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Cross entropy minimization in uninvadable states of complex populations

Immanuel M. Bomze

Institut für Statistik und Informatik, Universität Wien, Universitätsstraße 5, A-1010 Wien, Austria

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Abstract. Selection is often viewed as a process that maximizes the average fitness of a population. However, there are often constraints even on the phenotypic level which may prevent fitness optimization. Consequently, in evolutionary game theory, models of frequency dependent selection are investigated, which focus on equilibrium states that are characterized by stability (or uninvadability) rather than by optimality. The aim of this article is to show that nevertheless there is a biologically meaningful quantity, namely cross (fitness) entropy, which is optimized during the course of evolution: a dynamical model adapted to evolutionary games is presented which has the property that relative entropy decreases monotonically, if the state of a (complex) population is close to an uninvadable state. This result may be interpreted as if evolution has an "order stabilizing" effect.

Key words: Frequency dependent selection – Evolutionary game theory – Replicator dynamics

1 Introduction

Selection is often viewed as a process that maximizes the "good of a species", i.e. the average fitness of a population. This may be true in some elementary situations, but in general there is no evidence for a steady improvement. Apart from genetical obstacles like recombination which may yield a decrease in fitness (cf. Hutson/Law (1981) and Hofbauer/Sigmund (1988, p. 27)), there are also constraints on the phenotypic level which may prevent fitness optimization. The prototypic example is the meanwhile classical hawk/dove game as described in Maynard Smith/Price (1973).

To cope with these situations, game theoretical methods were applied to models of evolution, which have two essential features: (i) they mainly focus on phenotypes, thus avoid a detailed description of both the genotypic level and the transmission mechanism from genotype to phenotype; and (ii) they consider equilibrium states (attained by an adaptation process) which are characterized by stability rather than by optimality. Evolutionary game theory models frequency dependent selection: indeed, the "payoff" is nothing else than incremental

Darwinian fitness, which is influenced by the distribution of phenotypes ("strategies") within the population. Originally, strategies were interpreted as behavioural traits, particularly in pairwise conflicts, but it soon turned out that these concepts are advantageous also in more complex situations (often termed "playing the field"), e.g. if dispersal, size, or differences in resource allocation affect the individual's fitness in quite a complicated way.

The aim of this article is to show that – although evolutionary game theory favours stability instead of optimality – there is a biologically meaningful quantity, which is optimized during the course of evolution. To be more precise, a dynamical model adapted to evolutionary games, the so-called "replicator dynamics", is investigated which has the property that relative negentropy increases (and hence relative entropy decreases) monotonically, if the state of population is close to an evolutionary stable (more precisely: a strongly uninvadable) state. This result may be interpreted as if evolution counteracts the thermodynamical effect of increasing entropy, i.e. has an "order stabilizing" effect. Now (absolute) entropy need not have a unique (local) minimum, wherefore one is forced to consider an entropy measure relative to an ideal state, viz. an uninvadable state. Since there are situations where more than one state is uninvadable, it seems to be evident that the result can only hold locally, i.e. applies only to those states which are already close to an uninvadable state.

It should be stressed that the use of (fitness) entropy methods, particularly for dynamical systems applied to frequency-dependent selection models in genetics plays an important role; see, e.g. Ginzburg (1977), Desharnais/Costatino (1982), Desharnais (1986) and in particular Iwasa (1988); cf. Hines (1982). Although Akin (1982) already has proved a special case of the main result in the present paper, he interpreted it exclusively in terms of the *Kullback/Leibler* distance; hence it seems that this article for the first time explicitly relates cross entropy minimization with stability notions in the context of evolutionary game theory, i.e. on the phenotypic level.

The paper is organized as follows: in Sect. 2, the general setting of an evolutionary game, and the notion of strong uninvadability are introduced. Section 3 deals with the replicator dynamics, while in Sect. 4 the announced main result is stated and proved. Section 5 relates the notion of strong uninvadability to well-known solution concepts in evolutionary game theory.

2 Evolutionary games and strong uninvadability

Denote by X the set of strategies individuals are able to play. For the purpose of modelling the contest, the state of the population is then fully described by the distribution P of the strategies $x \in X$ within this population. Since our model – like most of the models investigated in the literature – is based on the assumption that populations are so large that they can be regarded ideally as infinite (see, e.g. Maynard Smith (1988) or Shaffer (1988) for a treatment of evolutionary stability in finite populations), there is no reason why, a priori, there should only be a finite number of strategies available to the individuals. Thus let $(X, \mathscr{X})$ be an arbitrary measurable space. Any state P then is a probability measure defined on the system $\mathscr{X}$, with $P(A)$ representing the relative frequency of strategies x belonging to a set $A \in \mathscr{X}$. The model now consists of a collection $\mathscr{P}$ of states, i.e. $\mathscr{P}$ is a set of distributions P on $(X, \mathscr{X})$. We assume throughout this paper that $\mathscr{P}$ is convex and exclude the trivial case where $\mathscr{P}$ contains no, or only one, element.

Let $F_P(x)$ denote the mean payoff to an individual playing $x \in X$ against members of a population in state $P \in \mathscr{P}$. In the simple case of pairwise conflicts, this mean payoff $F_P(x)$ is obtained by averaging the individuals' payoffs with respect to P (see Example 2 below). However, in more general situations like the "sex ratio game" as described, e.g. by Sigmund (1987), the averaging procedure is performed with respect to a more complicated probabilistic mechanism governing the contest. This mechanism is determined by both the structure of the underlying model and the state P of the population; cf. Maynard Smith (1982, p. 23). Thus, the quantity $F_P(x)$ may – but need not – depend on the state P in a rather complicated way.

Example 1 Finite number of admissible strategies. If the set of strategies available to each individual is finite, $X = \{x_1, \ldots, x_k\}$, say, then every state $P \in \mathscr{P}$ is given by the relative frequencies $p_j = P(\{x_j\})$, $1 \leqslant j \leqslant k$. Clearly the relative frequency $P(A)$ of a subset A of strategies is in this case given by the sum

$$P(A) = \sum_{j: x_j \in A} p_j.$$

If, particularly, in state P all individuals play the same strategy x_j, i.e. if P is a monomorphic state, then $p_j = 1$ and $p_i = 0$ for $i \neq j$. In this case P is given by the *Dirac* distribution (unit point mass) at x_j, denoted by $P = \delta_{x_j}$. In general, every state $P \in \mathscr{P}$ in this model is represented by a convex combination

$$P = \sum_{j=1}^{k} p_j \delta_{x_j}$$

of *Dirac* distributions; a state of this form is called "discrete polymorphism".

