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On equilibrium properties of evolutionary multi-player games with random payoff matrices

The Anh Han [a,*], Arne Traulsen [b,*], Chaitanya S. Gokhale [b]

[a] *Center of Artificial Intelligence, Department of Informatics, Faculty of Science and Technologies, New University of Lisbon, P-2829-516 Caparica, Portugal*

[b] *Evolutionary Theory Group, Max-Planck-Institute for Evolutionary Biology, August-Thienemann-Straße 2, D-24306 Plön, Germany*

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ABSTRACT

The analysis of equilibrium points in biological dynamical systems has been of great interest in a variety of mathematical approaches to biology, such as population genetics, theoretical ecology or evolutionary game theory. The maximal number of equilibria and their classification based on stability have been the primary subjects of these studies, for example in the context of two-player games with multiple strategies. Herein, we address a different question using evolutionary game theory as a tool. If the payoff matrices are drawn randomly from an arbitrary distribution, what are the probabilities of observing a certain number of (stable) equilibria? We extend the domain of previous results for the two-player framework, which corresponds to a single diploid locus in population genetics, by addressing the full complexity of multi-player games with multiple strategies. In closing, we discuss an application and illustrate how previous results on the number of equilibria, such as the famous Feldman–Karlin conjecture on the maximal number of isolated fixed points in a viability selection model, can be obtained as special cases of our results based on multi-player evolutionary games. We also show how the probability of realizing a certain number of equilibria changes as we increase the number of players and number of strategies.

1. Introduction

Since the formal inception of game theory by von Neumann and Morgenstern (1944, 1953), the study of equilibrium points has been of special interest (Nash, 1950). In biology, game theory took the form of evolutionary game theory, where instead of choosing strategies, individuals are "born" with them (Maynard Smith and Price, 1973; Maynard Smith, 1982). The payoffs from the game are translated into the fitness of each strategy, naturally leading to a dynamical approach. Evolutionary game theoretic formulations of biological situations stress one of the underlying principles of many biological systems, which is known as frequency dependence. Under frequency dependent selection, the fitness is contingent on the frequencies of the different types in the population. To study how the frequencies of the strategies change over time, we make use of the replicator equation (Taylor and Jonker, 1978; Zeeman, 1980; Hofbauer and Sigmund, 1998; Schuster and Sigmund, 1983). Due to its generality, the replicator equation encompasses a variety of biological contexts from ecology to population genetics and from prebiotic to social evolution (Schuster and Sigmund, 1983). From a dynamical systems point of view, the continuous time frequency dependent selection equations from population genetics, the Lotka–Volterra equations from ecology, and the replicator equations all are closely related (Sigmund, 1987; Cressman, 1988; Hofbauer and Sigmund, 1998; Page and Nowak, 2002; Cressman, 2003). This similarity sometimes allows us to transfer results from one field to another (Traulsen and Reed, 2011).

In evolutionary game theory, fixed points of the dynamical system predict the composition of strategy frequencies where all the strategies have the same average fitness. Biologically, these points can predict a co-existence of different types in a population and the maintenance of polymorphism. The study of the properties of these equilibrium points has a long-standing history in classical game theory, evolutionary game theory and population genetics (Kingman, 1961; Karlin and Feldman, 1970; Bishop and Cannings, 1976; Karlin, 1980; Cannings et al., 1993; Broom et al., 1993, 1997; Altenberg, 2010). One of the most significant advances has been the study of the maximal number of equilibrium points of a system and the attainability of the patterns of evolutionarily stable strategies in an evolutionary system (Maynard Smith, 1982; Karlin, 1980; Vickers and Cannings, 1988a,b; Cannings and Vickers, 1988; Karlin and Feldman, 1970; Broom et al., 1993, 1997; Altenberg, 2010). We provide an analytic estimation for the maximal number of equilibria of general multi-player multi-strategy systems, which generalizes existing results in the literature (Karlin and Feldman, 1970; Rowe, 1988; Feldman, 2009; Altenberg, 2010).

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* Corresponding authors.
E-mail address: traulsen@evolbio.mpg.de (A. Traulsen).

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Here, we study how natural and frequent internal equilibria are in a given class of games. That is, if we know the maximal number of equilibria possible in a system, what is the probability to obtain a certain number of equilibria when payoff matrices are randomly chosen (Berg and Engel, 1998; Eriksson and Lindgren, 2002; Broom, 2005; Gokhale and Traulsen, 2010; Huang and Traulsen, 2010; Haigh, 1988, 1989; Cannings and Vickers, 1988). Furthermore, we explore the probability that these equilibria are stable. Biologically, the presence of a stable internal equilibrium, involving all strategies, provides an estimate for the maximal level of biodiversity one can expect in a biological system (Levin, 2000, 2009; Gokhale and Traulsen, 2010). Our findings may have direct applications in the study of evolutionary, ecological or genetic systems in which very limited information is available, or the environment changes so rapidly and frequently that one cannot predict the payoffs of their inhabitants (May, 1973a,b; Fudenberg and Harris, 1992; Gross et al., 2009).

2. Model and results

2.1. Two-player evolutionary games

Consider two types A and B in an infinitely large population. In genetic terms, these could as well be considered as alleles (Sigmund, 1987; Cressman, 1992; Hofbauer and Sigmund, 1998; Weissing and van Boven, 2001; van Veelen, 2007; Traulsen and Reed, 2011). We begin with the simplest evolutionary game of two players and two strategies with the payoff matrix (payoffs for the row player)

$$\begin{array}{c} \\ \mathrm{A} \\ \mathrm{B} \end{array} \begin{array}{c} \begin{array}{cc} \mathrm{A} & \mathrm{B} \end{array} \\ \left(\begin{array}{cc} \beta_{A,A} & \beta_{A,B} \\ \beta_{B,A} & \beta_{B,B} \end{array} \right) \end{array}. \tag{1}$$

The frequencies of strategies A and B are given by x and $1 - x$, respectively. The average payoffs of the two strategies, π_A and π_B, can be written as

$$\pi_A = x\beta_{A,A} + (1-x)\beta_{A,B}$$
$$\pi_B = x\beta_{B,A} + (1-x)\beta_{B,B}. \tag{2}$$

We follow a usual convention in the replicator dynamics and equate payoff and fitness. The average fitness of the whole population is the weighted sum of these two fitnesses,

$$\langle \pi \rangle = x\pi_A + (1-x)\pi_B. \tag{3}$$

Comparing the average fitness of a strategy to that of the population, we can infer if the frequency of that strategy will increase or decrease. This is captured by the replicator equation (Hofbauer and Sigmund, 1998),

$$\dot{x} = x(\pi_A - \langle \pi \rangle) = x(1-x)(\pi_A - \pi_B). \tag{4}$$

From the replicator equation (4), we see that it has two trivial equilibria, $x = 0$ and $x = 1$. A third equilibrium is possible, as the average payoff difference is linear in x. Focusing our attention on the potential internal equilibrium, we ask: what is the probability that we obtain such an internal equilibrium if the payoff entries are randomly drawn from any given continuous distribution? Furthermore, what is the probability that it is stable?

