A coexistence criteria for the replicator equation

Daniel Bauman

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1 Introduction

This is based on a section of my senior thesis from Princeton University with Corina Tarnita; I rewrote the result in a cleaner fashion for a self-contained proof on my website.

2 Setup

An evolutionary game matrix $A \in \mathbb{R}^{n\times n}$ describes the pairwise interactions between n species. In an infinite population, we can describe a *community* of n species as a vector $x = (x_1, \dots, x_n)^t$, where x_i is the frequency of species i. I will refer to x as a *state*. Because x_i are frequencies, $\sum_{i=1}^n x_i = 1$. The *fitness* $s_i(x)$ of species i in a population at state x is $s_i(x) = (Ax)_i$, the $i-$th component of the vector Ax. The *average fitness* in the population $\bar{s}(x)$ is then given by $\bar{s}(x) = x^t Ax$. The dynamics of the community of species are governed by the *replicator equation*,

$$\frac{dx_i}{dt} = x_i\big((Ax)_i - x^t Ax\big) = x_i\big(s_i(x) - \bar{s}(x)\big). \tag{2.1}$$

An *equilibrium* of the replicator equation is a state x such that $\frac{dx_i}{dt} = 0$ for all $i \in \{1, \dots, n\}$. While this is trivially true for a given i if $x_i = 0$, and there are multiple equilibria corresponding to various subsets of coordinates of x being set to 0, I focus on the state x which satisfies the equation

$$(Ax)_1 = \cdots = (Ax)_n = \bar{s}(x). \tag{2.2}$$

When I subsequently refer to the equilibrium of the replicator equation, I refer to a solution of eq. 2.2, which clearly satisfies $\frac{dx_i}{dt} = 0$ for all i.

Biologically, a community x is only possible if each $x_i \geq 0$. Mathematically, however, eqs. 2.1, 2.2 are perfectly well-defined for any $x \in \mathbb{R}^n$. We say that x is a *feasible equilibrium* if x is an equilibrium and $x_i \geq 0$, and x is an *internal equilibrium* if x is a feasible equilibrium with $x_i > 0$ for all i.

Let x be a state with $x_i = 0$. We say that species i can *invade* the state x if species i is not present at x, but its *invasion growth rate* is positive, or $s_i(x) - \bar{s}(x) > 0$. This means that if a small amount ϵ of species i was introduced, it would have $\frac{dx_i}{dt} > 0$.

2.1 Notation and linear algebra background

I briefly review simple properties of the determinant of a matrix which will be used. All of the results can be found in a standard book on matrices, i.e. [2]. I will denote $A^{-i,j}$ to be the matrix A with row i and column j removed. So, $A^{-i,i}$ corresponds to a *subgame* which includes all species except i. Using this notation, for any $1 \leq i \leq n$, the Laplace expansion for the determinant of a matrix $A \in \mathbb{R}^{n\times n}$ can be written as a row expansion along the $i-$th row

$$\det(A) = \sum_{j=1}^{n} (-1)^{i+j}\, a_{ij}\, \det(A^{-i,j}), \tag{2.3}$$

or as a column expansion along the j-th column

$$\det(A) = \sum_{i=1}^{n} (-1)^{i+j}\, a_{ij}\, \det(A^{-i,j}). \tag{2.4}$$

If $A \in \mathbb{R}^{n\times n}$ is a matrix with columns $(a_1, \dots, a_n)$, then if we permutate the columns to matrix $A' = (a_{\pi(1)}, \dots, a_{\pi(n)})$ for some permutation π which has sign $\sigma(\pi) \in \{\pm 1\}$, then

$$\det(A') = \sigma(\pi)\,\det(A). \tag{2.5}$$

For example, swapping two columns corresponds to multiplying the determinant by -1.

If $M = \begin{pmatrix} A & B \\ C & D \end{pmatrix}$ is a block matrix, where A, B, C, D are matrices of dimension $m\times m$, $m \times n$, $n\times m$, $n \times n$, respectively, and A is invertible, then

$$\det(M) = \det(A)\,\det(D - CA^{-1}B). \tag{2.6}$$

If $A \in \mathbb{R}^{n\times n}$ is an invertible matrix and $b \in \mathbb{R}^n$ is a column vector, we can use *Cramer's rule* to write down the solution to the linear equation $Ax = b$. Cramer's rule says that

$$x_i = \frac{\det(A_i)}{\det(A)}, \tag{2.7}$$

where A_i is a matrix where column A is replaced by b.

