Higher-order equivalence of Lotka-Volterra and evolutionary games

Nrgssun

Topics:

- extension of the dimension from n to n + 1

- b matrix and fitness

General Description:

The Lotka–Volterra (LV) equations, which model absolute population sizes, and the replicator equation, which tracks relative strategy frequencies, are structurally equivalent. Hofbauer and Sigmund showed that the dynamics of an LV system with n species can be mapped exactly to an evolutionary game with n+1 strategies—without altering dynamic patterns like limit cycles or equilibrium points. The n to n+1 mapping:

To incorporate intrinsic growth rates ri and interaction coefficients aij into the replicator payoff matrix, one "extra strategy" (or fictitious species) is introduced. Its sole role is to enforce the normalization $\sum_i x_i = 1$ Any feature seen in the LV system—such as the classic predator–prey limit cycle—will appear identically in the corresponding evolutionary game. Even the two-species LV cycle corresponds to a rock–paper–scissors–like interaction in replicator form.

Although the mapping is mathematically exact, "species" in ecology and "strategies" in game theory are conceptually different. What does the (n+1)th strategy represent biologically? In LV, total population size is free to vary, whereas in replicator dynamics total relative frequency is fixed. That lost degree of freedom forces the addition of a normalization strategy when translating to the game

framework.

In predator-prey relationships, the presence of a third species can either strengthen or weaken the strength of the interaction between the other two species. This leads to higher-order nonlinear terms in the equations.

in evolutionary game theory, as in ecology, when we reach "multiplayer games," the dynamics can become very complex and non-fuzzy even with a small number of strategies (e.g., the "tragedy of the commons" becomes nonlinear in its multiplayer versions). Until now, the mathematical similarity between ecological models and evolutionary games has only been proven for pairwise or linear cases. If we also introduce higher-order terms—such as the Halling response function or the organic effect—in the LV equations, the same Hofbauer–Sigmund mapping still holds. It's just that the space and representation of the parameters become larger and more complex (e.g., three-dimensional or higher-dimensional tensors), and the biological interpretation of "species" in ecology and "strategy" in games on this new mapping requires more precision. Simply put: even the most complex ternary or multi-entity interactions in ecology can be mapped to a corresponding multiplayer game, but we must be careful not to misinterpret the meaning of each variable in each domain.

1. extension of the dimension from n to n + 1

In game theory, it is a bit difficult to combine the concept of strategy and the ideas of ecology. For further intuition, I have given the following example, which was

a continuation of a paper on this topic. Suppose we have an imaginary space with capacity k. This space contains two groups with populations p1 and p2. Also, apart from these two populations, we have empty spaces, which we call e.

In the paper, combining mixed strategies and blending them with the proposed ideas is somewhat difficult to follow. To build intuition, consider the following example:

1. Imaginary space of capacity K

Suppose we have an abstract space whose total capacity is K. Inside it we have two groups of sizes P_1 and P_2, and the remaining "empty" slots, which we denote by e. By definition,

$$P_1(t) + P_2(t) + e(t) = K.$$

2. Change of variables to a simplex

It is often more insightful to work with relative sizes rather than absolute ones, so we rescale. For example,

$$\frac{P_1(t)}{e(t)} + \frac{P_2(t)}{e(t)} + \frac{e(t)}{e(t)} = \frac{K}{e(t)} \implies y_i = \frac{P_i(t)}{e(t)},$$

Similarly, normalizing by K gives

$$\frac{P_1(t)}{K} + \frac{P_2(t)}{K} + \frac{e(t)}{K} = \frac{K}{K} \implies x_i = \frac{P_i(t)}{K},$$

$$\frac{y_1}{k'} + \frac{y_2}{k'} + \frac{1}{k'} = \frac{k'}{k'} \implies \begin{cases} x_i = \dfrac{y_i}{k'}, \\[2mm] k' = 1 + \displaystyle\sum_{k=1}^{n} y_k. \end{cases}$$

So far we have introduced a few changes of variables and, for instance, set

$$y_{n+1} = 1$$

in our notation. Now we wish to extend these steps in full generality.

Recall the standard *replicator equation* on the simplex:

$$\frac{dy_i}{dt} = y_i\Big(r_i + \sum_{j=1}^{n} a_{ij}\, y_j\Big),$$

which describes the frequency dynamics of n types.

By combining our evolutionary game theory ideas with this system, we need to make some changes. In general, according to the above equation, we are dealing with absolute values of yi. And with the n-dimensional simplex we are dealing with the n-group. According to game theory, we consider these populations as relative and we need to replace this n-dimension with the n+1 dimension that takes into account non-competitive effects.

$$\sum_{i=1}^{n+1} x_i = 1, \qquad k' = 1 + \sum_{i=1}^{n} y_i.$$

This framework allows us to work simultaneously with type frequencies and overall population size.

To present this interpretation, which in game theory we call strategy, I assume a simplex space plus one dimension. In mapping ecology, this definition can be likened to a space that changes the population of a species independently of the opposing group. For example, in addition to being eaten by the opposing group, the population can decrease due to flooding or grow by living in a favorable area. So if we consider a group of organisms, something separate from the effects of the opposing

groups and other groups is affecting their population and changing their ratio to the whole. On the other hand, we want the sum of the ratios of all groups in the space we have defined to remain 1. Because in the definition we gave at the beginning, our space with k parts always remains k parts.

Let's make the mathematics of the problem with these definitions, making the necessary changes to connect it to game theory, and see how to make the simplex n + 1 dimensional and look at relative absolute populations.

