

Evolutionary Stability of Ecological Hierarchy

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A self-similar hierarchical solution that is both dynamically and evolutionarily stable is found to the multi dimensional Lotka-Volterra equation with a single chain of prey-predator relations. This gives a simple and natural explanation to the key features of hierarchical ecosystems, such as its ubiquity, pyramidal population distribution, and higher aggressiveness among higher trophic levels.

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From bacterial colony to human society, hierarchical structure is one of the most universal features of ecological systems. It is typically realized as a *trophic pyramid* with exponentially larger populations for lower trophic levels. The ubiquity of this hierarchy in nature suggests the existence of a simple and robust mechanism behind it.

Let us consider an ecosystem of N species whose populations $x_1(t)$, $x_2(t)$, ..., $x_N(t)$ are described by a set of coupled differential equations with parameters that represent the environmental conditions [1, 2]. Then, the robustness of ecological structures is expressed as the presence and stability of fixed point solutions. The stability should be considered on two levels of different time-scales. The short-term dynamical stability is the stability against the perturbation in the dynamical variables x_n , while the long-term stability is related to the robustness of the solutions against the secular variation of environmental parameters. When some environmental parameters are at the disposal of a certain species, natural selection will lead to the realization of the parameter value that maximizes the population of that species. This is the concept of evolutionary stability [3, 4].

There are several numerical simulations of multi-species ecosystems that show the spontaneous emergence of multi-trophic structure [5, 6]. The models employ coupled differential equations with stochastic parameter variation subjected to evolutionary selection rules. These results indicate that pyramidal hierarchy is an evolutionarily stable configuration of ecosystems irrespective to the fine detail of the model. It is high time to search for a simple and clear theoretical explanation before further numerical calculations with increasingly “realistic” settings are to be pursued.

In this article, we consider ecosystems modeled by the Lotka-Volterra equation describing N species that form a single vertical chain of prey-predator relations. We intend to prove the existence of hierarchical solutions that are stable both dynamically and evolutionarily.

Let us begin with the two species prey-predator Lotka-

Volterra equation

$$\begin{aligned} \dot{x}_1 &= bx_1 - ax_1^2 - \rho_2 x_1 x_2 \\ \dot{x}_2 &= -d_2 x_2 + f_2 \rho_2 x_1 x_2. \end{aligned} \quad (1)$$

Here b is the reproduction rate of the prey x_1 and a the environmental limitation factor to its growth. The parameter d_2 is the decay rate of the predator x_2 which will not subsist without preying on x_1 with the rate of aggression ρ_2 . The factor f_2 represents the combination of the efficiency of the predation and the average mass ratio between prey and predator individuals. All parameters are positive real numbers. Although the dynamical variables x_n are treated as continuous quantities here, they are approximations of the actual integer populations. Moreover, in real life, there is a threshold number for a population under which a species is not viable. As is immediately identified, (1) has a nontrivial fixed point solution $x_1(t) = X_1$, $x_2(t) = X_2$ where X_1 and X_2 satisfy

$$\begin{aligned} b - aX_1 - \rho_2 X_2 &= 0, \\ -d_2 + f_2 \rho_2 X_1 &= 0. \end{aligned} \quad (2)$$

The eigenvalues λ of the linearized map around the fixed point are given by

$$\lambda = -\frac{1}{2q} \left(1 \pm \sqrt{1 - 4d_2 q (bq - 1)} \right), \quad q \equiv \frac{f_2 \rho_2}{ad_2}. \quad (3)$$

Therefore, the fixed point is dynamically stable when we have $f_2 \rho_2 b > ad_2$. Since, in this work, we are primarily concerned with the “populous” regime, $b \gg a$, this condition is almost always satisfied.