The last fact I will use is standard but a little bit nontrivial. If $A \in \mathbb{R}^{n\times n}$, and $\det(A)$, $\det(A^{-i,i})$ are both nonzero, then $\det(A)$ and $\det(A^{-i,i})$ are related as

$$\frac{\det(A^{-i,i})}{\det(A)} = (A^{-1})_{ii}, \tag{2.8}$$

the (i,i) element of matrix A^{-1}.

3 Coexistence in the replicator equation

The main result is the following theorem, which establishes a condition for an internal equilibrium of the replicator equation to exist.

Theorem 1. *For a set of n species with labels $i \in \{1, 2, \dots, n\}$, let A be an $n \times n$ game matrix. Let $\dot{x}_i = x_i((Ax)_i - x^t Ax)$, $1 \le i \le n$, be the corresponding replicator equation. Let $x = (x_1, \dots, x_n) \in \mathbb{R}^n$ with $\sum_{i=1}^n x_i = 1$ be an equilibrium point of the replicator equation such that*

$$(Ax)_1 = \cdots = (Ax)_n = \bar{s}(x). \tag{3.1}$$

For any $1 \le i \le n$, let $x^{(-i)} = \left(x_1^{(-i)}, \dots, x_{i-1}^{(-i)}, x_{i+1}^{(-i)}, \dots, x_n^{(-i)}\right) \in \mathbb{R}^{n-1}$, $\sum_{j\neq i} x_j^{(-i)} = 1$ be the equilibrium point of the replicator equation without species i, corresponding to matrix $A^{-i,i}$. Then $x^{(-i)}$ satisfies that for all $j \neq i$,

$$(A^{-i,i}x^{(-i)})_j = \bar{s}(x^{(-i)}). \tag{3.2}$$

Let the fitness of species i at the equilibrium $x^{(-i)}$ be

$$s_i\big(x^{(-i)}\big) = \sum_{j\neq i} a_{ij} x_j^{(-i)}. \tag{3.3}$$

Then the frequency of species i at the equilibrium in eq. 3.1 can be found by

$$x_i = -(A^{-1})_{ii}\,\frac{\bar{s}(x)}{\bar{s}\big(x^{(-i)}\big)}\left[s_i(x^{(-i)}) - \bar{s}(x^{(-i)})\right]. \tag{3.4}$$

This naturally leads to a criteria of coexistence in the replicator equation given by the following corollary.

Corollary 2. *The equilibrium point defined in the statement of Theorem 1 is an internal equilibrium if and only if one of the two conditions is satisfied:*

1) For all $1 \le i \le n$, species i can invade the equilibrium $x^{(-i)}$ of the without-i equation if $\frac{(A^{-1})_{ii}}{\bar{s}(x^{(-i)})} > 0$ and it cannot invade the equilibrium $x^{(-i)}$ if $\frac{(A^{-1})_{ii}}{\bar{s}(x^{(-i)})} < 0$.

2) For all $1 \le i \le n$, species i cannot invade the equilibrium $x^{(-i)}$ of the without-i equation if $\frac{(A^{-1})_{ii}}{\bar{s}(x^{(-i)})} > 0$ and it can invade the equilibrium $x^{(-i)}$ if $\frac{(A^{-1})_{ii}}{\bar{s}(x^{(-i)})} < 0$.

Condition 1 only holds when $\bar{s}(x) < 0$, and condition 2 only holds when $\bar{s}(x) > 0$.

This corollary follows immediately from Theorem 1 by recalling our invasion criteria, $s_i(x) - \bar{s}(x) > 0$. We now prove the theorem.

Proof. To prove the theorem, we first study the solution of a formal equilibrium given by eq. 3.1. Recall that an equilibrium of the replicator dynamics for matrix A is a point $x = (x_1, ..., x_n)$ such that $(Ax)_1 = (Ax)_2 = \cdots = (Ax)_n = c$. for some constant c which is equal to the average fitness of the population at that point. Since $x_1 + \cdots + x_n = 1$, we can write this system in the following form:

$$\left(\begin{array}{ccc|c} & & & -1 \\ & A & & \vdots \\ & & & -1 \\ \hline 1 & \cdots & 1 & 0 \end{array}\right) \begin{pmatrix} x_1 \\ \vdots \\ x_n \\ c \end{pmatrix} = \begin{pmatrix} 0 \\ \vdots \\ 0 \\ 1 \end{pmatrix} \tag{3.5}$$