Considering two strategies is the simplest case. For n strategies, we have a $n \times n$ payoff matrix $\{\beta_{j,k}\}_{j,k=1}^{n}$, where j is the strategy of the focal player and k is that of the opponent. The replicator dynamics with n strategies is given by

$$\dot{x}_i = x_i(\pi_i - \langle \pi \rangle) = x_i \sum_{j=1}^{n} x_j(\pi_i - \pi_j) \quad \text{for } i = 1, \ldots, n-1, \tag{5}$$

where x_i is the frequency of strategy i, $\sum_{i=1}^{n} x_i = 1$, $\pi_i = \sum_{k=1}^{n} x_k \beta_{ik}$ is the average payoff of strategy i, and $\langle \pi \rangle = \sum_{k=1}^{n} x_k \pi_k$ is the average payoff of the population. Note the similarity between the replicator equation and the continuous time selection equation (Crow and Kimura, 1970; Cressman, 2003) where x_i would denote the frequency while π_i is the fitness of genotype i in haploids. In diploids the same corresponds to the ith allele. In the diploid case however the fitness term has a more complex meaning as it is the average fitness of the ith allele. In the diploid case, it is usually reasonable to assume $\beta_{ik} = \beta_{ki}$, such that all heterozygotes have identical fitness. In evolutionary game theory, such games are called partnership games (Hofbauer and Sigmund, 1998). Here, we do not impose this symmetry on our random games for two reasons. First, this symmetry precludes distortions due to drive mechanisms (Traulsen and Reed, 2011). Second, it simplifies the extension to multi-player games, where such an obvious equivalent in genetics does not exist. The evolution of this system can be studied on a simplex with n vertices, S_n. The simplex S_n is defined by the set of all coordinates $(x_1, \ldots, x_n)$ satisfying $\sum_{i=1}^{n} x_i = 1$. The internal fixed points of this system are given by the points $(x_1, \ldots, x_n) \in S_n$ which satisfy

$$\pi_i = \pi_n \quad \text{for } i = 1, \ldots, n-1, \tag{6}$$

such that $x_i > 0$ for all i. There can exist at most one such isolated internal fixed point (Hofbauer and Sigmund, 1998), because in the non-degenerate case, a system of n linear equations in n variables ($n - 1$ distinct equations in (6) and $\sum_{i=1}^{n} x_i = 1$) has a unique solution. Next, we analyze the probability that such a fixed point occurs when the payoff entries $\beta_{j,k}$ are randomly chosen from an arbitrary continuous distribution. We call games with such random payoff matrices 'random games'.

We assume that all the payoff entries $\beta_{i,k}$ are continuous random variables with the *same* distribution, that is, with the same probability density function $f_\beta(\cdot)$. The coefficients of the difference $\pi_i - \pi_n$ are differences of two independent random variables with the same distribution. These random variables thus have a mean of 0, and are defined in a symmetric interval—denoted henceforth by $(-\alpha, \alpha)$, where α is a positive number or infinity. We first show that the density function of the payoff differences, denoted by $F_\beta(\cdot)$, is symmetric, i.e.,

$$F_\beta(x) = F_\beta(-x) \quad \text{for all } x. \tag{7}$$

Indeed, the density function of the difference of two independent random variables is the cross-correlation of their density functions (Grinstead and Snell, 1997a),

$$F_\beta(x) = \int_{-\infty}^{+\infty} f_\beta(y) f_\beta(x+y)\, dy. \tag{8}$$

We have

$$\begin{aligned} F_\beta(-x) &= \int_{-\infty}^{+\infty} f_\beta(z) f_\beta(-x+z)\, dz \\ &= \int_{-\infty}^{+\infty} f_\beta(x+y) f_\beta(y)\, dy = F_\beta(x). \end{aligned} \tag{9}$$

The latter equation is obtained by using a transformation $z = y + x$.

For simplicity, in our analysis we focus on payoff matrices with *continuous* random variables. However, our results can be extended for discrete random variables, except for the second part of the following theorem.

Theorem 1. *In a random two-player game with n strategies, the probability that there exists a (unique) isolated internal equilibrium is 2^{1-n}. Furthermore, the probability of having non-isolated equilibria is 0.*

Proof. Eq. (6) can be written as a system of linear equations

$$\begin{cases} \sum_{j=1}^{n} a_{i,j} x_j = 0 \quad \text{for } i = 1, \ldots, n-1 \\ \sum_{j=1}^{n} x_j = 1 \end{cases} \tag{10}$$

where $a_{i,j}$ are random variables with symmetric density function, $F_\beta(\cdot)$, defined in the interval $(-\alpha, \alpha)$. Consider the matrix

$$A = \begin{pmatrix} a_{1,1} & \cdots & a_{1,n} \\ \cdots & \cdots & \cdots \\ a_{n-1,1} & \cdots & a_{n-1,n} \\ 1 & \cdots & 1 \end{pmatrix}.$$

If $\det(A) \neq 0$, the system has a unique solution, which is given by Cramer's rule (Robinson, 1991)

$$x_j = \frac{\sigma_j}{\det(A)} \quad \text{for all } j = 1, \ldots, n \tag{11}$$

where

$$\sigma_j = (-1)^{n+j} \begin{vmatrix} a_{1,1} & \cdots & a_{1,j-1} & a_{1,j+1} & \cdots & a_{1,n} \\ \cdots & & \cdots & & \cdots & \\ \cdots & & \cdots & & \cdots & \\ a_{n-1,1} & \cdots & a_{n-1,j-1} & a_{n-1,j+1} & \cdots & a_{n-1,n} \end{vmatrix}.$$

We have $x_j > 0$ if and only if σ_j has the same sign as $\det(A)$. Furthermore, $\det(A) = \sum_{j=1}^{n} \sigma_j$. Thus, $x_j > 0$ for all j if and only if all σ_j have the same sign, $\sigma_j > 0$ for all $1 \le j \le n$ or $\sigma_j < 0$ for all $1 \le j \le n$.