Let us now assume that the aggression parameter ρ_2 is a quantity that is at the disposal of the predator x_2 through a long term “behavioral change”. That is, we regard X_1 and X_2 as functions of ρ_2 . Naturally, a change in ρ_2 would be directed toward the maximization of the predator population x_2 through evolutionary selection. We further assume that the time scale for the change of ρ_2 is substantially larger than the time scale for the variation of $x_1(t)$ and $x_2(t)$. Then, irrespective to the precise mechanism of the variation of ρ_2 , one eventually ends up with the value ρ_2^* that maximizes $X_2(\rho_2)$. With the notation $X_i^* \equiv X_i(\rho_2^*)$, we have

$$\rho_2^* = \frac{2ad_2}{f_2 b}, \quad X_2^* = \frac{f_2 b^2}{4ad_2}, \quad X_1^* = \frac{b}{2a}, \quad (4)$$

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which represents the evolutionarily stable solution. The solution is always dynamically stable, since, at these values, the real part of the eigenvalue of linearized map (3) never becomes positive. The stability against parametric variation of ρ_2 can be judged by

$$\frac{d^2 X_2^*}{d\rho_2^2} = -\frac{b}{\rho_2^{*3}}. \quad (5)$$

Our result shows that the optimal aggression rate from the stand point of the predator is to hunt the prey down to one half of its natural stability point b/a that is reached by x_1 when left alone. Already at this point, (4) gives us some insights. When b and d_2 are comparable quantities, the predator population X_2^* is suppressed by the factor $f_2/2$ compared to the prey X_1^* . Since f_2 is typically smaller than 1, we tend to have a small number of predators supported by a large pool of prey biomass as a stable configuration. Another interesting point is that the milder environment signified by a higher value of b/a will increase both X_1^* and X_2^* while reducing the optimal aggression rate ρ_2^* of the predator. This principle of *noblesse oblige* is a widely observed, but nonetheless non-trivial aspect of life. This is corroborated, for example, by recent field work observation on slave-making ants [7].

According to (4), the only way for the prey x_1 to increase its equilibrium population is to “improve the environment” by increasing b/a , when there is any such mean available to it. An intriguing fact is that “improving defensive shield” by decreasing f_2 will not benefit x_1 directly; it simply decreases the predator population X_2^* . However, when X_2 is close to the viability threshold, a decreasing f_2 would be a sensible strategy for x_1 , since that could drive x_2 out of existence, which would result in the instant doubling of X_1^* .

Next, we consider the case of $N = 3$ species that forms a single chain of prey-predator relations [8]:

$$\begin{aligned} \dot{x}_1 &= bx_1 - ax_1^2 - \rho_2 x_1 x_2, \\ \dot{x}_2 &= -d_2 x_2 + f_2 \rho_2 x_1 x_2 - \rho_3 x_2 x_3, \\ \dot{x}_3 &= -d_3 x_3 + f_3 \rho_3 x_2 x_3. \end{aligned} \quad (6)$$

The fixed point solution is obtained as

$$\begin{aligned} b - aX_1 - \rho_2 X_2 &= 0, \\ -d_2 + f_2 \rho_2 X_1 - \rho_3 X_3 &= 0, \\ -d_3 + f_3 \rho_3 X_2 &= 0. \end{aligned} \quad (7)$$

By rearranging the first two equations, we obtain

$$\begin{aligned} b_2 - a_2 X_2 - \rho_3 X_3 &= 0, \\ -d_3 + f_3 \rho_3 X_2 &= 0. \end{aligned} \quad (8)$$

with

$$a_2 \equiv \frac{f_2 \rho_2^2}{a}, \quad b_2 \equiv \frac{f_2 b \rho_2}{a} - d_2. \quad (9)$$

The problem is therefore reduced to the $N = 2$ case with the predator x_3 and effectively self-sustaining prey x_2

which has reproduction and limiting coefficients b_2 and a_2 . If the top predator, driven by evolutionary selection, tries to maximize its equilibrium population X_3 by varying ρ_3 , it will reach the optimum given by

$$\rho_3^{(*)} = \frac{2a_2 d_3}{f_3 b_2}, \quad X_3^{(*)} = \frac{f_3 b_2^2}{4a_2 d_3}, \quad X_2^{(*)} = \frac{b_2}{2a_2}. \quad (10)$$

The fact that these values are optimum only with a given ρ_2 is indicated by the bracketed asterisk. From the relation $\rho_3^{(*)} X_3^{(*)} = b_2/2$, one can rewrite the first two equations of (7) as

$$\begin{aligned} \frac{b}{2} - a \left(X_1 - \frac{b}{2a} \right) - \rho_2 X_2 &= 0 \\ -\frac{d_2}{2} + f_2 \rho_2 \left(X_1 - \frac{b}{2a} \right) &= 0. \end{aligned} \quad (11)$$