We name the corresponding matrix

$$B = \left(\begin{array}{c|c} A & -\mathbf{1} \\ \hline \mathbf{1}^t & 0 \end{array}\right), \tag{3.6}$$

where $B \in \mathbb{R}^{(n+1)\times(n+1)}$. Cramer's rule (eq. 2.7) tells us that the frequency x_i of type i at equilibrium is given by

$$x_i = \frac{\det(B_i)}{\det(B)}, \tag{3.7}$$

where B_i is the matrix B with column i replaced by $(0, \ldots, 0, 1)^t$. Furthermore, the population fitnes at equilibrium is given by

$$\bar{s}(x) = c = \frac{\det(B_{n+1})}{\det(B)}. \tag{3.8}$$

Because we assumed that A is invertible, we can use eq. 2.6 to see that

$$\det(B) = \det(A)\left(\mathbf{1}A^{-1}\mathbf{1}^t\right). \tag{3.9}$$

Furthermore, by a Laplace expansion (eq. 2.4) on the last column of B_{n+1}, we get that

$$\det(B_{n+1}) = \det\left(\begin{array}{c|c} A & \mathbf{0} \\ \hline \mathbf{1}^t & 1 \end{array}\right) = \det(A). \tag{3.10}$$

Combining eq. 3.8 with eqs. 3.9 and 3.10 gives us the population fitness at the equilibrium,

$$\bar{s}(x) = c = \frac{\det(A)}{\det(A)(\mathbf{1}A^{-1}\mathbf{1}^t)} = \frac{1}{\mathbf{1}A^{-1}\mathbf{1}^t}. \tag{3.11}$$

Next, we study the equilibrium frequencies x_i. From eq. 3.7, we must determine $\det(B_i)$. Recall that B_i is equal to matrix B (eq. 3.6) with column i replaced by $(0, \ldots, 0, 1)^t$. Using a Laplace expansion (eq. 2.3) on row i of B_i , we get that

$$\det(B_i) = \sum_{j=1}^{i-1}(-1)^{i+j}a_{ij}\det(B_i^{-i,j}) + \sum_{j=i+1}^{n}(-1)^{i+j}a_{ij}\det(B_i^{-i,j}) + (-1)^{i+(n+1)}(-1)\det(B_i^{-i,n+1}). \tag{3.12}$$

Now, notice that for $1 \le j \le n+1$, the matrix $B_i^{-i,j}$ is just equal to B with column j missing, column i having all 0's until the last row, and row i missing. If we permute the columns of $B_i^{-i,j}$ until the column with 0's is now where column j would be, then the resultant matrix is just $B_j^{-i,i}$. The sign of this permutation is just $(-1)^{i-j-1}$. Therefore,

$$\det(B_i^{-i,j}) = (-1)^{i-j-1}\det(B_j^{-i,i}) \tag{3.13}$$

So, we can substitute eq 3.13 into eq. 3.12 to get

$$\begin{aligned}\det(B_i) &= -\sum_{j=1}^{i-1} a_{ij}\det(B_j^{-i,i}) - \sum_{j=i+1}^{n} a_{ij}\det(B_j^{-i,i}) + \det(B_{n+1}^{-i,i}) \\ &= -\left[\sum_{j=1}^{i-1} a_{ij}\det(B_j^{-i,i}) + \sum_{j=i+1}^{n} a_{ij}\det(B_j^{-i,i})\right] + \det(B_{n+1}^{-i,i}). \end{aligned}\tag{3.14}$$

Next, consider the game without species i. This has game matrix $A^{-i,i}$. Let the corresponding equilibrium of the replicator dynamic be $x^{(-i)}$. By eq. 3.7, the frequency of species j at the equilibrium of the game without species i can be found by

$$x_j^{(-i)} = \frac{\det(B_j^{-i,i})}{\det(B^{-i,i})}. \tag{3.15}$$

By eq. 3.8, the average fitness of the population at the equilibrium $x^{(-i)}$ is

$$\bar{s}(x^{(-i)}) = c^{(-i)} = \frac{\det(B_{n+1}^{-i,i})}{\det(B^{-i,i})}. \tag{3.16}$$

