MUTUALISM AND COOPERATION

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Keywords: mutualism, cooperation, game theory, evolutionary game theory, prisoner's dilemma

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Summary

This article traces the formal development of mutualism and cooperation as theoretical foundations for explaining some types of behavior observed frequently in natural and social systems. Mutualism, or symbiosis, is a positive relationship between two or more species in a community that benefits all individuals of those species. However, theories based on traditional population models show that mutualistic relationships tend to have destabilizing effects on the dynamics and structure of a community. On the other hand, these destabilizing effects do not seem consistent with the types of cooperative behavior that are often observed. Recently, ecologists and economists have addressed these inconsistencies using game theory, and have gained new insights about the conditions under which cooperative behavior emerges as a stable outcome or equilibrium of a system. Results from games that are played once, or at most finitely repeated, show that noncooperative or competitive behavior tends to dominate cooperation. However for

indefinitely or infinitely repeated games, many types of equilibria exist with varying degrees of cooperative behavior. In repeated games with limited strategic complexity, cooperative behavior emerges as a best response. In these games, cooperation emerges through learning by adaptive agents or by evolutionary selection. In stochastic games where there is uncertainty about opponents' play, noncooperative behavior is less attractive to selfish players and cooperation can be an equilibrium. More generally, information differences among players or the possibility of preplay communication can also lead to cooperation.

1. Introduction

Mutualism and cooperation are important relationships in natural and social systems. Mutualism, or symbiosis, drives evolution and most organisms are mutualistic in some way. These interactions are essential for life. In social systems, organizations and institutions emerge as a result of cooperation towards common goals, and a functional society needs people to cooperate at many levels. A remarkable feature of both mutualism and cooperation is their emergence across different spatial, temporal, and organizational scales.

Plants and microorganisms participate in several types of mutualistic relationships, including nitrogen fixing and the uptake of other nutrients. For example, mycorrhizae are a mutualism involving plant roots and a fungus that occurs on more than 95% of all vascular plants. In fact, almost all terrestrial autotrophs, organisms such as plants that produce their own food, are symbiotic with fungi. Mutualisms also exist between animals and microorganisms. Herbivores such as cows, horses, and rabbits utilize a mixture of anaerobic microorganisms to aid digestion of cellulose. Humans also use bacteria, *Escherichia coli*, in their digestive system. Mutualistic relationships are very old but their stability is open to question. Since each partner in a mutualism is under evolutionary selection to increase exploitation of the other partners, conflict can arise. Theoretical models show that this conflict can cause evolutionary instability in the sense that one partner may gain, at least temporarily, by defecting from a mutualistic relationship.

One case has been studied in detail, the relationship between the yucca moth and the yucca plant. Female yucca moths are the exclusive pollinators of yucca plants. After collecting pollen, a female moth actively pollinates yucca flowers. Active pollination has obvious benefits for the reproductive efforts of the yucca plant, but is also important to the yucca moth because her larvae feed only on the developing seeds of the yucca plant. If the larvae consume only a modest proportion of seeds, then the yucca moth helps its host. In this way yucca moths and yucca plants have coevolved to complete mutual dependence on each other. However, some moths adopt selfish strategies such as overloading yucca flowers with larvae or not pollinating their hosts.

Cooperative behavior is essential for economic and other type of social interactions. The conflict or tension in mutualism is perhaps even starker in economic relationships than those from biology. Oligopolies and free riders are two fundamental problems in economics. In the oligopoly problem, two or more producers simultaneously determine output levels. These producers would like to coordinate their decisions and simultaneously restrict output to obtain monopoly profits. In this case, cooperation among producers is expressed by decisions to restrict output and keep prices, and therefore profits, high. However given the decision to cooperate, each partner has an ongoing incentive to defect from the monopolistic relationship and realize greater profits, at least in the short-run. For example, the Organization of Petroleum Exporting Countries (OPEC) attempts to control output from its member countries to keep oil prices and profits high. Control is fragile and members often sell more oil than is agreed upon, or sell below current market prices. While defection may be good for consumers, it reduces profits for all oil producers.

The free rider problem is also important in economics, particularly in environmental and natural resource economics. Public goods have the properties that consumption by one person does not preclude consumption by another, and no one person may be excluded from consumption. Many natural resources have these properties. For example, everybody can enjoy clean air and it would be impossible to exclude a single individual from consuming it without severely limiting that person's freedom. On the other hand, the atmosphere is a natural resource that is available to all people but keeping it clean is costly. The free rider problem arises when determining who should pay this cost. If a person is asked to voluntarily and anonymously contribute to the cost of maintaining a clean atmosphere, they may be likely to contribute less than their true willingness to pay. One reason may be this person believes that their contribution will be small relative to everyone else and will not be missed. Another reason may be this person believes that everyone else will make small contributions and they do not want to be penalized for their own honesty. In this context, cooperation means an individual contributes her true willingness to pay. The free rider problem is the tendency for people to not cooperate by contributing less than their true willingness to pay.

Like the atmosphere, many natural resources are owned publicly as common property. The tendency for publicly owned resources to be overexploited is called the Tragedy of the Commons. In marine fisheries, for example, overexploitation implies that excessive harvesting can keep stocks below sustainable levels, which can lead to a fishery's collapse or even to extinction of the stock. In this context, cooperation means that individual fishermen agree collectively to harvest sustainably. The conflict with cooperation in this case is between harvesting more fish today at the expense of fewer or even no fish tomorrow.

