

Suppression of Ecological Competition by Apex Predator

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In the framework of Lotka-Volterra dynamics with evolutionary parameter variation, it is shown that a system of two competing species which is evolutionarily unstable, if left to themselves, is stabilized by a common predator preying on both of them. Game-theoretic implications of the results are also discussed.

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From the dominant plants in forest vegetation to the wild beasts in savanna, an often encountered ecological paradox exists in the form of stabilizing influence of the top predator. While two species in direct competition rarely form a stable ecosystem, they often coexist under the dominance of a common predator [1]. The most illustrative example is found in the *trophic pyramids*, where the apex predator, the most savage aggressor of all, seem to act as the key guarantor of the stability of the whole system [2]. For species with intellectual capacity, this fact might be explained as a result of conscious effort of enlightened self-interest. But the peacekeeping function of the apex predator is so prevalent throughout ecosystems, that the existence of a simple and universal dynamics should be suspected.

The purpose of this paper is to understand the structure and stability of ecosystems composed of competing species in the framework of evolutionary population dynamics [3, 4]. The tool we employ is the Lotka-Volterra equation with adiabatic parameter variation [5]. In this approach, the ecological dynamics is determined by the time variation of the variables representing the population of the species, while the adiabatic parameter variation represents the behavioral evolution of the species. The viability of a species in this framework is judged both by the short-time ecological stability of the orbit and also by the long-term evolutionary stability of the shifting parameters.

We focus specifically on a system that consists of two self-sustaining but competing species and an apex predator who preys over both competitors. We show that the system evolves towards an evolutionarily stable configuration in which the warring preys are tamed into the peaceful coexistence. This is in contrast to the case of two competitors left to themselves, in which there are no evolutionarily stable solution for coexistence, and “arms race” drives one of the competitors into eventual extinction. We also show that our results can be interpreted in a game-theoretic language as the apex predator turning

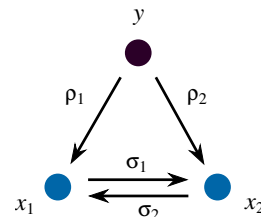


FIG. 1: A symbolic diagram showing the pecking order of the three species system described by (1). The arrows represent the aggression and predation with the specified intensities.

the prisoner’s dilemma between two competitors into a collaborative game.

Suppose there are two populations of competing species x_1 and x_2 which are preyed upon by a common predator population y (Fig. 1). We describe the ecological dynamics of this system by the standard Lotka-Volterra equation

$$\begin{aligned}\dot{x}_1 &= b_1 x_1 - a_1 x_1^2 - \sigma_2 x_1 x_2 - \rho_1 x_1 y, \\ \dot{x}_2 &= b_2 x_2 - a_2 x_2^2 - \sigma_1 x_1 x_2 - \rho_2 x_2 y, \\ \dot{y} &= -d y + f \rho_1 x_1 y + f \rho_2 x_2 y.\end{aligned}\quad (1)$$

Here, b_1, b_2 are the reproduction rates for species x_1, x_2 , and a_1, a_2 , the environmental limitation factor to their growth. The coefficient d is the decay rate for the predator y , and f , the efficiency of its predation. In the last equation, a term proportional to y^2 could be added for consistency with other equations, but this can be shown to introduce simply a technical complication without affecting the main line of our arguments. Also, specifying separate predation efficiencies for x_1 and x_2 makes no essential difference, because the result can be turned into the original form (1) with rescaling of variables. The parameters ρ_1 and ρ_2 are the aggression intensities of the apex predator y towards x_1 and x_2 , respectively. Similarly, σ_1 and σ_2 are the aggression intensities of x_1 to x_2 and of x_2 to x_1 , respectively. We assume all parameters to be positive real numbers. At this stage, we treat all of them as fixed numbers, making no distinction between the Roman denominated “environmental” parameters and Greek denominated “behavioral” parameters. A