Clearly one can think of more complicated situations where P consists of a continuous component and a discrete component, the latter corresponding to a finite or countably infinite convex combination of monomorphic states. An example is provided by the evolutionary stable state in the war of attrition with continuous time described in Bishop/Cannings (1978). The setting proposed simply allows us to treat all these different cases in a unified way. For instance, the average mean payoff of a (sub-)population in state Q against the (overall) population in state P is given by

$$E(Q, P) = E_Q(F_P) = \int_X F_P(x) Q(dx),$$

or, for short, $\int F_P \, dQ$. This quantity is essential in evolutionary game theory and also will be central in the definition of strong uninvadability given below.

According to Maynard Smith and Price (1973), a state $P \in \mathscr{P}$ of the population under consideration is evolutionarily stable, if occurrence of rare mutants results in an average mean payoff lower than the average mean payoff to the population in the original state P. The occurrence of rare mutants means that a subpopulation of (small) relative size ε, $0 < \varepsilon < 1$, switches from state P to a different state $Q \neq P$. Hence, the resulting "perturbed" state of the total population is given by

$$(1 - \varepsilon)P + \varepsilon Q.$$

(For convenience and in order to avoid lengthy arguments dealing with exceptional cases, we have made the assumption that $\mathscr{P}$ is convex at the beginning of this article; hence $(1-\varepsilon)P + \varepsilon Q \in \mathscr{P}$ whenever $Q \in \mathscr{P}$ and $0 \leqslant \varepsilon \leqslant 1$.) Now the statement that the average mean payoff to rare mutants is less than the average mean payoff to the remaining population (in state P) is reflected by the inequality

$$E(Q, (1-\varepsilon)P + \varepsilon Q) < E(P, (1-\varepsilon)P + \varepsilon Q).$$

Since the map $Q \mapsto E(Q, P)$ is affine, this relation is equivalent to

$$E(R, R) < E(P, R) \quad \text{with } R = (1-\varepsilon)P + \varepsilon Q.$$

Note that the variational distance $\|P - R\|$ between P and R is small because of

$$\|P - R\| = \varepsilon \|P - Q\| \leqslant 2\varepsilon.$$

Hence we are led to the following, stricter definition.

Definition 1 A state $P \in \mathscr{P}$ is said to be *strongly uninvadable*, if there is an $\alpha > 0$ such that for any $R \in \mathscr{P}$,

$$E(P, R) > E(R, R) \quad \text{whenever } 0 < \|R - P\| < \alpha.$$

To promote the flow of the argument, we defer discussion and formal definitions of other, usual solution concepts in evolutionary game theory to Sect. 5. Here let us only note that in some important special cases the above definition yields the usual evolutionary stability notions.

3 Replicator dynamics

The main idea behind any dynamical model for the evolution of behaviour based on games is as follows: assume that the state $Q \in \mathscr{P}$ favours strategies in a set $A \in \mathscr{X}$ in the sense that the average payoff on A exceeds the average mean payoff, i.e.

$$\int_A \varphi_Q(x) Q(dx) > 0 \quad \text{with } \varphi_Q(x) = F_Q(x) - E(Q, Q), \quad x \in X.$$

Then the frequency of strategies belonging to A should increase with time and vice versa. Replicator dynamics is the simplest formalization of this principle, and describes evolution of states $Q(t)$ over time t according to the relation

$$[Q(t)(A)]^{\cdot} = [\varphi_{Q(t)} \cdot Q(t)](A), \quad A \in \mathscr{X},$$

where a dot denotes derivative with respect to time t, and where

$$[\varphi \cdot Q](A) = \int_A \varphi(x) Q(dx), \quad A \in \mathscr{X},$$

for any bounded measurable function $\varphi: X \to \mathbb{R}$ and any $Q \in \mathscr{P}$. In order to avoid the highly technical differential geometric approach of Akin (1982), we rephrase the above relation in terms of a differential equation operating directly on a suitably chosen *Banach* space $\mathscr{L}$:

$$\dot{Q}(t) = \varphi_{Q(t)} \cdot Q(t), \tag{$\mathscr{R}$}$$

$\dot{Q}(t)$ being the signed measure on $(X, \mathscr{X})$ defined by

$$\|Q(t+h) - Q(t) - h\dot{Q}(t)\| = o(h) \quad \text{as } h \to 0.$$

For simplicity and parsimony, we choose $\mathscr{L}$ to be the smallest *Banach* space of signed measures on $(X, \mathscr{X})$ under variational norm, which contains all measures of the form $\varphi \cdot Q$, where $\varphi : X \to \mathbb{R}$ is bounded, measurable, and where $Q \in \mathscr{P}$. Then $\mathscr{L}$ is the so-called L-space of the experiment $(X, \mathscr{X}, \mathscr{P})$, upon which notion a functional analytical treatment of statistical decision theory is based: see Strasser (1985) and LeCam (1986); cf. Bomze (1990a, Proposition 1.1).

To ensure global existence and uniqueness of trajectories under $(\mathscr{R})$ in $\mathscr{L}$ (see, e.g. Lang (1972, p. 63)), we need some assumptions on the payoff structure F_Q, $Q \in \mathscr{P}$:

Lemma 1 *Assume that for any* $\mu \in \mathscr{L}$ *there is a bounded, measurable function* $\varphi_\mu : X \to \mathbb{R}$ *such that*
(i) $\varphi_Q(x) = F_Q(x) - E(Q, Q)$ *for all* $x \in X$, *all* $Q \in \mathscr{P}$;
(ii) $\varphi_\mu(x) = 0$ *for all* $x \in X$, *if* $\|\mu\| \geqslant 2$;
(iii) *there is some constant* $c > 0$ *such that*

$$\sup_{x \in X} |\varphi_\mu(x) - \varphi_\nu(x)| \leqslant c \|\mu - \nu\| \quad \textit{for all } \mu, \nu \in \mathscr{L}.$$

Then $\Phi(\mu) = \varphi_\mu \cdot \mu$ *defines a globally bounded Lipschitz map* $\Phi : \mathscr{L} \to \mathscr{L}$.