These examples highlight the diverse roles of mutualism and cooperation in biological evolution and social interactions. The following sections of this article formalize the concepts of mutualism and cooperation described above to clarify their meanings, give insight about when they emerge, and establish conditions under which they persist.

2. Mutualism and Ecosystem Models

Seminal work by Robert May connected population dynamics to ecosystem complexity and stability. A general theme of May's work is that mathematical models of multispecies communities tend to predict that greater species diversity implies diminished stability. Roughly speaking, May measures complexity by the number of individual links in the community food web, and stability by the tendency for population perturbations to return to a stationary or equilibrium state. Since their publication, May's results have challenged theorists in ecology and other fields to explain the apparent stability exhibited by complex systems. In fact, a positive relationship between trophic web complexity and community stability is one of the central themes of population biology.

2.1. Community Dynamics

May’s work uses a community matrix to describe community dynamics. He assumes that populations are described by linear dynamics and that an equilibrium exists. Let $x(t)$ be a vector that measures the abundance of n species at time t as differences from their equilibrium values. The notation $\dot{x}$ denotes the vector of time derivatives for each of the n species. An equilibrium is described by the condition $\dot{x} = 0$. The n by n community matrix A has components a_{ij} that describe the effect of each species j on the abundance of each species i. Population dynamics for the community of n species are given by the differential equation $\dot{x} = Ax$. The community matrix A provides a convenient framework for describing the different types of interactions that can occur between two species in terms of Odum's Classification. If $a_{ij} = 0$ and $a_{ji} = 0$, then species i and j are independent. Otherwise, the sign patterns between any given pair of species describe five distinct types of interaction. If the sign pattern is (+, +), then the interaction is mutualism or symbiosis; (+, 0) is commensalism; (-1, 0) is amensalism; (-, -) is competition; and (+, -) is general predator-prey including plant-herbivore, parasite-host, and other similar interactions.

2.2. Predator-Prey Dynamics and Community Stability

The community matrix also describes the stability properties of the linear community x described above. By definition, the linear system is stable if $x(t) \to 0$ as $t \to \infty$. This is true if and only if the eigenvalues of A, which are in general complex numbers, all have negative real parts. The special case of neutral stability, with sustained oscillatory dynamics, arises if at least one of the eigenvalues A is an imaginary number with its real part equal to zero and the other eigenvalues have negative real parts. More generally for many nonlinear systems, the community matrix represents a linear approximation of the true dynamics near the equilibrium. In this case, the stability properties of the linear approximation only apply locally. The relationship between complexity and stability may be illustrated with an example using the classical Lotka-Volterra nonlinear model of single predator-prey dynamics and its generalization with multiple species of predators and their prey.

In the Lotka-Volterra model, a pair of differential equations describes population dynamics. These equations represent a trophic web with a single link, and provide the simplest description with the essentials of nonlinear predator-prey interactions. Let p denote the abundance of the predator, and q the abundance of the prey. Let a, α, b, and β be positive constants. The differential equations that describe predator-prey dynamics are $\dot{p} = p\left(a - \alpha q\right)$ and $\dot{q} = q\left(-b + \beta p\right)$. The Lotka-Volterra model is nonlinear and its equilibrium values are obtained by solving the pair of linear equations associated with the conditions $\dot{p} = 0$ and $\dot{q} = 0$, which gives equilibrium values for the predator and prey of $\overline{p} = a/\alpha$ and $\overline{q} = b/\beta$. Therefore, the community matrix that gives a linear approximation of the Lotka-Volterra model is

$$\begin{pmatrix} 0 & -\frac{\alpha b}{\beta} \\ \frac{\beta a}{\alpha} & 0 \end{pmatrix} \tag{1}$$

The eigenvalues of this matrix are the complex conjugate pair of purely imaginary numbers $\pm i\sqrt{ab}$. Since real parts of this pair are zero, the dynamics of the Lotka-Volterra model are neutrally stable. In this case, a system perturbed from equilibrium will not return. Instead, the perturbed system will cycle around the equilibrium forever.

To consider the effects of trophic complexity, the case with two species is extended to a system with *n*-predators and *n*-prey where dynamics are given by the *n* pairs of equations

$$\dot{p}_i = p_i\left(a_i - \sum_{j=1}^{n} \alpha_{ij} q_j \right) \tag{2}$$

$$\dot{q}_i = q_i\left(-b_i + \sum_{j=1}^{n} \beta_{ij} p_j \right) \tag{3}$$

In this case, a_{ij}, α_{ij}, b_{ij}, and β_{ij} are all positive constants, and the equilibrium values $\overline{p}_i$ and $\overline{q}_i$ are obtained by solving the above system of equations with $\dot{p}_i = 0$ and $\dot{q}_i = 0$, for all $i = 1,\ldots, n$. The $2n \times 2n$ community matrix consists of four $n \times n$ blocks. In this case, the two diagonal blocks have all zero components. The upper off-diagonal block has components $-\overline{p}_i\alpha_{ij}$, and the lower off-diagonal block has components $\overline{q}\beta_{ij}$. The $2n$ eigenvalues for this community matrix occur in n pairs with the form $\pm(\eta + i\xi)$. If any eigenvalues has a nonzero real part, then an eigenvalue with a positive real part exists and the system is unstable. Therefore, the multi predator-prey generalization has, at best, the neutral stability properties of the single predator-prey Lotka-Volterra model but also includes cases with unstable equilibria.

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Biographical Sketch

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