The determinant σ_j is a continuous function in its variables $a_{i,k}$. In addition, by changing all the elements in a row or column to the opposite sign, σ_j changes to its opposite sign. Thus, the range of σ_j is a symmetric interval. For any symmetric distribution of $a_{i,k}$ (see Eq. (7)), the probability of σ_j obtaining a positive value is $P(\sigma_j > 0) = 1/2$. Furthermore, the probability, p_i, that σ_i has the same sign as all σ_j with $j < i$, given that all σ_j with $j < i$ already have the same sign, is

$$p_i = \frac{1}{2} \quad \text{for all } i \ge 3. \tag{12}$$

This is because there exists a column common to all $\sigma_j,\ j < i$, that is not contained in σ_i. We can switch the sign of all its entries to change the sign of all $\sigma_j,\ j < i$. Now, by applying Bayes' chain rule (Russell and Norvig, 2009, pages 495–499), the probability that all σ_i have the same sign reads

$$P(\sigma_1, \ldots, \sigma_n \text{ have the same sign}) = P(\sigma_1, \sigma_2 \text{ have the same sign}) \prod_{i=3}^{n} p_i. \tag{13}$$

Since σ_1 and σ_2 each has a column that is not contained in the other, the two events $\sigma_1 > 0$ and $\sigma_2 > 0$ (respectively for <0) are independent. Thus,

$$P(\sigma_1, \sigma_2 \text{ have the same sign}) = P(\sigma_1 > 0)P(\sigma_2 > 0) + P(\sigma_1 < 0)P(\sigma_2 < 0) = \frac{1}{2}. \tag{14}$$

Thus, from Eqs. (12)–(14), the probability of having a single (thus, isolated) internal equilibrium in a random game is 2^{1-n}. This result is independent of the distributions of the payoff entries.

We now move to the second part of the theorem. The equation $\det(A) = 0$ defines a hyper-surface in the simplex $(-\alpha, \alpha)^{(n-1)^2}$, since at least one payoff entry can be defined as a function of the remaining ones. The probability that $\det(A) = 0$ is the probability of a point randomly drawn belonging to a hyper-surface within a simplex thus equals 0, independent of the (continuous) distribution. Indeed, the volume of the hyper-surface is a multivariable integral over all variables in $\det(A)$ (Gut, 2009, Chapter 1), which contains one integral with coinciding upper and lower limits—the one of the variables that is defined as the function of the remaining variables.[1] □

Note that this second part of the theorem is not valid in general if the payoff entries are chosen from discrete distributions instead of continuous ones, as previously discussed. The probability that the equation $\det(A) = 0$ holds is positive if there exist values of the payoff entries in their discrete space satisfying the equation. The probability remains 0 otherwise.

This result implies that in nature, the case of non-isolated fixed points should not be observed in generic cases. This reassures the appropriateness of previous work that omits the case of non-isolated fixed points, focusing on studying *isolated* fixed points only. This argument has also been put forward by Haigh (1988). Similar arguments can be used for the case of closed orbits in the Rock–Paper–Scissors game (Hofbauer and Sigmund, 1998; Reichenbach et al., 2007a,b; Claussen and Traulsen, 2008). In the symmetric Rock–Paper–Scissors game, closed orbits occur if and only if the time derivative of the quantity $V = x_1 x_2 x_3$ is zero, i.e., $\dot{V} = 0$ for all x_1, x_2, and x_3 (Hofbauer and Sigmund, 1998; Sigmund, 2010). The quantity $\dot{V}$ depends on the payoff entries. From the equation we can similarly show that there is a payoff entry that can be represented as a function of the remaining ones. Thus, if the payoff entries are randomly drawn from continuous distributions, the probability that the equation holds is 0. In other words, closed orbits will not arise if payoffs are random, even in the absence of noise.

Next, we focus on the stability of the unique isolated internal equilibrium. As mentioned earlier, stable fixed points have attracted special interest, since biologically they denote a co-existence of different types. In the following, we assess the probability that an internal equilibrium in a random two-player n-strategy game is stable.

Theorem 2. *The probability that a random two-player n-strategy game has a stable internal equilibrium is at most 2^{-n}. In the case $n = 2$, this probability is exactly $2^{-2} = \frac{1}{4}$.*

Proof. Recall that for a two-player game with n strategies, the replicator equations are (Hofbauer and Sigmund, 1998; Sigmund, 2010)

$$\dot{x}_i = x_i (\pi_i - \langle \pi \rangle) \quad \text{for } i = 1, \ldots, n-1. \tag{15}$$

We denote $\boldsymbol{x} = (x_1, \ldots, x_n)$. Suppose $\boldsymbol{x}^* = (x_1^*, \ldots, x_n^*)$ is the isolated internal equilibrium of the system, i.e. $x_i^* > 0$ for all $1 \le i \le n$. The point $\boldsymbol{x}^*$ is a stable equilibrium if and only if all the eigenvalues of the Jacobian matrix

$$J(\boldsymbol{x}) = \begin{pmatrix} \frac{\partial \dot{x}_1}{\partial x_1} & \cdots & \frac{\partial \dot{x}_1}{\partial x_{n-1}} \\ \cdots & \cdots & \cdots \\ \frac{\partial \dot{x}_{n-1}}{\partial x_1} & \cdots & \frac{\partial \dot{x}_{n-1}}{\partial x_{n-1}} \end{pmatrix} \tag{16}$$

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[1] The simplest case for a univariate distribution of a continuous random variable, say X, is usually seen in textbooks (Feller, 1968, pages 1–5) (Grinstead and Snell, 1997b, pages 55–59). Namely, suppose X has a probability density function $h(x)$, then its probability to fall into a given interval, say $[a, b]$, is given by the integral: $P(a \le X \le b) = \int_a^b h(x)dx$. Hence, the probability with which X 'falls into' any particular point a is $P(X = a) = \int_a^a h(x)dx = 0$. The argument can be readily generalized for the general case of multivariate distributions.