Proof. Putting $\nu = o$ in (iii) we get

$$|\varphi_\mu(x)| \leqslant c \|\mu\| + d \quad \text{with } d = \sup_{x \in X} |\varphi_o(x)|. \tag{$*$}$$

This and (ii) yields clearly $\|\Phi(\mu)\| \leqslant 2(2c + d)$ for all $\mu \in \mathscr{L}$. If $\mu, \nu \in \mathscr{L}$ satisfy $\|\mu\| \leqslant 2$ and $\|\nu\| \leqslant 2$, then from (iii), from $(*)$, and from

$$\Phi(\mu) - \Phi(\nu) = (\varphi_\mu - \varphi_\nu) \cdot \mu + \varphi_\nu \cdot (\mu - \nu)$$

we get

$$\|\Phi(\mu) - \Phi(\nu)\| \leqslant (4c + d) \|\mu - \nu\|.$$

Finally observe that for any measures $\mu, \nu \in \mathscr{L}$ with $\|\mu\| \leqslant 2 < \|\nu\|$ there is a number λ with $0 \leqslant \lambda \leqslant 1$ and $\|\nu'\| = 2$, if $\nu' = \lambda\mu + (1 - \lambda)\nu$. Hence $\Phi(\nu') = o = \Phi(\nu)$ and with the help of the above relation we obtain

$$\begin{aligned} \|\Phi(\mu) - \Phi(\nu)\| &= \|\Phi(\mu) - \Phi(\nu')\| \leqslant (4c + d) \|\mu - \nu'\| \\ &= \lambda(4c + d) \|\mu - \nu\| \leqslant (4c + d) \|\mu - \nu\|. \end{aligned}$$

Hence also the *Lipschitz* condition is met. □

A mild sufficient condition for the assumption of Lemma 1 to hold in an important class of evolutionary games is specified in Theorem 7 of Sect. 5. For this class, where $X \subseteq \mathbb{R}^n$, the replicator dynamics was introduced in a slightly different way by Zeeman (1981), who considered the values of the n-variate distribution functions, i.e.

$$Q(t)(\{x \in X : x_i \leqslant y_i,\ 1 \leqslant i \leqslant n\}), \quad y \in X,$$

instead of $Q(t)(A)$ for general $A \in \mathscr{X}$. Within the same framework, Akin (1982) and Hines (1980a) investigated dynamics $(\mathscr{R})$ for the special case where $E(Q, P)$ is bilinear, and where every state $Q \in \mathscr{P}$ is dominated by P; Akin even requires a condition implying P to be equivalent to all states $Q \in \mathscr{P}$ (as usual, we say that P dominates Q, in symbols $Q \ll P$, if $P(A) = 0$ entails $Q(A) = 0$ for any $A \in \mathscr{X}$, and say P and Q to be equivalent, abbreviated by $Q \approx P$, if both $P \ll Q$ and $Q \ll P$ hold). Due to bilinearity of $E(Q, Q)$ – which according to Bomze/

Pötscher (1989, p. 14) means the contest is pairwise – Akin obtained in (1982, p. 399) a global version of the main Theorem 4 below for this special case. See also Hines (1980b, 1982).

Example 1, continued. Replicator dynamics in games with finitely many strategies. In this case, we may and do put $X = \{x_1, \dots, x_k\}$. Furthermore, every state $Q(t) \in \mathscr{P}$ is a discrete polymorphism of the form

$$Q(t) = \sum_{j=1}^{k} q_j(t)\delta_{x_j}$$

and hence uniquely determined by the vector of relative frequencies

$$q(t) = [q_1(t), \dots, q_k(t)]' \in S^k,$$

where

$$S^k = \left\{ q = [q_1, \dots, q_k]' \in \mathbb{R}^k : q_i \geqslant 0, \sum_{i=1}^{k} q_i = 1 \right\}$$

is the k-standard simplex (by $'$ we denote transposition of a column vector). For simplicity, we assume that $\mathscr{P}$ consists of all distributions on X, so that every $q(t) \in S^k$ gives rise to a state $Q(t) \in \mathscr{P}$. Defining $h_j(q(t)) = F_{Q(t)}(x_j)$, $1 \leqslant j \leqslant k$, we obtain

$$E(Q(t), Q(t)) = \sum_{j=1}^{k} q_j F_{Q(t)}(x_j) = q(t)'h(q(t)),$$

and thus it is not surprising that ($\mathscr{R}$) takes the form

$$\dot{q}_j(t) = q_j(t)[h_j(q(t)) - q(t)'h(q(t))], \quad 1 \leqslant j \leqslant k.$$

This is the game dynamics introduced by Taylor and Jonker (1978).

Example 2 Pairwise conflicts in games with finitely many strategies. This is a special case of the situation considered in Example 1. The fact that the game consists in pairwise conflicts yields linearity of the payoff function h considered above: see Bomze/Pötscher (1989, p. 14). Thus there is an $n \times n$ payoff matrix A such that $h(q(t)) = Aq(t)$. Consequently, the replicator dynamics ($\mathscr{R}$) takes the form

$$\dot{q}_j(t) = q_j(t)[(Aq(t))_j - q(t)'Aq(t)], \quad 1 \leqslant j \leqslant n.$$

Models of this type belong to those investigated most frequently in the literature: cf. e.g. Maynard Smith (1982), or Hofbauer/Sigmund (1988).