This is essentially the same relationship as in the $N = 2$ case (2), with an extra factor $1/2$ in front of the first terms, and the shift in X_1 in the second. We should now suppose that the middle predator x_2 will, in a long run, adjust its aggression rate ρ_2 toward the prey x_1 and maximize X_2 . We then obtain the solution

$$\rho_2^* = \frac{2ad_2}{f_2 b}, \quad X_2^* = \frac{f_2 b^2}{8ad_2}, \quad X_1^* = \frac{3b}{4a}, \quad (12)$$

which in turn yields

$$\rho_3^* = \frac{8ad_2 d_3}{f_2 f_3 b^2}, \quad X_3^* = \frac{f_2 f_3 b^2}{16ad_3}. \quad (13)$$

Note the fact that ρ_2^* here is identical to the $N = 2$ case. We also obtain parametric stability measures as

$$\frac{d^2 X_2^*}{d\rho_2^2} = -\frac{b}{2\rho_2^{*3}}, \quad \frac{d^2 X_3^*}{d\rho_2^2} = -\frac{d_2}{\rho_3^{*3}}, \quad (14)$$

which indeed prove the evolutionary stability of the solution. In Fig.1, the phase space profile of one such example of evolutionarily stable $N = 3$ system is depicted. With consideration at each stage (8) and (11), it is easy to see that this evolutionarily stable solution is also dynamically stable for all parameter values. In effect, the single-chain $N = 3$ Lotka-Volterra equation is broken into two $N = 2$ equations with essentially the same structure, albeit with an additional factor for the lower chain.

When d_2 and d_3 are comparable quantities, the population of the top trophic level X_3^* is inherently suppressed by the factor $f_3/2$ compared to that of X_2^* , giving a pyramidal profile to the trophic structure. It is amusing to note that, from the stand point of the lowest trophic species, an $N = 3$ system, in which two thirds of its natural population is left alive, is considerably more “benign” than an $N = 2$ system.

The preceding proof for the $N = 3$ solution suggests its generalization to arbitrary N . This is achieved through the realization that the fixed point equation for any

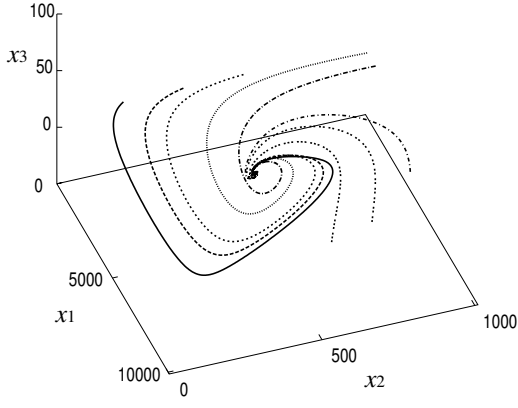


FIG. 1: The phase space profile of a $N = 3$ system at evolutionarily stable parameter value. The parameters are set to be $b = 1$, $a = 1/10000$, $d_2 = 1/3$, $d_3 = 1/5$, $f_2 = 1/10$, $f_3 = 1/5$. The optimal aggression rates are calculated as $\rho_2^* = 1/1500$ and $\rho_3^* = 1/375$. All orbits approach the fixed point $(X_1^*, X_2^*, X_3^*) = (7500, 375, 64.5)$.

mid-level population x_n can have both purely prey-like and purely predator-like representations. Let us start with the N vertically-coupled Lotka-Volterra equation with evolutionarily adjustable aggression parameter ρ_n for each species x_n

$$\begin{aligned} \dot{x}_1 &= bx_1 - ax_1^2 - \rho_2 x_1 x_2, \\ \dot{x}_2 &= -d_2 x_2 + f_2 \rho_2 x_1 x_2 - \rho_3 x_2 x_3, \\ &\vdots \\ \dot{x}_n &= -d_n x_n + f_n \rho_n x_{n-1} x_n - \rho_{n+1} x_n x_{n+1}, \\ &\vdots \\ \dot{x}_N &= -d_N x_N + f_N \rho_N x_{N-1} x_N. \end{aligned} \quad (15)$$

