=x^*} + \left.\frac{\partial^2 s_x(y)}{\partial x \partial y}\right|_{y=x=x^*}$ reduces to $\left.\frac{\partial^2 s_x(y)}{\partial y^2}\right|_{y=x^*}$, which is negative. Finally, since the second term in Equation (11b) is zero and the third term is negative, the first term $\left.\frac{\partial^2 s_x(y)}{\partial x^2}\right|_{x=x^*}$ must be positive. This implies that the singular strategy x^* has the potential to invade any other resident population with a strategy that is similar to itself. Notice that, because all mixed partial derivatives vanish, the conditions for asymptotic stability, for evolutionary stability, and for invading potential are all equivalent.

4.2. Matrix games

In matrix games, the components of the vector $\boldsymbol{x}$ represent the probabilities of playing different pure strategies. This implies $x_1+...+x_n=1$, and therefore the n components are not independent of each

other. The adaptive dynamics in Equation (7) thus has to be constrained to the set of vectors with $x_1+...+x_n=1$, called the n-dimensional simplex, S_n. This amounts to a constraint that has to be imposed on the mutational variance-covariance matrix $\boldsymbol{C}$: Mutations in the different components of $\boldsymbol{x}$ cannot be independent because the resulting mutant strategy must still satisfy $x_1+...+x_n=1$.

This means that $x_1,...,x_n$ cannot change in an uncorrelated manner, because if some elements of $\boldsymbol{x}$ increase then it is necessary for others to decrease in order to maintain a constant sum. Constraining $\boldsymbol{C}$ in this manner affects the stability conditions (8), (9), and (10) such that negative or positive definiteness is required only for vectors with $x_1+...+x_n=1$. (More precisely, instead of requiring that a matrix $\boldsymbol{M}$ is positive definite, we only need to require that $\boldsymbol{xMx}$ is a positive definite quadratic form for $\boldsymbol{x}\in S_n$.) In this subsection, we shall use negative or positive definiteness in this sense. (Alternatively, one can rewrite the theory in terms of $n-1$ independent strategy variables, say $x_1,\ldots,x_{n-1}$, and replace x_n by $1- x_1-\ldots-x_{n-1}$. The resulting fitness function $s_x(\boldsymbol{y})$ remains linear in the independent variables $y_1,\ldots,y_{n-1}$.)

In order to simplify the analysis, we have assumed that the evolutionarily singular strategy of the adaptive dynamics lies in the interior of the strategy space and not on its boundary. Accordingly, we restrict attention here to fully mixed ESSs, which contain each pure strategy with positive probability ($x_i^* > 0$ for all i).

According to the Bishop–Cannings theorem, all (pure or mixed) strategies are neutral in the resident population of a fully mixed singular strategy $\boldsymbol{x}^*$. In Condition (6a), therefore, equality holds for all $\boldsymbol{y}$. Evolutionary stability thus depends on Condition (6b): $\boldsymbol{x}^*$ as a rare mutant must be able to invade any other strategy. In matrix games, evolutionary stability and invading potential are thus intimately linked.

Asymptotic stability follows from evolutionary stability and invading potential not only in the generic case (see previous section) but, by analogous reasoning, also in the degenerate case of matrix games. For matrix games $\left[\dfrac{\partial^2 s_{\mathbf{x}}(\mathbf{y})}{\partial y_i \partial y_j}\right]=\mathbf{0}$ holds, because $s_x(\boldsymbol{y})$ is linear in $\boldsymbol{y}$ (Equation (4)). According to Condition (10), $\boldsymbol{x}^*$ as a rare mutant is able to invade all nearby resident strategies and hence is an ESS of the matrix game if $\left[\left.\dfrac{\partial^2 s_{\mathbf{x}}(\mathbf{y})}{\partial x_i \partial x_j}\right|_{\mathbf{y}=\mathbf{x}=\mathbf{x}^*}\right]$ is positive definite. Notice that since $s_x(\boldsymbol{y})$ is quadratic in $\boldsymbol{x}$, this is a global condition. In Equation (11a), the first term is positive definite and the last term vanishes. The remaining terms, $\left[\left.\dfrac{\partial^2 s_{\mathbf{x}}(\mathbf{y})}{\partial y_i \partial x_j}\right|_{\mathbf{y}=\mathbf{x}=\mathbf{x}^*}+\left.\dfrac{\partial^2 s_{\mathbf{x}}(\mathbf{y})}{\partial x_i \partial y_j}\right|_{\mathbf{y}=\mathbf{x}=\mathbf{x}^*}\right]$, must then be negative definite, which implies that Condition (8) is satisfied (see also Hines, 1980; Cressman and Hines, 1984; Hofbauer and Sigmund, 1990). In case of one-dimensional strategies (i.e. in 2×2 games with mixing probabilities x and $1-x$, respectively), we have $\dfrac{\partial^2 s_x(y)}{\partial y^2}=0$ since $s_x(y)$ is a linear function of y and $\left.\dfrac{\partial^2 s_x(y)}{\partial x^2}\right|_{y=x=x^*}$ must be positive for x^* to be able to invade other strategies and hence to be the ESS. Equation (11b) then guarantees that $\left.\dfrac{\partial^2 s_x(y)}{\partial x \partial y}\right|_{y=x=x^*}$ is negative, which, together with $\dfrac{\partial^2 s_x(y)}{\partial y^2}=0$, implies that Condition (8) is satisfied.