Remark. Although there is a statistical aspect of the game within the population at every point of time t, described by the state $Q(t)$ as a distribution of strategies displayed by the individuals, we assume in this setting that evolution over time of the whole population is governed by a purely deterministic mechanism. This means that we are not concerned, for instance, with the way in which the states $Q(s)$ and $Q(t)$ are correlated over time. A model taking into account these aspects would have to investigate a stochastic dynamics, describing a stochastic process with marginal distributions $Q(t)$. However, if the time scale at which mutations occur at a reasonable rate (to induce the evolution of the states $Q(t)$ with varying time t) is large compared to the time scale at which individuals and their offspring receive the payoff (resulting from repeated contests in a population in state $Q(t)$, practically at instant t) then this payoff will approximately correspond to the mean response $F_{Q(t)}(x)$ and comparison of this quantity with the average mean payoff $E(Q(t), Q(t))$ makes sense; furthermore, this is the only way in which the state $Q(t)$ may influence the payoffs by a significant amount. Hence – at least in this setting – a model employing the replicator dynamics ($\mathscr{R}$) seems to make sense: the stochastic process mentioned above may be uncorrelated or even stochastically independent over time.

Before passing to cross entropy, we specify an important auxiliary result.

Lemma 2 *If* $(Q(t))_{t\geqslant 0}$ *is a trajectory in* $\mathscr{S}$ *satisfying* ($\mathscr{R}$) *and starting in* $Q(0) \in \mathscr{P}$, *then*
(a) $Q(t) \approx Q(0)$ *with Radon/Nikodym density*

$$\frac{dQ(t)}{dQ(0)}(x) = \exp\left(\int_0^t \varphi(s, x)\, ds\right),$$

where $\varphi(t, x) = \varphi_{Q(t)}(x)$ *for* $t \geqslant 0$ *and* $x \in X$;
(b) *in particular, every* $Q(t)$ *is a probability measure satisfying* $P \ll Q(t)$ *whenever* $P \ll Q(0)$; *in this case,*

$$\log\frac{dP}{dQ(t)}(x) = \log\frac{dP}{dQ(0)}(x) - \int_0^t \varphi(s, x)\, ds \quad \textit{for } Q(0)\textit{-almost all } x \in X.$$

Proof. (a) For all $t \geqslant 0$ and $x \in X$, let

$$\tilde{\varphi}_t(x) = \exp\left(\int_0^t \varphi(s, x)\, ds\right) \geqslant 0$$

and put $\tilde{Q}(t) = \tilde{\varphi}_t \cdot Q(0) \in \mathscr{S}$. Since the map $s \mapsto Q(s)$ from $\mathbb{R}$ to $\mathscr{S}$ is $\|\cdot\|$-continuous, we obtain from the assumption (iii) of Lemma 1 that the functions $s \mapsto \varphi(s, x)$ are uniformly bounded and equicontinuous as $x \in X$. Hence

$$\int_t^{t+h} \varphi(s, x)\, ds - h\varphi(t, x) = o(h) \quad \text{uniformly in } x \text{ as } h \to 0,$$

showing

$$\begin{aligned}\tilde{\varphi}_{t+h}(x) - \tilde{\varphi}_t(x) &= \tilde{\varphi}_t(x)[\exp(h\varphi(t, x) + o(h)) - 1]\\ &= h\tilde{\varphi}_t(x)\varphi(t, x) + o(h) \quad \text{uniformly in } x \text{ as } h \to 0,\end{aligned}$$

which entails

$$\begin{aligned}[\tilde{Q}(t)(A)]^{\cdot} &= \lim_{h\to 0}\int_A \frac{1}{h}[\tilde{\varphi}_{t+h}(x) - \tilde{\varphi}_t(x)]Q(0)(dx)\\ &= \int_A \varphi(t, x)\tilde{\varphi}_t(x)Q(0)(dx)\\ &= [\varphi_{Q(t)} \cdot \tilde{Q}(t)](A) \quad \text{uniformly in } A \in \mathscr{X},\end{aligned}$$

and therefore $[\tilde{Q}(t)]^{\cdot} = \varphi_{Q(t)} \cdot \tilde{Q}(t)$ as well as $\tilde{Q}(0) = Q(0)$. From the uniqueness theorem – see Lang (1972, p. 63) – we thus get $\tilde{Q}(t) = Q(t)$ for all $t \geqslant 0$. Hence $Q(t) \ll Q(0)$ with *Radon/Nikodym* density $dQ(t)/dQ(0) = \tilde{\varphi}_t$. Now pick a $\gamma > 0$ such that $|\varphi(s, x)| \leqslant \gamma$ for all $s \geqslant 0$, all $x \in X$. Then

$$e^{-\gamma t} \leqslant \tilde{\varphi}_t(x) \leqslant e^{\gamma t} \quad \text{for all } x \in X, \tag{$*$}$$

which shows also $Q(0) \ll Q(t)$. Hence (a) is proved.

(b) follows from (a) and from the chain rule for *Radon/Nikodym* densities. □

From relation (∗) in the preceding proof it follows that every function ψ on X, which is integrable w.r.t. $Q(0)$, is also integrable w.r.t. $Q(t)$ for all t. Then the time derivative of its integral is given by

$$\left[\int_X \psi \, dQ(t)\right]^{\cdot} = \int_X \psi \, d\dot{Q}(t) = \int_X \psi \varphi_{Q(t)} \, dQ(t) = \operatorname{Cov}_{Q(t)}[\psi, F_{Q(t)}], \qquad (\mathscr{E})$$

because of $\varphi_{Q(t)}(x) = F_{Q(t)}(x) - \int_X F_{Q(t)} \, dQ(t)$. Relation $(\mathscr{E})$ is a counterpart of Price's (1970) phenotypical evolution equation, and has the interpretation that the instantaneous time variation of the average of an observable quantity ψ equals the covariance, i.e. the measure for the common (spatial) variation, of ψ with the fitness function F_Q in the current state Q.

In the case of frequency independent selection, where $F_Q = F$ for all $Q \in \mathscr{P}$, inserting $\psi = F$ in the evolution equation $(\mathscr{E})$ shows that the average mean fitness $E(Q, Q)$ increases monotonically along $(\mathscr{R})$-trajectories. Furthermore, in a wide class of models the following result holds true: if m is the unique maximizer of the fitness function F, and if the starting state $Q(0)$ has full support, then the states $Q(t)$ evolve towards the monomorphism δ_m yielding the highest fitness at $t \to \infty$: see Bomze (1990b, Example 1). However, this result is false in general if selection is frequency dependent. In the next section we shall show that in this more general set-up, negative cross entropy increases along $(\mathscr{R})$-trajectories, similarly to average mean fitness in the frequency independent selection model.