The first assumption is to relativize the Y-s with the following simple definition:

$$x_i = \frac{y_i}{\sum_{j=1}^{n} y_j}.$$

On the other hand, the sum of all these ratios must eventually add up to 1, and we want to add a new dimension in addition to population to give us the effect of other strategies, or in ecology, something other than the effect of the opposing group on population. So we assume that another fixed x is added to the sum of all the Xis to include these changes.

Now we need to get the value of this new parameter. Given the definition we made for xi:

$$\sum_{i=1}^{n+1} x_i = 1 \iff \sum_{i=1}^{n} x_i + x_{n+1} = 1.$$

$$\sum_{i=1}^{n} x_i \; + \; x_{n+1} \; = \; \frac{\sum_{k=1}^{n} y_k}{1 + \sum_{k=1}^{n} y_k} \; + \; \frac{1}{1 + \sum_{k=1}^{n} y_k} \; = \; 1.$$

$$x_i = \frac{y_i}{1 + \sum\limits_{j=1}^{n} y_j}, \qquad x_{n+1} = \frac{1}{1 + \sum\limits_{j=1}^{n} y_j} \implies x_i = \frac{y_i}{\sum\limits_{j=1}^{n+1} y_j}.$$

That's all we need to put into the equation to make it relative.

$$\frac{dy_i}{dt} = y_i \Big(r_i + \sum_{j=1}^{n} a_{ij}\, y_j \Big),$$

$$\frac{dx_i}{dt} = \frac{d}{dt}\Big(\frac{y_i}{\sum_{j=1}^{n+1} y_j} \Big) = \frac{1}{\sum\limits_{j=1}^{n+1} y_j} \frac{dy_i}{dt} - \frac{y_i}{\Big(\sum\limits_{j=1}^{n+1} y_j\Big)^2} \sum_{j=1}^{n+1} \frac{dy_j}{dt}$$

$$= x_{n+1}\, y_i \Big(r_i + \sum_{j=1}^{n} a_{ij}\, y_j \Big) - y_i\, x_{n+1}^2 \sum_{j=1}^{n+1} y_j \Big(r_j + \sum_{k=1}^{n} a_{jk}\, y_k \Big) \implies$$

$$x_i \left[\Big(\sum_{j=1}^{n+1} b_j\, x_j \Big) - \Big(\sum_{j,k=1}^{n+1} b_{jk}\, x_j\, x_k \Big) \right]$$

Here, after simplification, we see a new definition that introduces the matrix B. We will now discuss its meaning.

2. b matrix and fitness

In the evolutionary game literature, ri is usually called the "baseline fitness" or "intrinsic fitness." It is also sometimes called the "constant payoff" or "fitness offset" for strategy i.

We define matrix b as follows:

$$b_{n+1,i} = 0, \qquad b_{i,n+1} = r_i.$$

Parameter Substitution in the Matrix b

We define the entries of B as follows:

$$\begin{aligned}
b_{ij} &= a_{ij}, && 1 \le i, j \le n \quad \text{(pairwise interaction)}, \\
b_{i,n+1} &= r_i, && 1 \le i \le n \qquad \text{(intrinsic growth)}, \\
b_{n+1,j} &= 0, && 1 \le j \le n+1.
\end{aligned}$$

So, below are the equations before simplification:

$$\frac{dx_i}{dt} = y_i\, x_{n+1} \left[\sum_{j=1}^{n+1} b_{ij}\, y_j \; - \; x_{n+1} \sum_{j,k=1}^{n+1} b_{jk}\, y_j\, y_k \right]$$

with $y_i = \dfrac{x_i}{x_{n+1}} \quad \Longrightarrow \quad \dfrac{dx_i}{dt} = x_i \left[\sum_{j=1}^{n+1} b_{ij}\, x_j - \sum_{j,k=1}^{n+1} b_{jk}\, x_j\, x_k \right].$

Now we define growth rate or fitness:

$$\bar{f}(\mathbf{x}) = \sum_{i=1}^{n+1} x_i\, f_i(\mathbf{x}) = \sum_{i,j=1}^{n+1} b_{ij}\, x_i\, x_j.$$

$$\frac{\dot{x}_i}{x_i} = f_i - \bar{f} \qquad \bar{f} = \sum_{k=1}^{n+1} x_k\, f_k.$$

For our own example, which is decades old, if the average growth rate is higher than the total population, its share has increased, and vice versa.

Also in higher dimensions we can show that we have:

$$\frac{dx_i}{dt} = x_i\left[\sum_{j,k=1}^{n+1} b_{ijk}\, x_j\, x_k \;-\; \sum_{j,k,l=1}^{n+1} b_{jkl}\, x_j\, x_k\, x_l\right].$$

$$f_i \;=\; \sum_{j,k=1}^{n+1} b_{ijk}\, x_j\, x_k, \qquad \bar{f} \;=\; \sum_{i=1}^{n+1} x_i\, f_i \;=\; \sum_{i,j,k=1}^{n+1} b_{ijk}\, x_i\, x_j\, x_k.$$

General d-player Form

For interactions up to order d (a dth-order Lotka–Volterra system), we consider a d-player game with $n+1$ strategies and a payoff tensor

$$b = \left(b_{i_1 i_2 \cdots i_d}\right) \in \mathbb{R}^{(n+1)\times\cdots\times(n+1)}.$$

The replicator equation then reads

$$\dot{x}_i = x_i\left(\sum_{j_2,\ldots,j_d=1}^{n+1} b_{i\, j_2\cdots j_d}\, x_{j_2}\cdots x_{j_d} \;-\; \sum_{j_1,\ldots,j_d=1}^{n+1} b_{j_1\cdots j_d}\, x_{j_1}\cdots x_{j_d}\right).$$