5. Discussion

The simplest version of optimisation models amount to an unconditional maximisation of fitness: strategies with higher fitness always replace strategies with lower fitness until the optimal strategy is established. This is the most straightforward formalisation of the Darwinian idea of survival of the fittest, and it is easily visualised as evolution moving uphill on a fixed adaptive landscape. Optimisation, however, is applicable only if a measure of fitness, $W(\boldsymbol{x})$ in Equation (1), can be found that characterises each strategy independently of the actual composition of the population (Fig. 1).

A universally applicable measure of fitness is the long-term per capita growth rate of a rare mu-

tant strategy (Metz et al., 1992). This growth rate depends not only on the strategy of the mutant but also on the environment in which such a mutant lives. This environment is characterised in terms of variables like the abundance and quality of resources, abundance and satiation status of predators, presence and harmfulness of pathogens, behavioural actions undertaken by conspecifics, etc. These environmental variables, in turn, tend to be affected by the number and strategy of other individuals present in the population. Therefore, the existence of a good fitness measure that is independent of the resident population is more the exception than the rule. Instead, environmental feedback and the resulting density and frequency dependence of selection pressures are important phenomena in a wide variety of ecosystems.

A rare mutant's long-term growth rate depends on the resident population even in those ecological situations where optimisation models apply. A negative feedback necessarily exists between population growth and population density: Otherwise populations would exhibit sustained exponential growth, which is biologically impossible. Optimisation models may be applicable if growth rates depend on a *single* density parameter (such as total population density). In this case, equilibrium densities are maximised (Charlesworth, 1980; Mylius and Diekmann, 1995). Under even more specific assumptions, the growth rate r or the lifetime reproductive success R_0 can be expressed as the product of a density-dependent and a strategy-dependent component (Mylius and Diekmann, 1995; Pásztor et al., 1996). Notice, however, that from a mathematical point of view it is often most straightforward to retain the long-term growth rate of a strategy when it is rare as the ultimate measure of fitness and consider density dependence explicitly; this choice, of course, does not alter the nature of the optimisation problem. If a population is limited by a single resource, then the abundance of this resource will be minimised by the evolutionarily optimal strategy (Tilman, 1982; Mylius and Diekmann, 1995). If, however, the environment is characterised by two or more variables, then optimisation is no longer possible: Any fitness measure then necessarily depends on the strategy (or strategies) established in the population (Tilman, 1982; Kisdi and Meszéna, 1993, 1995; Metz et al. 1996b; Heino et al., 1998; Meszéna and Metz, in press).

Frequency-dependent selection was first studied in the context of evolutionary game theory (Hamilton, 1967; Maynard Smith and Price, 1973; Bishop and Cannings, 1978; Taylor and Jonker, 1978; Zeeman, 1980; Hines, 1980, 1987; Maynard Smith, 1982; Hofbauer and Sigmund, 1998). Similarly to game theory, adaptive dynamics theory considers fitness as being determined by the strategy of a focal individual as well as by the strategies of the resident population. However, while fitness functions are often linear in game theory, adaptive dynamics theory is based on generic, non-linear fitness functions. Indeed, frequency-dependent selection with a non-linear dependence of fitness values on strategies is ubiquitous: it occurs, for example, in the context of resource competition (Christiansen and Loeschcke 1980, 1984; Loeschcke and Christiansen, 1984; Brown and Vincent, 1987b; Christiansen, 1991, 1998; Taper and Case, 1992; Vincent et al. 1993; Doebeli, 1996; Metz et al., 1996a; Dieckmann and Doebeli, 1999), predator-prey systems (Brown and Vincent, 1992; Matsuda and Abrams, 1994a; Doebeli and Dieckmann, 2000), multiple habitats (Brown and Pavlovic, 1992; Meszéna et al., 1997; Kisdi and Geritz, 1999), stochastic environments (Ellner, 1985; Cohen and Levin, 1991; Kisdi and Meszéna, 1993, 1995; Doebeli and Ruxton, 1997), asymmetric competition (Maynard Smith and Brown, 1986; Abrams and Matsuda, 1994; Matsuda and Abrams, 1994b; Law et al., 1997; Kisdi, 1999), mutualistic interactions (Law and Dieckmann, 1998; Doebeli and Dieckmann, 2000) and sex-ratio evolution (Van Tienderen and De Jong, 1986).