at $\boldsymbol{x}^*$ have negative real parts (Hofbauer and Sigmund, 1998). Note that due to normalization of frequencies, $x_n = 1 - \sum_{i=1}^{n-1} x_i$, it is sufficient to consider a Jacobian with dimension $(n-1) \times (n-1)$. Keeping the additional row and column in the Jacobian would simply lead to an additional eigenvalue zero. Since $(\pi_i - \langle\pi\rangle)|_{x^*} = 0$, we obtain

$$\left.\frac{\partial \dot{x}_i}{\partial x_j}\right|_{\boldsymbol{x}^*} = x_i^* \left.\frac{\partial\left(\pi_i - \langle\pi\rangle\right)}{\partial x_j}\right|_{\boldsymbol{x}^*}. \tag{17}$$

We have

$$\frac{\partial \pi_i}{\partial x_j} = \frac{\partial\left(\sum_{k=1}^{n-1} \beta_{ik} x_k + \beta_{in} x_n\right)}{\partial x_j} = \beta_{ij} - \beta_{in},$$

$$\frac{\partial \langle\pi\rangle}{\partial x_j} = \frac{\partial\left(\sum_{k=1}^{n} x_k \pi_k\right)}{\partial x_j} = \sum_{k=1}^{n} x_k\left(\beta_{kj} - \beta_{kn}\right) + \pi_j - \pi_n.$$

Since $\boldsymbol{x}^*$ is an equilibrium, it follows $\pi_j(\boldsymbol{x}^*) = \pi_n(\boldsymbol{x}^*)$. Thus,

$$\left.\frac{\partial\left(\pi_i - \langle\pi\rangle\right)}{\partial x_j}\right|_{\boldsymbol{x}^*} = \beta_{ij} - \beta_{in} - \sum_{k=1}^{n} x_k^*\left(\beta_{kj} - \beta_{kn}\right). \tag{18}$$

The addition of a constant to each column of the payoff matrix $\{\beta_{ij}\}_{i,j=1}^n$ does not change Eq. (15) on S_n (Hofbauer and Sigmund, 1998). Therefore, we add $-\beta_{nj}$ to column j and transform the matrix such that the last row is made up of zeros. Without loss of generality we can therefore assume that $\beta_{nk} = 0$ for all $k = 1, \ldots, n$ and $\beta_{ij} \in (-\alpha, \alpha)$ for all $i \leq n-1$. Hence, the terms $\beta_{nj} = \beta_{nn} = 0$ can be removed from Eq. (18). Now the terms β_{ij} are equivalent to a_{ij} in the proof of Theorem 1. As a result of such a transformation, all payoffs are zero at the equilibrium point,

$$\begin{aligned} 0 &= \sum_{k=1}^{n} \beta_{ik} x_k^* = \sum_{k=1}^{n-1} \beta_{ik} x_k^* + \beta_{in}\left(1 - \sum_{k=1}^{n-1} x_k^*\right) \\ &= \beta_{in} + \sum_{k=1}^{n-1} (\beta_{ik} - \beta_{in}) x_k^*. \end{aligned}$$

Thus, Eq. (18) can be rewritten as

$$\left.\frac{\partial(\pi_i - \langle\pi\rangle)}{\partial x_j}\right|_{\boldsymbol{x}^*} = \beta_{ij} + \sum_{k=1}^{n-1} x_k^* (\beta_{ik} - \beta_{in} - \beta_{kj} + \beta_{kn}). \tag{19}$$

Ergo, from Eqs. (17) and (19) the trace of the Jacobian matrix can be simplified as

$$\begin{aligned} \mathrm{Tr}(J(\boldsymbol{x}^*)) &= \sum_{i=1}^{n-1} x_i^* \left.\frac{\partial(\pi_i - \langle\pi\rangle)}{\partial x_i}\right|_{\boldsymbol{x}^*} \\ &= \sum_{i=1}^{n-1} x_i^* \beta_{ii} + \sum_{i=1}^{n-1}\sum_{k=1}^{n-1} x_i^* x_k^* (\beta_{ik} - \beta_{in} - \beta_{ki} + \beta_{kn}) \\ &= \sum_{i=1}^{n-1} x_i^* \beta_{ii} + \sum_{i=1}^{n-1}\sum_{k=1}^{n-1} x_i^* x_k^* (\beta_{ik} - \beta_{ki}) \\ &\quad + \sum_{i=1}^{n-1}\sum_{k=1}^{n-1} x_i^* x_k^* (\beta_{kn} - \beta_{in}) \\ &= \sum_{i=1}^{n-1} x_i^* \beta_{ii}. \end{aligned} \tag{20}$$

Note that the double sums are zero as a result of the symmetry of the summation indices i and k in the under-sum terms, $x_i^* x_k^* (\beta_{ik} - \beta_{ki})$ and $x_i^* x_k^* (\beta_{kn} - \beta_{in})$.

The trace is actually the sum of all the eigenvalues of the Jacobian matrix, and thus also equals the sum of their real parts. Therefore, in order for all the eigenvalues of the matrix to have negative real parts, it is necessary that

$$\mathrm{Tr}(J(\boldsymbol{x}^*)) < 0. \tag{21}$$

Notice that a system admits the same equilibrium point $\boldsymbol{x}$ if we change the sign of all β_{ij} $(1 \leq i \leq n-1,\ 1 \leq j \leq n)$ simultaneously (see Eq. (11)). As all β_{ij} have a symmetric probability density function (see Eq. (7)), this inequality holds with probability 1/2. Since the inequality is a necessary condition for the given equilibrium to be stable, the equilibrium is stable with probability at most 1/2. From Theorem 1, it follows that the probability that the system has a stable equilibrium is at most $\frac{1}{2} \cdot 2^{1-n} = 2^{-n}$.

In the case $n = 2$, inequality (21) is also the sufficient condition for $\boldsymbol{x}^*$ to be stable. Hence, in this case the probability of having a stable internal equilibrium is $2^{-2} = 1/4$, as expected. A numerical investigation of random games shows that for $n \geq 3$, the upper bound 2^{-n} is not reached, namely, for the uniform (Gokhale and Traulsen, 2010) and Gaussian distributions. This suggests an upper bound that is smaller than 2^{-n} for $n \geq 3$. □

2.2. Multi-player evolutionary games

Now we move on to the case of multi-player games. In this context, a special class of multi-player evolutionary games has been extensively studied, public goods games and their generalizations (Hardin, 1968; Szabó and Hauert, 2002; Hauert et al., 2002, 2006a,b; Santos et al., 2008; Pacheco et al., 2009; Souza et al., 2009; Kurokawa and Ihara, 2009; Chiong and Kirley, 2011; Lessard, 2011).