4 Cross entropy decreases

In the sequel we consider a strongly uninvadable state P and an arbitrary trajectory $(Q(t))_{t \geqslant 0}$ of states evolving according to $(\mathscr{R})$, which starts in a (suitably small) vicinity of P. The main result states that then cross entropy of $Q(t)$ with respect to P decreases with increasing time. Cross entropy – some authors, e.g. Kullback (1959), Fano (1961), Csiszár (1967, 1975), also speak of directed divergence – of a state Q with respect to P is defined whenever $P \ll Q$ and is nothing else than the well-known Kullback/Leibler (1951) information

$$K_{Q:P} = E_P\left(\log \frac{dP}{dQ}\right).$$

Remark. Assume for the moment that $\mathscr{P}$ is dominated by a measure μ on $(X, \mathscr{X})$, and denote by $\psi_Q = dQ/d\mu$ the *Radon/Nikodym* densities. Given μ, one can define the entropy of a state Q relative to P via the *Boltzmann/Gibbs/Shannon* formula, see e.g. Wehrl (1978):

$$H_{Q:P} = E_P(-\log \psi_Q) = -\int \psi_P \log \psi_Q \, d\mu,$$

as well as cross entropy by

$$K_{Q:P} = E_P\left(\log\left(\frac{\psi_P}{\psi_Q}\right)\right) = \int \psi_P \log\left(\frac{\psi_P}{\psi_Q}\right) d\mu.$$

If $H_{Q:P}$ is well defined and if $H_{P:P}$ is finite, relative entropy and cross entropy are related by the identity

$$K_{Q:P} = H_{Q:P} - H_{P:P}$$

(the quantity $H_{P:P}$ is the usual (absolute) entropy; cf., e.g. Rényi (1970) for the information theoretical background, or Good (1953) for applications in population biology). In any case, the quantity $K_{Q:P}$ itself is well defined and finite if and only if the function $\psi_P \log(\psi_P/\psi_Q)$ is integrable with respect to μ. Integrability yields in turn the relation $\psi_Q(x) > 0$ for P-almost all strategies $x \in X$, which means $P \ll Q$.

If $P \ll Q$, then $K_{Q:P}$ is nonnegative and vanishes if and only if $Q = P$. Hence $K_{Q:P}$ may be viewed as a measure of distance between the states Q and P called the *Kullback/Leibler* distance (note however that $K_{Q:P}$ is asymmetric in Q and P). The following inequality relates this distance to the variational distance.

Lemma 3 *Let Q, P be two states satisfying $P \ll Q$. Then*

$$\|Q - P\|^2 \leqslant K_{Q:P}.$$

Proof. The assertion follows, e.g. from formulae (3.3.6) and (3.3.9) in Reiss (1989). □

The arguments preceding Lemma 3 show that it is reasonable to regard the set

$$\mathscr{U}_P = \{Q \in \mathscr{P} : K_{Q:P} \text{ exists and fulfills } 0 \leqslant K_{Q:P} < \delta\}$$

as a vicinity of the state P. Here we choose $\delta = \alpha^2$, where $\alpha > 0$ is the tolerance number from Definition 1. Note that the sets $\mathscr{U}_P, \delta > 0$, do not define a topology, see Csiszár (1967). This is the reason why we use the term "vicinity" instead of "neighbourhood". Nevertheless, the sets $\mathscr{U}_P$ – in a certain geometrical sense – are the counterpart to spheres in *Euclidean* spaces, cf. Csiszár (1975).

The following main result now states that along any evolutionary path $Q(t)$ of states obeying the replicator dynamics ($\mathscr{R}$) and starting in $Q(0) \in \mathscr{U}_P$, *Kullback/Leibler* information $K_{Q(t):P}$ decreases monotonically as time t increases. This observation perfectly corresponds to the minimum cross entropy approach in inference, which has various applications in chemistry and biology, and which can be derived axiomatically, see Shore/Johnson (1980, 1981).

Theorem 4 *Suppose that the states $Q(t) \in \mathscr{P}$ satisfy ($\mathscr{R}$) for $0 \leqslant t \leqslant T$, and that $Q(0) \in \mathscr{U}_P$ holds. If $P \in \mathscr{P}$ is a strongly uninvadable state, then*
(1) *also the states $Q(t) \in \mathscr{U}_P$ for all t, $0 \leqslant t \leqslant T$, i.e. belong to the vicinity of P;*
(2) *the Kullback/Leibler information $K_{Q(t):P}$ decreases monotonically as time t increases.*

Proof. If $Q(0) \in \mathscr{U}_P$, then $K_{Q(0):P}$ exists, so that $P \ll Q(0)$ holds. By Lemma 2(a) we know that then for all t we have $P \ll Q(t)$, thus $K_{Q(t):P}$ is well defined and nonnegative. Now note that for any $Q \in \mathscr{U}_P$ different from P, we get using Lemma 3

$$0 \leqslant \|Q - P\| \leqslant \sqrt{K_{Q:P}} < \sqrt{\delta} = \alpha,$$

whence $E(P, Q) > E(Q, Q)$ results, due to strong uninvadability of P. Thus the relation $Q \in \mathscr{U}_P$ yields $E(Q, Q) \leqslant E(P, Q)$. Furthermore we obtain from Lemma 2(b) using *Fubini*'s theorem

$$K_{Q(t):P} = K_{Q(0):P} - \int_X \int_0^t \varphi(s, x)\, ds\, P(dx) = K_{Q(0):P} - \int_0^t E_P(\varphi_{Q(s)})\, ds.$$

In the proof of Lemma 2, we established equicontinuity of the functions $s \mapsto \varphi(s, x)$ as $x \in X$, which in turn yields continuity of $s \mapsto E_P(\varphi_{Q(s)})$. Therefore the time derivative of $K_{Q(t):P}$ at time t exists and equals

$$E_P(-\varphi_{Q(t)}) = -E(P, Q(t)) + E(Q(t), Q(t)) \leqslant 0.$$

Hence $K_{Q(t):P}$ decreases, and $0 \leqslant K_{Q(t):P} \leqslant K_{Q(0):P} < \delta$ for all $t, 0 \leqslant t \leqslant T$. $\square$