In general, a trophic level can comprise several competing species. In our simplified treatment, however, such species are lumped into a single population variable. The equations for the nontrivial fixed point (X_1, \dots, X_N) are

$$\begin{aligned} b - ax_1 - \rho_2 x_2 &= 0, \\ -d_2 + f_2 \rho_2 x_1 - \rho_3 x_3 &= 0, \\ &\vdots \\ -d_n + f_n \rho_n x_{n-1} - \rho_{n+1} x_{n+1} &= 0, \\ &\vdots \\ -d_N + f_N \rho_N x_{N-1} &= 0. \end{aligned} \quad (16)$$

Apart from the species with the highest trophic level x_N , each of these can be transformed to the “slave” form

$$b_n - a_n X_n - \rho_{n+1} X_{n+1} = 0, \quad (17)$$

with the recursive definition

$$a_n = f_n \rho_n^2 \frac{1}{a_{n-1}}, \quad b_n = f_n \rho_n \frac{b_{n-1}}{a_{n-1}} - d_n. \quad (18)$$

It can be further rewritten into the form

$$\eta_n b_n - a_n \left(X_n - (1 - \eta_n) \frac{b_n}{a_n} \right) - \rho_{n+1} X_{n+1} = 0 \quad (19)$$

for $n = 1, \dots, N - 1$. Let us now *assume* the relation

$$\rho_{n+1}^{(*)} X_{n+1}^{(*)} = \frac{\eta_n b_n}{2}. \quad (20)$$

This assumption results in another form of (16):

$$-\frac{2 - \eta_{n+1}}{2} d_{n+1} + f_{n+1} \rho_{n+1} \left(X_n - \frac{\eta_{n+1} b_n}{2 a_n} \right) = 0 \quad (21)$$

If we require the relation

$$1 - \eta_n = \frac{\eta_{n+1}}{2}, \quad (22)$$

we obtain the “master” form

$$-\eta_n d_{n+1} + f_{n+1} \rho_{n+1} \left(X_n - (1 - \eta_n) \frac{b_n}{a_n} \right) = 0 \quad (23)$$

for $n = 1, \dots, N - 1$. The equations (16) are now decoupled to $(N - 1)$ pairs of prey-predator equations (19) and (23). We then have

$$\rho_{n+1}^{(*)} = \frac{2a_n d_{n+1}}{f_{n+1} b_n}, \quad (24)$$

and

$$X_{n+1}^{(*)} = \eta_n \frac{f_{n+1} b_n^2}{4a_n d_{n+1}}, \quad X_n^{(*)} = (2 - \eta_n) \frac{b_n}{2a_n}. \quad (25)$$

This result justifies the assumption (20) *a posteriori*, and the whole procedure becomes consistent. From the last equation of (16), we observe that η_{N-1} should be set to one, which results in $\eta_{N-2} = 1/2$, $\eta_{N-3} = 3/4$, \dots . We finally obtain the following explicit forms for the evolutionarily and dynamically stable solution:

$$\begin{aligned} X_1^* &= \frac{B_N b}{2^{N-1} a}, \\ X_2^* &= \frac{B_{N-1} f_2 b^2}{2^N a d_2}, \quad \rho_2^* = \frac{2ad_2}{f_2 b}, \\ &\vdots \\ X_N^* &= \frac{B_1 f_2 \dots f_N b^2}{2^{2N-2} a d_3}, \quad \rho_N^* = \frac{2^{2N-3} a d_2 d_3}{f_2 \dots f_N b^2}. \end{aligned} \quad (26)$$

The stability with respect to the variation ρ_n is given by

$$\begin{aligned} \frac{d^2 X_2^*}{d\rho_2^2} &= -\frac{B_{N-1} b}{2^{N-2} \rho_2^{*3}}, \quad \frac{d^2 X_3^*}{d\rho_3^2} = -\frac{B_{N-2} b}{2^{N-3} \rho_3^{*3}}, \\ &\dots \quad \frac{d^2 X_N^*}{d\rho_N^2} = -\frac{B_1 b}{\rho_N^{*3}}. \end{aligned} \quad (27)$$

Here the coefficient B_n is a variant of the Fibonacci series defined by

$$B_{n+2} = B_{n+1} + 2B_n, \quad B_1 = B_2 = 1. \quad (28)$$