Therefore, substituting eqs. 3.15, 3.16 into eq. 3.14 gives

$$\begin{aligned}\det(B_i) &= -\left[\sum_{j=1}^{i-1} a_{ij}\det(B^{-i,i})x_j^{(-i)} + \sum_{j=i+1}^{n} a_{ij}\det(B^{-i,i})x_j^{(-i)}\right] + \bar{s}(x^{(-i)})\det(B^{-i,i}) \\ &= -\det(B^{-i,i})\left[\left(\sum_{j=1}^{i-1} a_{ij}x_j^{(-i)} + \sum_{j=i+1}^{n} a_{ij}x_j^{(-i)}\right) - \bar{s}(x^{(-i)})\right] \\ &= -\det(B^{-i,i})\big[s_i(x^{(-i)}) - \bar{s}(x^{(-i)})\big], \end{aligned}\tag{3.17}$$

where $s_i(x^{(-i)})$ is the fitness of species i at the equilibrium without species i from eq. 3.3. Notice that

$$s_i(x^{(-i)}) - \bar{s}(x^{(-i)}) > 0 \iff \frac{dx_i}{dt}(x^{(-i)}) > 0, \tag{3.18}$$

our invasion criterion of species i in the equilibrium without species i.

Now, combining eqs. 3.17 and 3.7 gives us

$$x_i = \frac{\det(B_i)}{\det(B)} = \frac{-\det(B^{-i,i})}{\det(B)}\big[s_i(x^{(-i)}) - \bar{s}(x^{(-i)})\big]. \tag{3.19}$$

Applying equation 3.9 to both $\det(B)$ and $\det(B^{-i,i})$ (because they are both in the same form; I write $\mathbf{1}_n$ and $\mathbf{1}_{n-1}$ for the dimensions of the all-1 vectors for clarity) gives

$$\begin{aligned}x_i &= -\frac{\det(A^{-i,i})\left(\mathbf{1}_{n-1}(A^{-i,i})^{-1}\mathbf{1}_{n-1}^t\right)}{\det(A)\left(\mathbf{1}_n A^{-1}\mathbf{1}_n^t\right)}\left[s_i(x^{(-i)}) - \bar{s}(x^{(-i)})\right] \\ &= -\frac{\det(A^{-i,i})}{\det(A)}\frac{\bar{s}(x)}{\bar{s}(x^{(-i)})}\left[s_i(x^{(-i)}) - \bar{s}(x^{(-i)})\right] && (3.20) \\ &= -(A^{-1})_{ii}\frac{\bar{s}(x)}{\bar{s}(x^{(-i)})}\left[s_i(x^{(-i)}) - \bar{s}(x^{(-i)})\right], && (3.21)\end{aligned}$$

where we used eq. 3.11 to get to eq. 3.20 and eq. 2.8 to get to eq. 3.21. This proves the theorem. □

4 Discussion

This result finds a formula for the composition of an n-species equation, where the frequency of species i is given by eq. 3.4. It does this by relaxing the assumptions of the replicator equation to assume that the without-i species community could be a "virtual" community which contains negative frequencies. Therefore, it potentially lacks biological interpretability. However, rewriting eq. 3.4

$$x_i = -(A^{-1})_{ii} \frac{\bar{s}(x)}{\bar{s}(x^{(-i)})} \left[s_i(x^{(-i)}) - \bar{s}(x^{(-i)}) \right],$$

we see that many parts of this do relate to "nice" quantities. The term $s_i(x^{(-i)}) - \bar{s}(x^{(-i)})$ is just the invasion growth rate of species i in community $x^{(-i)}$. The term $\frac{\bar{s}(x)}{\bar{s}(x^{(-i)})}$ just relates the fitness of the without-i community to the fitness of the n species community. We lack a biological interpretation of $(A^{-1})_{ii}$.

Corollary 2 says that this equation provides a necessary/sufficient equation for coexistence in the n-species community: either all species can invade the without-i community (up to a sign determined by $\frac{(A^{-1})_{ii}}{\bar{s}(x^{(-i)})}$) or they all cannot invade the without-i community up to this sign. It would be interesting to potentially relate this invasion criteria for some stability or instability in the without-i community. According to Hofbauer and Sigmund [1], Theorem 13.5.3, if we take $a_{ii} = 0$, the replicator equation is *permanent*, with an interior rest point $\hat{x}$, then the mean fitness $\bar{s}(\hat{x}) > 0$. Therefore, the two cases may, in fact (if we rescale A appropriately, which we can always do by adding a constant to each column without changing the dynamics) correspond directly to stability/instability. However, I have not attempted to simulate/study these dynamics and whether this implies stability.

References

[1] Josef Hofbauer and Karl Sigmund. *Evolutionary games and population dynamics.* Cambridge university press, 1998.

[2] Roger A. Horn and Charles R. Johnson. *Matrix Analysis.* Cambridge University Press, 1985.