Example 1, continued. Replicator dynamics of *Taylor/Jonker* type. To be compatible with the remark preceding Lemma 3, choose as a dominating measure $\mu = \sum_{j=1}^{k} \delta_{x_j}$. In this setting the entropy of $Q = \sum_{j=1}^{k} q_j \delta_{x_j}$ relative to $P = \sum_{j=1}^{k} p_j \delta_{x_j}$ is given by the expression

$$H_{Q:P} = -\sum_{j:p_j>0} p_j \log q_j$$

which is well defined (and finite) if $p_j > 0$ yields $q_j > 0$. This is evidently true if the *Euclidean* distance $|q - p|$ between q and p is small enough. In particular, absolute entropy $H_{P:P}$ is always finite in this type of game. Thus the vicinity $\mathscr{U}_P$ here corresponds to a *Euclidean* neighbourhood of p in S^n. The function $e^{-H_{Q:P}}$, which strictly increases along the trajectories $Q(t) \in \mathscr{U}_P$ unless $Q(t) = P$, is used as a *Lyapunov* function, e.g. in Bomze/Pötscher (1989, Theorem 44), to establish convergence of $q(t)$ to p as $t \to \infty$ for any trajectory starting with $Q(0) \in \mathscr{U}_P$, i.e. to prove dynamical stability of uninvadable states. This *Lyapunov* function was introduced first in Hofbauer et al. (1979) in the context of Example 2, i.e. for pairwise conflicts with finitely many strategies, to show that every evolutionarily stable state is dynamically stable. This result is wrong if the game does not consist of pairwise conflicts: see Bomze/Pötscher (1989, Example 18).

5 Evolutionary stability and (strong) uninvadability

In Sect. 2, we discussed Maynard Smith's notion of evolutionary stability, which can be formalized in the following definition taken from Taylor/Jonker (1978):

Definition 2 $P \in \mathscr{P}$ is said to be an *evolutionarily stable state*, if for all $Q \in \mathscr{P}$, $Q \neq P$, there is an $\varepsilon(Q), 0 < \varepsilon(Q) \leqslant 1$, such that

$$h_{Q:P}(\varepsilon) = E(Q, (1-\varepsilon)P + \varepsilon Q) - E(P, (1-\varepsilon)P + \varepsilon Q) < 0$$

whenever $0 < \varepsilon \leqslant \varepsilon(Q)$. This is equivalent to the condition that

$$\varepsilon_P(Q) = \inf\{1\} \cup \{\varepsilon : 0 < \varepsilon \leqslant 1 \text{ and } h_{Q:P}(\varepsilon) \geqslant 0\} > 0 \quad \text{for all } Q \in \mathscr{P}, Q \neq P.$$

We call $\varepsilon_P(Q)$ the "invasion barrier" for P against Q. Vickers and Cannings (1987) proposed to consider a uniform version of evolutionary stability called "uninvadability" in Bomze/Pötscher (1989) (note that, in contrast, Maynard Smith (1982, p. 205) and Thomas (1985) use the terms "uninvadable" and "evolutionarily stable" synonymously). According to Definition 3 below, a state P is uninvadable if it is protected by a positive global invasion barrier

$$\varepsilon_P^* = \inf_{Q \in \mathscr{P}, Q \neq P} \varepsilon_P(Q),$$

i.e., if immunity against mutants is uniform.

Definition 3 If $P \in \mathscr{P}$ fulfills $\varepsilon_P^* > 0$, we call P *uninvadable*; if $\varepsilon_P^* = 0$, P is said to be *invadable*.

Of course, every uninvadable state P is evolutionarily stable in the sense of Definition 2. Models in which invadable evolutionarily stable states exist are well known, see, e.g. Vickers/Cannings (1987). However, in some important special cases it turns out that both concepts do not differ much from each other. But beforehand let us relate the notions introduced in Definitions 1 and 3:

Theorem 5 (a) *Every strongly uninvadable state $P \in \mathscr{P}$ is also uninvadable.*
(b) *Let $P \in \mathscr{P}$ be an uninvadable state such that there is an $\alpha > 0$ satisfying*

$$\left(1 - \frac{1}{\delta}\right)P + \frac{1}{\delta} R \in \mathscr{P} \quad \textit{for some positive } \delta = \delta(R) < \varepsilon_P^*,$$

whenever $R \in \mathscr{P}$ fulfills $\|R - P\| < \alpha$. Then P is also strongly uninvadable.

Proof. (a) From Definitions 1 and 3 it is clear that $\varepsilon_P(R) = 1$ holds for any state $R \in \mathscr{P}$ fulfilling $0 < \|R - P\| < \alpha$. Consider any state $Q \in \mathscr{P}$ differing from P. If $0 < \varepsilon < \alpha/2 < 1$, then $R = (1 - \varepsilon)P + \varepsilon Q$ satisfies

$$\|R - P\| = \varepsilon \|Q - P\| \leqslant 2\varepsilon < \alpha,$$

yielding $\varepsilon_P(Q) \geqslant \alpha/2$ and thus the assertion.
(b) If $R \in \mathscr{P}$ and $0 < \|R - P\| < \alpha$, then choose δ as in the condition and let $Q = (1 - 1/\delta)P + (1/\delta)R \in \mathscr{P}$. Then $R = (1 - \delta)P + \delta Q$, and since $0 < \delta < \varepsilon_P^* \leqslant \varepsilon_P(Q)$, we obtain $E(R, R) < E(P, R)$. □

Example 13 in Bomze/Pötscher (1989) shows that the converse of (a) above is not true in general. Note that the condition in (b) implies that for every state $R \in \mathscr{P}$ sufficiently close to P in variational distance,

$$\left(1 - \frac{1}{\delta}\right) P(A) + \frac{1}{\delta} R(A) \geqslant 0 \quad \text{holds for all } A \in \mathscr{X}.$$

This is equivalent to $P \ll R$ with *Radon/Nikodym* derivative dP/dR that is R-almost surely bounded by $(1 - \delta)^{-1} < (1 - \varepsilon_P^*)^{-1}$. Given this property to hold for some δ not depending on R with $0 < \delta < \varepsilon_P^*$, the condition of Theorem 5(b) follows if P lies in the interior (w.r.t. variational norm) of $\mathscr{P}$ relative to the set of all probability measures on $(X, \mathscr{X})$.