We consider multi-player games with multiple strategies. Let $d \geq 2$ be the number of participants in a game and $n \geq 2$ the number of possible strategies.

Suppose that the game is symmetrical among all players, such that the order of the players is irrelevant. Let $\beta_{i_0,i_1,\ldots,i_{d-1}}$ denote the payoff of the focal player, where i_0 is the strategy of the focal player, and i_p, $1 \leq p \leq d-1$, is the strategy of the player in position p. These payoffs form a $(d-1)$-dimensional payoff matrix. For the game symmetry, the payoff entries must satisfy

$$\beta_{i_0,i_1,\ldots,i_{d-1}} = \beta_{i_0,i'_1,\ldots,i'_{d-1}}$$

for any permutation $(i'_1, \ldots, i'_{d-1})$ of $(i_1, \ldots, i_{d-1})$. This means that only the fraction of each strategy of the other participants matters.

The average payoff (fitness) of the focal player is given by

$$\pi_{i_0} = \sum_{i_1,\ldots,i_{d-1}=1}^{n} \left(\beta_{i_0,i_1,\ldots,i_{d-1}} \prod_{k=1}^{d-1} x_{i_k}\right). \tag{22}$$

Hereafter the calculations leading to the replicator dynamics and the arguments for the interior fixed points are the same as in Eqs. (5)–(7). The system in Eq. (6) for this case is generalized into a system consisting of n multivariate polynomials of degree $d-1$ and with n variables.

2.3. d-player games with two strategies

We first consider multi-player games with an arbitrary number of players d, but only two strategies $(n = 2)$. In this case, solving Eq. (6) consists in solving a univariate polynomial equation with $x \in (0, 1)$ (Broom et al., 1997; Bukowski and Miekisz, 2004; Hauert et al., 2006b; Pacheco et al., 2009; Kurokawa and Ihara, 2009; Gokhale and Traulsen, 2010),

$$\sum_{k=0}^{d-1} \beta_k \binom{d-1}{k} x^k (1-x)^{d-1-k} = 0, \tag{23}$$

where x is the fraction of strategy 1 (i.e., $1 - x$ is that of strategy 2) and β_k is specifically the payoff to strategy 1 minus that to strategy 2 obtained in a d-player interaction with k other participants using strategy 1.

Let $y = \frac{x}{1-x}$, $0 < y < \infty$. With this, Eq. (23) is simplified to

$$\sum_{k=0}^{d-1} \beta_k \binom{d-1}{k} y^k = 0. \tag{24}$$

The polynomial on the left hand side has a degree of $d - 1$. Thus, according to the fundamental theorem of algebra (Courant and Robbins, 1996), the system has at most $d - 1$ equilibria (Hauert et al., 2006b). From this equation one also can see that a system admits the same set of equilibria if we change the sign of all β_k simultaneously.

For $d = 2$, we recover the result for two-player games wherein at most one internal isolated equilibrium can be attained.

Next, we consider the special cases $d = 3$ and $d = 4$ and calculate the probability that we obtain the maximal number of equilibria therein (2 and 3, respectively). It is known that univariate polynomials of order greater than 4 cannot be solved analytically (Abel, 1826; Stewart, 2004). Thus, it would be challenging to provide analytical computation of the probabilities of having a particular number of equilibria for the case $d > 5$.

Example 2.1 (*Three-Player Game with Two Strategies*)**.** Compute the probability of having two internal equilibria.

Solution. The system has two equilibria if and only if the quadratic equation (see Eq. (24))

$$\beta_2 y^2 + 2\beta_1 y + \beta_0 = 0$$

has two distinct positive roots. This is equivalent to:

$$\begin{cases} {\beta_1}^2 > \beta_0\beta_2 \\ \beta_1\beta_2 < 0 \\ \beta_0\beta_2 > 0. \end{cases} \tag{25}$$

The first condition guarantees the equation has two distinct real roots, and the last two make sure that these two roots are positive. These inequalities define two separate spaces,

$$D_1 = \Big\{ (\beta_0, \beta_2, \beta_1) \in \mathbb{R}^3 : 0 < \beta_0 < \alpha;\ 0 < \beta_2 < \alpha; \\ -\alpha < \beta_1 < -\sqrt{\beta_0\beta_2} \Big\}$$

and

$$D_2 = \Big\{ (\beta_0, \beta_2, \beta_1) \in \mathbb{R}^3 : -\alpha < \beta_0 < 0; \\ -\alpha < \beta_2 < 0;\ \alpha > \beta_1 > \sqrt{\beta_0\beta_2} \Big\}.$$

Recall that β_0, β_1 and β_2 are independent, and have the same probability density function $F_\beta(\cdot)$. Hence, the random variable $(\beta_0, \beta_1, \beta_2)$ has a joint probability density function given by Gut (2009, Chapter 1)

$$g(\beta_0, \beta_1, \beta_2) = F_\beta(\beta_0)F_\beta(\beta_1)F_\beta(\beta_2). \tag{26}$$

The probability that $(\beta_0, \beta_1, \beta_2)$ falls into the space $D_1 \cup D_2$ is given by

$$p_\beta = \int_{D_1 \cup D_2} g(\beta_0, \beta_1, \beta_2)\, d\beta_0\, d\beta_1\, d\beta_2. \tag{27}$$

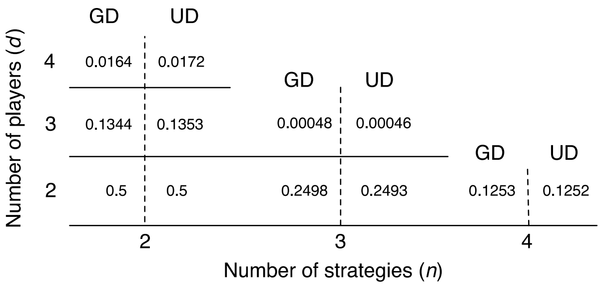

Fig. 1. *Probabilities to obtain the maximum possible number of isolated internal equilibria.* For a system with d players and n strategies the maximum number of isolated internal equilibria are given by $(d-1)^{n-1}$. The probability to obtain this upper bound can be derived by following the calculation provided in Example 2.1. For instance, for a three-player game with two strategies we calculate the probability of having two internal isolated equilibria to be $61/450 = 0.1355$ which is well corroborated by the simulation results (0.1353). The simulation results are based on sampling 1 000 000 payoff matrices where the payoff entries were drawn from a Gaussian distribution with variance 1 and mean 0 (GD) and from a standard uniform distribution (UD).