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nontrivial fixed point $x_i(t) = X_i$, $y(t) = Y$ ($\dot{X}_i = \dot{Y} = 0$) with $i = 1, 2$ is given by

$$\begin{aligned} X_1 &= \frac{1}{f} \cdot \frac{d(a_2\rho_1 - \sigma_2\rho_2) - f(b_2\rho_1 - b_1\rho_2)\rho_2}{a_2\rho_1^2 + a_1\rho_2^2 - (\sigma_1 + \sigma_2)\rho_1\rho_2}, \quad (2) \\ X_2 &= \frac{1}{f} \cdot \frac{d(a_1\rho_2 - \sigma_1\rho_1) + f(b_2\rho_1 - b_1\rho_2)\rho_1}{a_2\rho_1^2 + a_1\rho_2^2 - (\sigma_1 + \sigma_2)\rho_1\rho_2}, \\ Y &= -\frac{d}{f} \cdot \frac{a_1a_2 - \sigma_1\sigma_2}{a_2\rho_1^2 + a_1\rho_2^2 - (\sigma_1 + \sigma_2)\rho_1\rho_2} \\ &\quad + \frac{(a_2b_1 - b_2\sigma_2)\rho_1 + (a_1b_2 - b_1\sigma_1)\rho_2}{a_2\rho_1^2 + a_1\rho_2^2 - (\sigma_1 + \sigma_2)\rho_1\rho_2}. \end{aligned}$$

The stability of the fixed point is determined by the behavior of the linearized map

$$M = \begin{pmatrix} -a_1X_1 & -\sigma_2X_1 & -\rho_1X_1 \\ -\sigma_1X_2 & -a_2X_2 & -\rho_2X_2 \\ f\rho_1Y & f\rho_2Y & 0 \end{pmatrix}. \quad (3)$$

Namely, the fixed point is stable when real part of all the eigenvalues λ of M determined by

$$|\lambda I - M| = 0 \quad (4)$$

is negative.

When the fixed point is of stable, attracting sort, neighboring orbits form an absorbing spiral in phase space. We now assume that evolutionary pressure of selection and adaptation are at work. We can then regard aggression intensities ρ_1 , ρ_2 , σ_1 and σ_2 as *evolutionarily adjustable parameters* which evolve along the path that simultaneously increase the functions $X_1[\sigma_1]$, $X_2[\sigma_2]$ and $Y[\rho_1, \rho_2]$ until they reach the optimal values. There are several indirect pieces of evidence supporting the existence of this type of adiabatic evolution among real-life ecosystems [6, 7]. It is convenient to start with the maximization condition for the apex predator $\partial Y/\partial \rho_1|_{\rho_1^*} = 0$ and $\partial Y/\partial \rho_2|_{\rho_2^*} = 0$. We then have the relations

$$\begin{aligned} \rho_1^* &= \frac{d}{f} \cdot \frac{2a_1a_2b_1 - b_1\sigma_+\sigma_1 + a_1b_2\sigma_-}{a_2b_1^2 + a_1b_2^2 - b_1b_2\sigma_+}, \quad (5) \\ \rho_2^* &= \frac{d}{f} \cdot \frac{2a_1a_2b_2 - b_2\sigma_+\sigma_2 - a_2b_1\sigma_-}{a_2b_1^2 + a_1b_2^2 - b_1b_2\sigma_+}. \end{aligned}$$

These conditions give the expressions

$$\begin{aligned} X_1^* &= \frac{2a_2b_1 - b_2\sigma_+}{4a_1a_2 - \sigma_+^2}, \quad (6) \\ X_2^* &= \frac{2a_1b_2 - b_1\sigma_+}{4a_1a_2 - \sigma_+^2}, \\ Y^* &= \frac{f}{d} \cdot \frac{a_2b_1^2 + a_1b_2^2 - b_1b_2\sigma_+}{4a_1a_2 - \sigma_+^2}. \end{aligned}$$

The quantities $-X_1^*$ and $-X_2^*$ as functions of σ_1 and σ_2 act as the ‘‘potential surface’’ for the variation of σ_1 and σ_2 . In (5) and (6), the notation $\sigma_{\pm} \equiv \sigma_1 \pm \sigma_2$ is used. With the definitions $\alpha \equiv \sqrt{a_1a_2}$ and $\beta \equiv \sqrt{a_2/a_1} \cdot b_1/b_2$,