Nevertheless, there is an important class of evolutionary games, where (b) is true even if P is not dominated by $\mathscr{P}$, or if P lies on the boundary of $\mathscr{P}$. These "evolutionary mixed strategy games" can be described as follows:

Suppose there is only a finite number n of elementary actions available to individuals participating in a certain game. For reasons that will become clear soon, we represent these elementary actions, or "pure strategies", by the standard basis (column) vectors e_i in n-dimensional *Euclidean* space $\mathbb{R}^n$, $e_i := [0, \ldots, 1, \ldots, 0]'$ (only the ith coordinate non vanishing, $1 \leqslant i \leqslant n$. Assume that each individual is able to play a mixed strategy $x = [x_1, \ldots, x_n]'$, i.e., to display e_i with a certain probability x_i, $1 \leqslant i \leqslant n$. Some authors use the term "complex population" in this situation. One may interpret the probabilities x_i associated with a mixed strategy x in several ways; see, e.g. Maynard Smith (1982, p. 68). The strategy set X then is a subset of the n-standard simplex $S^n \subseteq \mathbb{R}^n$ and $\mathscr{X}$ is the system of *Borel* subsets of X.

For the sake of clarity let us note here that it is important to distinguish between

- (population) states describing the distribution of behaviour within a population, and
- mixed (individual) strategies, which include probabilities x_i for an individual to display behaviour pattern e_i.

Hence, states describe a statistical aspect while strategies refer to an individualistic aspect of behaviour.

In evolutionary mixed strategy games, the dependence of $F_P(x)$ on the strategy x is of very simple type: by definition of a mixed strategy, the payoff $F_P(x)$ to an individual displaying x is the weighted sum of payoffs $f_i(P) = F_P(e_i)$ to the elementary actions e_i, $1 \leqslant i \leqslant n$:

$$F_P(x) = \sum_{i=1}^{n} x_i f_i(P) = x'f(P),$$

where $f(P) = [f_1(P), \ldots, f_n(P)]'$ is the response vector to the elementary actions in state P. As a consequence, the expression for the average mean payoff simplifies to

$$E(Q, P) = \int_{S^n} x'f(P)Q(dx) = \left[\int_{S^n} xQ(dx)\right]' f(P) = \bar{x}'_Q f(P),$$

where $\bar{x}_Q = E_Q(x) = \int xQ(dx)$ denotes the average strategy played in a population in state Q, the so-called "population strategy". In the arguments presented below, the set

$$\bar{X} = \{\bar{x}_Q : Q \in \mathscr{P}\}$$

of all population strategies in the model will play an important role. For simplicity of exposition, we shall in the sequel always assume that $\bar{X}$ is polyhedral. This is certainly true, if for instance $\bar{X}$ is the whole of S^n.

An evolutionary mixed strategy game is said to be a "population game", if the response depends on the state P only through its population strategy $\bar{x}_P$, i.e. if $f(P) = \bar{f}(\bar{x}_P)$ for some function $\bar{f} : \bar{X} \to \mathbb{R}^n$. As a consequence, the average mean payoffs $E(Q, P)$ depend in this case only on the population strategies $\bar{x}_Q$ and $\bar{x}_P$, namely via the formula

$$E(Q, P) = \bar{x}'_Q f(P) = \bar{x}'_Q \bar{f}(\bar{x}_P).$$

Similarly, the mean response to strategy x in a population game takes the form

$$F_P(x) = x'f(P) = x'\bar{f}(\bar{x}_P), \quad x \in X.$$

In a population game with polyhedral $\bar{X}$, the notions of evolutionary stability and uninvadability do not differ too much from each other, provided the response function $\bar{f}$ is differentiable at $x = \bar{x}_P$: cf. Bomze/Pötscher (1989, Theorem 35 (a) through (c), Corollary 39(a)). For instance, in the setting of Example 2 every evolutionarily stable state is already uninvadable, due to bilinearity of the average mean payoff $E(Q, P)$ in Q and P, see Bomze/Pötscher (1989, Corollary 39(b)).

Furthermore, as we shall show now, the notions of uninvadability and strong uninvadability coincide in this case. To this end, we next specify an auxiliary result relating closeness of population strategies to closeness of states in the following sense: denote by $|u| = \sqrt{u'u}$ the *Euclidean* norm of a vector $u \in \mathbb{R}^n$, so that $|\bar{x}_R - \bar{x}_P|$ is the *Euclidean* distance between $\bar{x}_R \in \bar{X}$ and $\bar{x}_P$; then, given an arbitrarily small barrier $\varrho > 0$, any population strategy $\bar{x} \in \bar{X}$ can be represented as a population strategy of a perturbed state resulting from mutations which occur with relative frequency ε less than ϱ, provided $|\bar{x}_R - \bar{x}_P|$ is small enough.

Lemma 6 *Consider a population game with polyhedral $\bar{X}$ and let $\varrho > 0$ be an arbitrary positive number. Then there is an $\alpha > 0$ such that for any $\bar{x}_R \in \bar{X}$ satisfying $|\bar{x}_R - \bar{x}_P| < \alpha$ there is a state $Q \in \mathscr{P}$ and an ε, fulfilling $0 \leqslant \varepsilon < \varrho$, with*

$$x = (1 - \varepsilon)\bar{x}_P + \varepsilon\bar{x}_Q = \bar{x}_{(1-\varepsilon)P + \varepsilon Q}.$$

Proof. If $\bar{X} = S^n$, this follows from Bomze/Pötscher (1989, Remark 7.5(ix) and Lemma 42). For general polyhedral $\bar{X}$, the proof is obtained by straightforward generalization and will therefore be omitted. □

Theorem 7 *In a population game with polyhedral $\bar{X}$, a state P is strongly uninvadable if and only if P is uninvadable.*

Proof. All we have to show is the converse of Theorem 5(a). Put $\varrho = \varepsilon_P^*$ and choose α as in Lemma 6. Then

$$|\bar{x}_R - \bar{x}_P| = \left| \int_X xR(dx) - \int_X xP(dx) \right| \leqslant \int_X |x|\,|R - P|(dx) \leqslant \|R - P\| < \alpha$$