We now consider three distinct probability distributions of the payoff entries and show that the probability of realizing the maximal number of equilibria for three-player random games with two strategies depends on the distributions. This contrasts multi-player games with two-player random games (see Theorem 1).

First, if the payoff entries are such that all the β_i's ($i = 0, 1, 2$) have uniform distributions in the interval $[-\alpha, \alpha]$ (i.e. $F_\beta(x) = \frac{1}{2\alpha}$ if $-\alpha \le x \le \alpha$ and 0 otherwise), then

$$\begin{aligned} p_\beta &= \frac{1}{8\alpha^3}\Bigg(\int_0^\alpha \int_0^\alpha \int_{-\alpha}^{-\sqrt{\beta_0\beta_2}} d\beta_1\, d\beta_0\, d\beta_2 \\ &\quad + \int_{-\alpha}^0 \int_{-\alpha}^0 \int_{\sqrt{\beta_0\beta_2}}^{\alpha} d\beta_1\, d\beta_0\, d\beta_2 \Bigg) \\ &= \frac{5}{36} \approx 0.138889. \end{aligned} \tag{28}$$

If the payoff entries originally have uniform distributions, by applying the cross-correlation formula as given in Eq. (8) we obtain a probability density function for β_i

$$\begin{aligned} F_\beta(x) &= \int_{-\infty}^{+\infty} f(y)f(x+y)dy = \frac{1}{2\alpha}\int_{-\alpha}^{\alpha} f(x+y)dy \\ &= \begin{cases} \dfrac{\alpha + x}{\alpha^2} & \text{for } -\alpha \le x \le 0, \\ \dfrac{\alpha - x}{\alpha^2} & \text{for } 0 \le x \le \alpha, \\ 0 & \text{for } x < -\alpha \text{ or } x > \alpha. \end{cases} \end{aligned}$$

Now, resolving Eq. (27), we obtain

$$\begin{aligned} p_\beta &= \frac{1}{\alpha^6} \int_0^\alpha \int_0^\alpha \int_{-\alpha}^{-\sqrt{\beta_0\beta_2}} (\alpha - \beta_0)(\alpha - \beta_2) \\ &\quad \times (\alpha + \beta_1) d\beta_1\, d\beta_0\, d\beta_2 + \frac{1}{\alpha^6} \int_{-\alpha}^0 \int_{-\alpha}^0 \int_{\sqrt{\beta_0\beta_2}}^{\alpha} \\ &\quad \times (\alpha + \beta_0)(\alpha + \beta_2)(\alpha - \beta_1)\, d\beta_1\, d\beta_0\, d\beta_2 \\ &= \frac{61}{450} \approx 0.135556. \end{aligned} \tag{29}$$

Note that this result is corroborated by a numerical investigation for random games with uniformly distributed payoff entries in Gokhale and Traulsen (2010) (see also Fig. 1).

Next, if all the payoff entries have the Gaussian distribution with variance 1 and mean 0 we obtain

$$\begin{aligned} p_\beta &= \left(\frac{1}{2\sqrt{\pi}}\right)^3 \int_0^{+\infty} \int_0^{+\infty} \int_{-\infty}^{-\sqrt{\beta_0\beta_2}} e^{-\frac{\beta_0^2+\beta_1^2+\beta_2^2}{4}}\, d\beta_1\, d\beta_0\, d\beta_2 \\ &\quad + \left(\frac{1}{2\sqrt{\pi}}\right)^3 \int_{-\infty}^{0} \int_{-\infty}^{0} \int_{\sqrt{\beta_0\beta_2}}^{+\infty} e^{-\frac{\beta_0^2+\beta_1^2+\beta_2^2}{4}}\, d\beta_1\, d\beta_0\, d\beta_2 \\ &= 0.134148, \end{aligned} \tag{30}$$

which is different from the result for the uniform distribution, despite being numerically close to Eqs. (28) and (29). However, we note that even for more exotic distributions that can only be analyzed numerically, we have not obtained results that differ substantially from the values given above. Based on this approach one can derive such probabilities for any given probability distribution of the payoff entries.

Example 2.2 (*Four-Player Game with Two Strategies*)**.** Compute the probability of having three internal equilibria.

Solution. In a similar fashion, we can compute the probability of having three internal equilibria in a four-player game with two strategies, noting that the system has three equilibria if and only if the cubic equation (see Eq. (24))

$$\beta_3 y^3 + 3\beta_2 y^2 + 3\beta_1 y + \beta_0 = 0$$

has three distinct positive roots, which is in turn equivalent to the following system of inequalities (Irving, 2004)

$$\begin{cases} 18\beta_0\beta_1\beta_2\beta_3 - 12{\beta_2}^3\beta_0 + 9{\beta_2}^2{\beta_1}^2 - 12\beta_3{\beta_1}^3 - 3{\beta_3}^2{\beta_0}^2 > 0 \\ \beta_2\beta_3 < 0 \\ \beta_1\beta_3 > 0 \\ \beta_0\beta_3 < 0. \end{cases}$$

Analyzing these inequalities to reach the probability of seeing the maximal number of equilibria is a task mechanically similar to the case of three players, but considerably more complicated. Thus, we will not elaborate further on that computation here, but provide numerical results for the uniform and Gaussian distribution in Fig. 1.

Next we approach the question of stability of the equilibria in multi-player two-strategy games. For two strategies the simplex of the system is just a one-dimensional line. In a single dimension a fixed point can be either stable or unstable (we exclude the non-generic case of neutrally stable fixed points). If all the payoff entries are randomly chosen from the same distribution, an equilibrium is stable or unstable with a probability of 1/2, even for a multi-player game.