Since a mutant can only invade if it has a higher fitness than the resident, each small evolutionary step is made uphill on the adaptive landscape, entailing some resemblance to optimisation models. Under frequency dependence, however, the adaptive landscape depends on the resident population and therefore changes with each replacement of a resident strategy with a mutant strategy (see, for example, Brown and Pavlovic, 1992; Brown and Vincent, 1992; Dieckmann 1994; Geritz and Kisdi, in press). Evolution comes to a halt if the population cannot be invaded by any new mutant, i.e. if an evolutionarily stable strategy is established.

Generically, the ESS is located at a peak of the adaptive landscape that results from the resident ESS population. In other words, the fitness of the ESS is the highest possible *provided that the ESS is the resident*. The ESS is thus characterised by a conditional maximisation of fitness. Evolutionarily stable polymorphisms, comprising several strategies, can be defined analogously (Brown and Vincent, 1987a, b; Metz et al., 1996a; Geritz, 1998).

Matrix games are part of an important but special class of frequency-dependent models in which fitness is a linear function of the mutant strategy and for which the adaptive landscape is therefore described by a straight line or hyperplane (Hines, 1987; see also Fig. 2). Other members of this class are games in which the mutant's payoff is nonlinear in the opponent's strategy but still linear in the strategy of the mutant itself, $E(\boldsymbol{y},\boldsymbol{x})=\boldsymbol{y}\cdot\boldsymbol{f}(\boldsymbol{x})+\text{const.}$ For example, the sex ratio game (Maynard Smith, 1982) has a payoff function of this form. If the adaptive landscape is linear, then it cannot have an internal maximum and therefore must be flat once the (fully mixed) ESS is established. When infinitesimally rare, alternative strategies are neutral in the population of the ESS. Consequently, an additional condition is necessary to ensure that alternative mutants decline in number whenever they are present at a small but positive frequency. For matrix games, the payoff to a strategy can be decomposed into a sum of the payoff received in encounters with the resident and the payoff from encounters with the rare mutant. The first term is equal for all strategies when the resident is the (fully mixed) ESS. All the fitness difference between the ESS and the alternative mutants therefore comes from the second term: If the mutant is to die out, the ESS must perform better when encountering the alternative strategy than the alternative strategy against itself. This means that the ESS as a rare mutant must be able to invade the established population of the alternative strategies (Condition (6b); Maynard Smith and Price, 1973; Maynard Smith, 1982; Pohley and Thomas, 1983). Notice that the described decomposition of fitness is valid only in matrix games: There no simple criterion is available similar to Condition (6b) if the payoff is given by $\boldsymbol{y}\cdot\boldsymbol{f}(\boldsymbol{x})+\text{const.}$ with non-linear $\boldsymbol{f}(\boldsymbol{x})$.

In the context of matrix games, the linearity of fitness is a consequence of the assumption that fitness is determined by the average payoff gained in independent encounters in well-mixed populations. The fragility of this assumption is underscored by the fact that in iterated and/or spatially extended games the encounters are no longer independent of each other; consequently, the fitness function becomes nonlinear (Hofbauer and Sigmund, 1990, 1998; Nowak and May, 1992; Szabó and Tőke, 1998; Brauchli et al., 1999; Szabó et al., 2000). The linearity of fitness is also lost if payoffs fluctuate over generations (Metz, unpublished).

When the shape of the fitness function $s_x(\boldsymbol{y})$ is unrestricted, the properties of evolutionary singularities (asymptotic stability, evolutionary stability, and invading potential) are pairwise independent (Eshel, 1983; Taylor, 1989; Christiansen, 1991; Geritz et al., 1998). For example, evolutionarily stable strategies are not necessarily attractors and thus may be unreachable by evolution. Eshel (1983), Nowak (1990) and Kisdi and Meszéna (1995) provide examples for such 'Garden of Eden' singularities (see also Fig. 3). On the other hand, there exist convergence stable strategies that are not evolutionarily stable: The evolutionary process then converges towards a local *minimum* instead of maximum of the adaptive landscape; see Hofbauer and Sigmund (1990), Nowak (1990), Christiansen (1991), Brown and Pavlovic (1992), Brown and Vincent (1992), Abrams et al. (1993), Day (in press) for examples. Disruptive selection near these points can lead to *evolutionary branching*, a process during which an initially monomorphic population splits up into two distinct strategies that become separated by a widening gap (Metz et al., 1996a; Geritz et al., 1997, 1998). Examples for evolutionary branching have been found e.g. by Metz et al. (1992), Doebeli and Ruxton (1997), Meszéna et al. (1997), Boots and Haraguchi (1999), Geritz et al. (1998, 1999), Kisdi (1999), Kisdi and Geritz (1999), Parvinen (1999), Mathias and Kisdi (2001), Mathias et al. (2001) and Cheptou and Mathias (in press). Evolutionary branching accompanied by the evolution of reproductive isolation has been suggested as a basis for adaptive speciation that may occur in sympatry (Dieckmann and Doebeli, 1999; Doebeli and Dieckmann, 2000; Kisdi and Geritz, in press; Geritz and Kisdi, 2000).