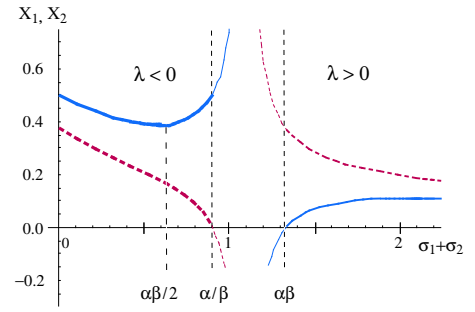


FIG. 2: Fixed point coordinates X_1^* and X_2^* as functions of $\sigma_1 + \sigma_2$. The parameters are $a_1 = 1$, $b_1 = 1$, $a_2 = 1.2$, $b_2 = 0.9$ and $d = 2$. Solid line represents X_1^* and the dashed X_2^* . The fixed point is stable in the region below α/β but unstable above α/β . The region in between is unphysical.

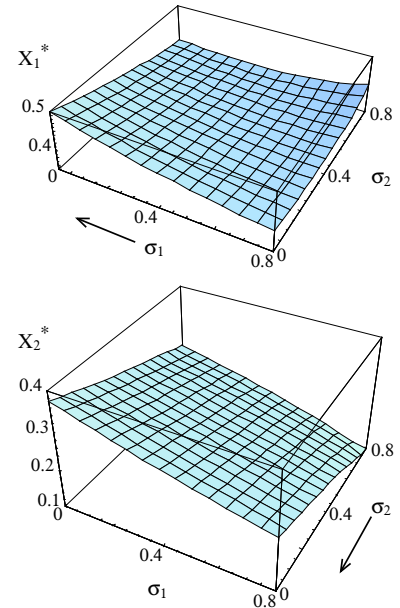


FIG. 3: Fixed point coordinates X_1^* and X_2^* as functions of σ_1 and σ_2 . The parameters are $a_1 = 1$, $b_1 = 1$, $a_2 = 1.2$, $b_2 = 0.9$ and $d = 2$. In the region $\sigma_1 + \sigma_2 < \sigma_{cr} = \alpha\beta/2 = a_2b_1/b_2$, both σ_1 and σ_2 have to be decreased to make X_1 and X_2 larger.

valid parameter range for X_i and Y being positive and stable ($\Re\lambda < 0$) is given by

$$\sigma_1 + \sigma_2 < \min\{\alpha\beta, \alpha/\beta\}. \quad (7)$$

That stability requirement is satisfied can be checked by the fact that all the coefficients of the third order polynomial equation (4) are of same sign within this parameter range.

The evolution of σ_1 and σ_2 depends on their starting

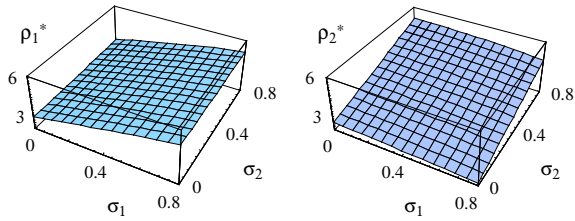


FIG. 4: Aggression intensities ρ_1^* and ρ_2^* as functions of σ_1 and σ_2 . The parameters are $a_1 = 1$, $b_1 = 1$, $a_2 = 1.2$, $b_2 = 0.9$, $d = 2$ and $f = 0.7$.

values. With a straightforward calculation, we obtain

$$\begin{aligned} \frac{\partial X_1^*}{\partial \sigma_1} < 0, \quad \frac{\partial X_2^*}{\partial \sigma_2} < 0 & : \sigma_1 + \sigma_2 < \sigma_{cr}, \\ \frac{\partial X_1^*}{\partial \sigma_1} \cdot \frac{\partial X_2^*}{\partial \sigma_2} < 0 & : \sigma_1 + \sigma_2 > \sigma_{cr}, \end{aligned} \quad (8)$$

within the range of (7). The critical aggression intensity σ_{cr} is given by

$$\sigma_{cr} \equiv \max \{ \alpha\beta/2, \alpha/2\beta \}. \quad (9)$$

If the sum $\sigma_1 + \sigma_2$ is below σ_{cr} , both σ_1 and σ_2 will move toward $\sigma_1 = \sigma_2 = 0$. Namely, two competing species shall settle for a peaceful coexistence as the common preys of a predator y . On the other hand, if the sum starts above critical value, σ_1 and σ_2 will increase until one of the competing species is extinct at that critical value. The situation becomes immediately clear with a glance at numerical example depicted in Fig. 2 and Fig. 3.