Theorem 3 (*Stability of Equilibria in Two-Strategy Multi-Player Games*)**.** *For multi-player games with two strategies, the probability that a given equilibrium is stable is* 1/2*. That is, given an equilibrium of the game, it is equally likely to be stable or unstable.*

Proof. For a d-player game with two strategies, the replicator equation is given by Hauert et al. (2006b), Pacheco et al. (2009) and Gokhale and Traulsen (2010)

$$\dot{x} = x(1-x)\sum_{k=0}^{d-1} \beta_k \binom{d-1}{k} x^k (1-x)^{d-1-k}. \tag{31}$$

Suppose $x^* \in (0,1)$ is an internal equilibrium of the system. Let $f(x)$ be the polynomial on the right hand side of the equation. Thus, $f(x^*) = 0$. Furthermore, x^* is stable if and only if $f'(x^*) < 0$. Let $y = \frac{x}{1-x}$ (and denote $y^* = y(x^*)$ accordingly) and $\beta'_k = \beta_k \binom{d-1}{k}$. We have

$$f(x) = x(1-x)^d \sum_{k=0}^{d-1} \beta'_k y^k. \tag{32}$$

Taking the derivative of $f(x)$ we obtain

$$\begin{aligned} f'(x) &= (1-x)^{d-1}(1-x-dx)\sum_{k=0}^{d-1}\beta'_k y^k \\ &\quad + x(1-x)^{d-2}\sum_{k=1}^{d-1} k\beta'_k y^{k-1}. \end{aligned} \tag{33}$$

Since $f(x^*) = 0$ and $x^* \in (0,1)$, from Eq. (32) we have that $\sum_{k=0}^{d-1} \beta'_k {y^*}^k = 0$. Hence,

$$f'(x^*) = x^*(1-x^*)^{d-2}\sum_{k=1}^{d-1} k\beta'_k {y^*}^{k-1}. \tag{34}$$

Consequently, $f'(x^*) < 0$ holds if and only if

$$\sum_{k=1}^{d-1} k\beta'_k {y^*}^{k-1} < 0. \tag{35}$$

Note that a system admits the same set of equilibria if we change the sign of all β'_k simultaneously (see Eq. (24)). If the payoff entries have the same distribution, such that all β'_k satisfy (7) (i.e., their probability density function is symmetric), the inequality (35) holds with probability 1/2. An equilibrium that is stable becomes unstable when we change the signs of all β'_k (and vice versa). □

So far we have considered an arbitrary equilibrium and then discussed its stability. It would be of interest to confine our analysis to equilibria for which we have more information, such as the number of evolutionarily stable states (ESS). For example if we consider a four-player case with two strategies, there can be at most three internal equilibria. Thus if we are interested in the patterns of possible ESS as in Broom et al. (1994), there are two possible configurations if no pure ESSs are present. Either there can be just a single internal equilibrium which has to be a mixed ESS or there can be two mixed ESS and one unstable equilibrium. Hence, the probability to obtain a single mixed ESS or two mixed ESS will depend on the probabilities of first having a single internal equilibrium or three internal equilibria. These probabilities have been provided in Gokhale and Traulsen (2010) for payoff matrices with entries drawn from a uniform distribution. Furthermore, these probabilities need to be multiplied by the probability of getting a single stable equilibrium or two stable equilibria. The probability of getting a single internal equilibrium is 0.48 (Gokhale and Traulsen, 2010). The probability that this single equilibrium is stable is 0.366 and conversely that it is unstable is 0.634. We have computed these probabilities by choosing 1 000 000 payoff matrices with entries chosen from a standard uniform distribution. The probability to get a single stable internal equilibrium is 0.1761. Similarly, the probability to obtain three internal equilibria is 0.0172 (Fig. 1). The probability that of those three, two are stable is 0.5. Thus, the probability to obtain three internal equilibria of which two are ESS is just 0.0086. This was just an example for a four-player game with two strategies. To explore all possible patterns of ESS for an arbitrary number of players and strategies would require a sophisticated numerical exploration of the parameter space. Our focus is on the equilibria in general and not on ESS, therefore interested readers are referred to Broom et al. (1994) for an in-depth discussion on this topic.

2.4. Multi-player games with an arbitrary number of strategies

Now we approach the full complexity of the evolutionary system of multi-player games with multiple strategies (arbitrary n and d). First we provide a formal proof of the result for the maximal number of isolated equilibria in a d-player n-strategy system which has been numerically (Broom et al., 1997) and intuitively (Gokhale and Traulsen, 2010) explored before. Once the maximal number of internal isolated equilibria is known, it is important to know whether these maxima are attainable. In other words, are the bounds sharp?

Theorem 4 (*Maximal Number of Internal Isolated Equilibria*)**.** *A d-player n-strategy game has at most* $(d-1)^{n-1}$ *isolated internal equilibria, and this bound is sharp.*

Proof. The proof of this theorem is a direct consequence of the famous Bézout's theorem (Bézout, 1779b,a; Kollár, 2008; Altenberg, 2010), which can be stated as (Kollár, 2008; Altenberg, 2010) Let $f_1(\boldsymbol{x}), \ldots, f_n(\boldsymbol{x})$ be n polynomials in n variables, and for each i let d_i be the degree of f_i. Then either

1. the equation(s) $f_1(\boldsymbol{x}) = \cdots = f_n(\boldsymbol{x}) = 0$ have at most $d_1 \cdots d_n$ solutions; or
2. the f_i vanish identically on an algebraic curve C, and so there is a continuous family of solutions.

In our case, the equilibria are the solutions of the system of multivariate polynomials of n variables

$$\begin{cases} \pi_i - \pi_n = 0 \quad \text{for } i = 1, \ldots, n-1 \\ \sum_{j=1}^{n} x_j = 1. \end{cases} \tag{36}$$

This gives $n-1$ polynomial equations of degree $d-1$, and one of degree 1. Since we are interested in systems with isolated internal fixed points, the second case of Bézout's theorem is excluded. Hence, the system can have at most $(d-1)^{n-1} * 1 = (d-1)^{n-1}$ isolated internal equilibria.

To prove that this bound is sharp, it is enough to construct a single payoff matrix which exhibits such a property. Indeed, in the following we provide a way to construct a family of such matrices.