By contrast, in optimisation models the optimal strategy is always evolutionarily stable, asymptoti-

cally stable and can invade nearby resident strategies, i.e. these three properties are linked (Kisdi and Meszéna, 1993, 1995; Kisdi, 1998). Asymptotic stability, evolutionary stability, and invading potential are also linked in matrix games, but in a slightly different sense. In optimisation models, asymptotic stability and invading potential are implied by evolutionary stability. In matrix games, however, invading potential is necessary for evolutionary stability, since the model is degenerate with respect to the generic condition for evolutionary stability. Since invading potential is thus part of the ESS definition for matrix games, only asymptotic stability remains to be regarded as a consequence of evolutionary stability (Hines, 1980; Cressman and Hines, 1984; Hofbauer and Sigmund, 1990).

If an optimisation model is perturbed such that Equation (1) does not hold anymore, but the perturbation is small, then the model still has a convergence stable singular strategy that is an ESS and that also can invade other nearby strategies. This can be seen from the fact that Conditions (8), (9), and (10) are satisfied in optimisation models as strict inequalities. An illustration for this structural stability is given by Kisdi and Meszéna (1993). They consider a density-dependent life-history model, where optimisation is applicable when the environment is stable; for temporally fluctuating environments, however, selection in the model becomes frequency dependent. If the temporal fluctuations are weak (i.e. if the optimisation model is only slightly perturbed), then there is still a strategy near the original optimum that is attracting, evolutionarily stable and has invading potential.

Matrix games do not possess this kind of structural stability. Since equality holds in Condition (9), the singularity of a matrix game can lose its evolutionary stability due to the slightest perturbation. Asymptotic stability and invading potential will be retained because strict inequalities hold in Conditions (8) and (10). In case of one-dimensional strategies, loss of evolutionary stability implies that the singularity bifurcates into an evolutionary branching point (Geritz et al., 1998). Dieckmann and Metz (in prep.) provide examples for such bifurcations in perturbed matrix games.

In this paper, we have considered monomorphic resident populations only. Coexistence of strategies is not possible in optimisation models: The strategy with the highest fitness $W(\boldsymbol{x})$ outcompetes all others, or, in case of density-dependent optimisation under the described monotonicity condition, the strategy with the highest equilibrium density (lowest equilibrium resource level) wins over the rest. Coexistence requires frequency dependent selection. In case of resource competition, this requirement translates into the well-known ecological requirement of having more than one resources to sustain more than one consumer (MacArthur and Levins, 1964; Levin, 1970; Tilman, 1982; Meszéna and Metz, in press). Optimisation models are structurally unstable in the sense that an arbitrarily weak frequency dependence may result in the coexistence of certain strategies in the neighbourhood of the ESS. These strategies, however, undergo convergent evolution such that ultimately the ESS will be established (Geritz et al., 1998).

In matrix games strategies can coexist. New mutants are neutral against a set of resident strategies if the frequencies of pure strategies, averaged over the entire population (and thus called the population strategy), correspond to the ESS frequencies (Thomas, 1984). Starting with a single resident strategy and with small mutations, however, the ESS population strategy will not be reached until the individual strategies themselves are near the ESS. Directional evolution will thus proceed until it arrives at the neighbourhood of the ESS. Near the ESS, several strategies may form a polymorphism that generates the ESS population strategy where further mutations are neutral.

In the generic case of frequency-dependent selection with non-linear fitness function, the notions of ESS and environment-dependent optimality are equivalent: they are the general rendering of the Darwinian idea of the “survival of the fittest”. Linear models, such as matrix games, represent an important, but mathematically degenerate, special case when the ESS cannot be considered as an optimum.

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Note added in proof: The relation between matrix games and an alternative framework of adaptive dynamics, the so-called *G*-function approach, is discussed by VINCENT, T. and CRESSMAN, R. (2000): An ESS maximum principle for matrix games. *Theor. Pop. Biol.* **58**:173–186.

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