A crucial point is that the master y acts as a punisher, according to (5), that inhibits the increase of σ_1 and σ_2 . Fig. 4 serves as a graphical illustration of this effect; Increasing σ_i will induce an increase of ρ_i that incur the damage upon x_i . We stress that no special mechanism is assumed for y to police the system in the outset, yet the dynamics seems to explain our common sense observation about apex predators.

An intriguing fact is that the critical value σ_{cr} is inversely proportional to the natural population of one of the prey species, b_1/a_1 or b_2/a_2 . This means that the coexistence of competing species under common predator becomes a less likelier outcome for a system with richer resources. This seems to give a partial explanation to the decrease of species at the base levels of trophic pyramids.

We next consider the case where the predator leaves the scene, namely $y = 0$ (Fig. 5). By setting $\rho_1 = \rho_2 = 0$, we obtain, in place of (6),

$$\begin{aligned} X_1^* &= \frac{a_2 b_1 - \sigma_2 b_2}{a_1 a_2 - \sigma_1 \sigma_2} \\ X_2^* &= \frac{a_1 b_2 - \sigma_1 b_1}{a_1 a_2 - \sigma_1 \sigma_2}. \end{aligned} \quad (10)$$

The linearized map now takes a two-by-two matrix form

$$M = \begin{pmatrix} -a_1 X_1 & -\sigma_2 X_1 \\ -\sigma_1 X_2 & -a_2 X_2 \end{pmatrix}, \quad (11)$$

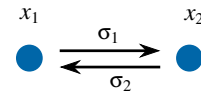


FIG. 5: A symbolic diagram showing the two competing species described by (1) with $\rho_1 = \rho_2 = 0$.

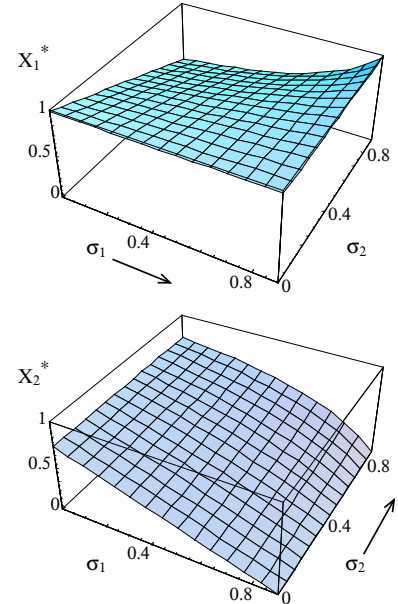


FIG. 6: Fixed point coordinates X_1^* and X_2^* for the case without the apex predator as functions of σ_1 and σ_2 . X_1^* will increase σ_1 and X_2^* will increase σ_2 to achieve local advantage, which will eventually doom X_2^* to extinction. The parameters are $a_1 = 1$, $b_1 = 1$, $a_2 = 1.2$, and $b_2 = 0.9$.

in place of (3). The straightforward calculation gives the condition for X_1^* and X_2^* to be a viable fixed point, namely, $X_1^*, X_2^* > 0$, $\Re \lambda < 0$, in terms of the allowed region for the aggression intensity as

$$\sigma_1 < \min \{ \alpha, \alpha\beta \}, \quad \sigma_2 < \min \{ \alpha, \alpha/\beta \}. \quad (12)$$

However, within this region, we can easily check the relation

$$\frac{\partial X_1^*}{\partial \sigma_1} > 0, \quad \frac{\partial X_2^*}{\partial \sigma_2} > 0. \quad (13)$$