Let us consider, for $i = 1, \ldots, n-1$, the polynomials

$$\pi_i - \pi_n = \frac{1}{U_i}\prod_{k=1}^{d-1}(x_i - \eta_{ki}) = \frac{1}{U_i}\prod_{k=1}^{d-1}\left(x_i - \eta_{ki}\sum_{j=1}^{n} x_j\right), \tag{37}$$

where $\eta_{ki} \in (0,1)$ such that $\eta_{ki} \neq \eta_{hi}$ for all $k \neq h \in \{1, \ldots, d-1\}$ and $\sum_{i=1}^{n-1} \eta_{k_i i} < 1$ for all $k_i \in \{1, \ldots, d-1\}$. It is easily seen that each term of the polynomials is of degree $d-1$. We choose positive constants U_i to be large enough so that coefficients of the polynomials are in the interval $(-\alpha, \alpha)$. Clearly, the set of zeros of the system of polynomial equation (36), Ξ, is given by

$$\left\{ \left(\eta_{k_1 1}, \ldots, \eta_{k_{n-1} n-1}, 1 - \sum_{i=1}^{n-1} \eta_{k_i i} \right) \middle| \; k_i = 1, \ldots, d-1 \; \forall i = 1, \ldots, n-1 \right\}. \tag{38}$$

We have $|\Xi| = (d-1)^{n-1}$. □

Throughout the article, we did not take into account the isolated equilibria that are on the boundaries of the simplex. Since we now know the maximal possible number of *internal* equilibria in a general multi-player multi-strategy system, we can recursively find the maximal number of internal equilibria in the subsystems with fewer strategies. These can be summed up to obtain the maximal possible total number of equilibria of a system. The following corollary provides a general formula allowing us to compute the maximal number of isolated equilibria, including those that belong to the boundaries and finally the vertices of the simplex.

Corollary 1 (*Maximal Number of Isolated Equilibria*)**.** *A d-player n-strategy game has at most* $\frac{d^n-1}{d-1}$ *isolated equilibria.*

Proof. In the boundary of the simplex with $i < n$ strategies having non-vanishing frequency, it is reduced to a d-player i-strategy game. There are $\binom{n}{i}$ such boundaries. Therefore, applying Theorem 4 for $i = 2, \ldots, n-1$ the number of isolated equilibria of a d-player n-strategy game is bounded by

$$\begin{aligned} &(d-1)^{n-1} + \binom{n}{1}(d-1)^{n-2} + \cdots + \binom{n}{n-2}(d-1) \\ &\quad + \binom{n}{n-1}(d-1)^0 \\ &= \frac{1}{d-1}\left[\left(\sum_{i=0}^{n}\binom{n}{i}(d-1)^{n-i}\right) - 1\right] = \frac{d^n-1}{d-1}. \quad \square \end{aligned} \tag{39}$$

3. Discussion

The famous Feldman and Karlin's conjecture (Karlin and Feldman, 1970; Karlin, 1980; Feldman, 2009) and its recent proof by Altenberg (2010) show that the maximal number of isolated fixed points for a deterministic viability selection model along with recombination between n haplotypes has an upper bound of $2^n - 1$. Here, we have recasted this into a game theoretic framework, where the different haplotypes correspond to different strategies (Cressman, 1992, Chapter 4) (Cressman, 2003, pages 53–57). Usually, it is assumed that there is no position effect, i.e. there is no difference between the fitness of genotypes $\beta_{i,j}$ and $\beta_{j,i}$. In game theoretic terms these games are termed partnership games (Hofbauer and Sigmund, 1998, page 82) and (Weissing and van Boven, 2001). Since this symmetry is natural from a genetic point of view, but not generic in evolutionary game theory, we relax this assumption. This also facilitates the extension to games with more than two players.

The proof provided by Altenberg works even for imperfect transmission, which can be caused by recombination, mutation, segregation distortion, etc. Altenberg introduces the transformation matrix $[T_{i,j,k}]$, which gives the probability of a genotype jk producing a gamete of type i. This matrix can encompass various genetic distortions such as recombination, mutation, gene conversions, etc. Hence, the proof by Altenberg goes much further than the original constraints of the Feldman and Karlin conjecture and also beyond the scope of our present game theoretic formulation. Our approach is not able to handle such complexities. Hence, we compare our work to Altenberg's only in the case of perfect transmission. In this case, we obtain from Corollary 1 that the maximum number of isolated equilibria for $d = 2$ is $\frac{2^n-1}{2-1} = 2^n - 1$, as shown previously by Altenberg (2010).

If we are interested in the changes in allele frequencies then we need to look at the dynamics at the level of the alleles. For a single locus n alleles model, each diploid individual will have two copies. Hence at the level of the alleles this is a four-player game with two alleles in each mating partner. Again we do not assume the symmetry $\beta_{i,j} = \beta_{j,i}$. For an n alleles model, this would give us a maximum of $\frac{4^n-1}{4-1} = \frac{1}{3}(4^n - 1)$ as shown in Rowe (1988), which is also a special case of Corollary 1 for $d = 4$. For a polyploid system with a perfect transmission system, we can determine the upper bound for n alleles with $d = 2 \times$ ploidy. The 2 still remains in determining d, representing the fact that a zygote is formed from two gametes. It would be interesting, but challenging to develop the model provided by Altenberg for a polyploid system and to check the maximum number of equilibria derived for arbitrary transmission processes.

As discussed earlier, knowing the maximal number of equilibria of an evolutionary process is insightful (Levin, 2000, 2009; Gokhale and Traulsen, 2010). But if we do not know the precise interaction of the evolving agents, then it is relevant to ask for the probability to obtain a certain number of internal equilibria and to assess their stability. In other words, even if we know the maximum, how probable is it to attain it when we choose the payoff entries randomly? We can answer these questions precisely in two different limits. (i) For a game with $d = 2$ and an arbitrary number of strategies n, from Theorems 1 and 2, the probability that a randomly drawn payoff matrix will have an equilibrium in the interior is 2^{1-n} and the probability that there is a stable equilibrium is *at most* 2^{-n} (for $n = 2$ it is *exactly* $\frac{1}{4}$). (ii) For a game with $n = 2$ and arbitrary d, if we are given an equilibrium in the interior, the probability that it is stable is always $1/2$. For such a game with more than two players $d > 2$, we can have multiple equilibria in the interior of the simplex. The probability of seeing the maximum can be calculated up to $d = 5$. For $d > 5$, the polynomials are of degree 5 or greater, and hence cannot be solved analytically.

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