(the second inequality is due to $|x| \leqslant 1$ for all $x \in S^n$). Lemma 6 yields $\bar{x}_R = \bar{x}_{(1-\varepsilon)P+\varepsilon Q}$ for some $Q \in \mathscr{P}$ and some $\varepsilon, 0 \leqslant \varepsilon < \varepsilon_P^*$. Now $R \neq P$ entails $\bar{x}_R \neq \bar{x}_P$, see Bomze/Pötscher (1989, Proposition 25(a)). Thus

$$\varepsilon(\bar{x}_Q - \bar{x}_P) = \bar{x}_R - \bar{x}_P \neq o,$$

whence we deduce $\varepsilon > 0$ and $Q \neq P$. Furthermore we have $0 < \varepsilon < \varepsilon_P^* \leqslant \varepsilon_P(Q)$. Therefore we arrive at

$$\begin{aligned} E(P, R) - E(R, R) &= (\bar{x}_P - \bar{x}_R)'\bar{f}(\bar{x}_R) \\ &= (\bar{x}_P - \bar{x}_{(1-\varepsilon)P+\varepsilon Q})'\bar{f}(\bar{x}_{(1-\varepsilon)P+\varepsilon Q}) \\ &= \varepsilon(\bar{x}_P - \bar{x}_Q)'f((1 - \varepsilon)P + \varepsilon Q) \\ &= \varepsilon(E(P, (1 - \varepsilon)P + \varepsilon Q) - E(Q, (1 - \varepsilon)P + \varepsilon Q)) > 0, \end{aligned}$$

establishing the desired inequality. □

Turning finally towards the replicator dynamics, it might be convenient to note that, for mixed strategy games, $(\mathscr{R})$ can be written in the following, simpler way:

$$\dot{\varphi}_{Q(t)}(x) = \varphi_{Q(t)}(x)[x'f(Q(t)) - \bar{x}_{Q(t)}{}'f(Q(t))], \quad x \in X.$$

Moreover, in a population game we can simplify further to the form

$$\dot{\varphi}_{Q(t)}(x) = \varphi_{Q(t)}(x)[x - \bar{x}_{Q(t)}]'\bar{f}(\bar{x}_{Q(t)}), \quad x \in X.$$

Example 1, continued. Games with finitely many strategies as population games. For simplicity, we again assume that $\mathscr{P}$ consists of all distributions concentrated on $X = \{x_1, \ldots, x_k\}$, so that every $q \in S^k$ gives rise to a state $Q = \sum_{j=1}^k q_j\delta_{x_j} \in \mathscr{P}$. Identifying $\{x_1, \ldots, x_k\}$ with $\{e_1, \ldots, e_k\} \subset \mathbb{R}^k$, we pass to the model where $\mathscr{P}$ consists of all discrete polymorphisms Q concentrated on $\{e_1, \ldots, e_k\} \subset S^k$. Consequently,

$$\bar{x}_Q = q \quad \text{if and only if} \quad Q = \sum_{j=1}^{k} q_j \delta_{e_j},$$

and hence $\bar{X} = S^k$ is polyhedral. Moreover, the response function is given by $\bar{f}(\bar{x}_Q) = h(q)$. Therefore a game with finitely many strategies can be viewed as a population game with polyhedral $\bar{X}$ and thus Theorem 7 is in force. Finally note that the replicator dynamics takes the form

$$\dot{q}_j(t) = q_j(t)[x_j - \bar{x}_{Q(t)}]'\bar{f}(\bar{x}_{Q(t)}), \quad 1 \leqslant j \leqslant k.$$

Now we show that the assumptions of Lemma 1 in Sect. 3 are satisfied if the response function is smooth:

Theorem 8 *Consider a population game with response function $\bar{f}$, which is defined in an open neighbourhood U of $\bar{X}$, and which is continuously differentiable there. Then the assumption of Lemma* 1 *holds.*

Proof. At first note that due to $|x| \leqslant 1$ for all $x \in X \subseteq S^n$, we have $|\bar{x}_\mu| \leqslant \|\mu\|$ for any $\mu \in \mathscr{L}$, if $\bar{x}_\mu = \int_X x\mu(dx) \in \mathbb{R}^n$. Denote by $B = \{x \in \mathbb{R}^n : |x| \leqslant 2\}$ and assume without loss of generality that $U \subset B$. Pick a closed set V such that $\bar{X} \subset V \subset U \subset B$, and choose a smooth function $\psi : B \to [0, 1]$ which vanishes outside of U, and is equal to unity on V. Define

$$\bar{g}(x) = \begin{cases} \psi(x)\bar{f}(x), & \text{if } x \in U, \\ 0, & \text{otherwise.} \end{cases}$$

Then $\bar{g}$ is bounded and *Lipschitz* on B. Now put for $\mu \in \mathscr{L}$

$$g(\mu) = \begin{cases} (2 - \|\mu\|)\bar{g}(\bar{x}_\mu), & \text{if } \|\mu\| \leqslant 2, \\ 0, & \text{otherwise.} \end{cases}$$

If $\varphi_\mu(x) = (x - \bar{x}_\mu)'g(\mu)$ for $x \in X$, then $\varphi_\mu : X \to \mathbb{R}$ is bounded, measurable, and

$$\varphi_Q(x) = (x - \bar{x}_Q)'\bar{f}(\bar{x}_Q) = F_Q(x) - E(Q, Q) \quad \text{for all } x \in X.$$

Therefore conditions (i) and (ii) of Lemma 1 are satisfied. From

$$\varphi_\mu(x) - \varphi_\nu(x) = (x - \bar{x}_\mu)'[g(\mu) - g(\nu)] + (\bar{x}_\nu - \bar{x}_\mu)'g(\nu),$$

and from

$$g(\mu) - g(\nu) = (2 - \|\mu\|)[\bar{g}(\bar{x}_\mu) - \bar{g}(\bar{x}_\nu)] + (\|\nu\| - \|\mu\|)\bar{g}(\bar{x}_\nu),$$

we see also that condition (iii) holds. ☐

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