Therefore, in this case, both σ_1 or σ_2 shall eventually be increased beyond the range (12), and there is no evolutionarily stable coexisting solutions for two competing species. Namely, in the absence of the common master, one of the competing species is always driven to extinction by arms race of increasing σ_1 and σ_2 . An example of this case is illustrated in Fig. 6

In order to fully understand the generic shape of the ecosystem, we would have to generalize our arguments to more trophic levels than two, and also more species than two within a single trophic level. To this end, this work,

TABLE I: The game table $X_1^*[\sigma_1, \sigma_2]$ for x_1 discretized at $\sigma_1, \sigma_2 = a/3$ (low aggressiveness, “dove”) and $2a/3$ (high aggressiveness, “hawk”). Left hand side is the table for the case with apex predator (6), and the right hand side, without apex predator (10). The game table $X_2^*[\sigma_1, \sigma_2]$ for x_2 is obtained by transposition of row and column. The Nash equilibrium is indicated with boldface.

With Apex Predator			No Apex Predator		
$\sigma_1 \setminus \sigma_2$	$a/3$ <i>dove</i>	$2a/3$ <i>hawk</i>	$\sigma_1 \setminus \sigma_2$	$a/3$ <i>dove</i>	$2a/3$ <i>hawk</i>
$a/3$ <i>dove</i>	$\frac{3b}{8a}$	$\frac{3b}{9a}$	$a/3$ <i>dove</i>	$\frac{6b}{8a}$	$\frac{6b}{14a}$
$2a/3$ <i>hawk</i>	$\frac{3b}{9a}$	$\frac{3b}{10a}$	$2a/3$ <i>hawk</i>	$\frac{6b}{7a}$	$\frac{6b}{10a}$

in combination to our previous work, is but a modest start. More sophisticated approach of both numerical and analytical nature may have to be called for [6, 8]. In the current work, no precise specification for the evolutionary dynamics of behavioral parameters has been required. While we stress that this is an advantage, construction and analysis of more detailed models with such specifications are attractive possibilities.

Finally, some remarks in the broader context of game theory [9] are in order. There is an obvious game-theoretic interpretation of the results (6) and (10). For the sake of simplicity, let us set $a_1 = a_2 = a$ and $b_1 = b_2 = b$. We now regard σ_i ($i = 1, 2$) as the control parameter of the strategy of population x_i for the game played between x_1 and x_2 whose payoff tables are given by $X_1^*[\sigma_1, \sigma_2]$ and $X_2^*[\sigma_1, \sigma_2]$. To facilitate the un-

derstanding, the game tables for two discretized points for σ_1 and σ_2 are tabulated in Table I. For the case without the common predator, (10), the game is a continuous strategy version of prisoner’s dilemma [10, 11], whose outcome is $\sigma_1 \rightarrow a, \sigma_2 \rightarrow a$ which leads to the extinction of either x_1 or x_2 . With the introduction of the apex predator, the game table is turned into one of collaborative game, whose outcome is the coexistence $\sigma_1 \rightarrow 0$ and $\sigma_2 \rightarrow 0$. Note that the game table is symmetrized under the presence of the apex predator; $X_2^*[\sigma_1, \sigma_2] = X_1^*[\sigma_2, \sigma_1]$. This could be interpreted as the sign of altruistic behavior [12]. Advantage of having the apex predator as a “law enforcer” is evident, and the loss of half of the populations to the predation would be an acceptable tradeoff.

The application of Lotka-Volterra equation (1) is not limited to the ecological population dynamics. Indeed, with the help of replicator dynamics [4], a game-theoretic interpretation of (1) itself is possible in terms of mixed strategy in a generalized prisoner’s dilemma [12]. As such, the current analysis of the stabilizing effect of the apex predator should have direct pertinence to the problem in social and economic settings.

In summary, we have established, for Lotka-Volterra systems with evolutionary parameter variation, that two competing species are evolutionarily unstable, but can be stabilized by the introduction of an apex predator. We hope this to be a start for systematic understanding of stable ecosystems.

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