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The Origin of Synergistic Symbiosis

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A dominant theme in the history of life has been the evolutionary innovations of cooperative symbioses: the first genomes near the origin of life, integrated prokaryotic cells, the complex symbiotic communities that evolved into modern eukaryotic cells, lichens, mycorrhizae, and so on. In this paper, a model of cooperative symbiosis that shows a threshold condition for the evolution of cooperation is analyzed. The threshold is not easily passed, but cooperative evolution proceeds rapidly once a symbiosis overcomes the threshold. In the model presented here, each species has genetic variability for a symbiotic trait. The trait imposes a reproductive cost on its bearer but enhances the reproduction of its partner species. For example, in the origin of genetic systems, the trait may cause biochemical synergism for the rate of replication of primitive RNA strands as in Eigen and Schuster's hypercycle model. Models of growth synergism, which are most appropriate for the evolution of genetic systems and for mutualisms such as lichens, with the strategic and psychological applications of the Prisoner's Dilemma model.

are contrasted

Introduction

Game theory models, such as the Prisoner's Dilemma, are frequently used to study the evolution of cooperation (Axelrod, 1984; Mesterton-Gibbons & Dugatkin, 1992). These behavioral models focus on how individuals adjust their actions in response to the history of cooperation and cheating in past encounters. Game theory analysis shows that the origin and subsequent spread of cooperative behavior requires that individuals start with a certain innate (genetic) tendency to cooperate (Axelrod & Hamilton, 1981). If, for example, most individuals fail to reciprocate, then a rare, cooperative individual will always be aiding its neighbors but never receiving any return benefits. Thus there is a threshold for the innate, cooperative tendency that must be passed before further cooperative evolution can occur.

Many complicated aspects of spatial interaction and behavior have been analyzed to determine how the threshold for cooperative evolution may be overcome (Mesterton-Gibbons & Dugatkin, 1992; Nowak & May, 1992). Two factors appear most important (Alexrod & Hamilton, 1981). The first is the average distance of the population from the threshold. The second is the tendency of the initial, mutant individuals above the threshold to interact with each other. Spatial association of cooperators most likely occurs when relatives interact.

A different kind of cooperative evolution occurs between simple symbionts that lack behavioral flexibility. Each partner contributes a fixed, genetically determined proportion of its energy to aid partners. For example, biochemical symbionts may enhance the replication rate of partner species (hypercycles, Eigen & Schuster, 1979) or provide partners with important nutrients. An individual may gain by aiding a partner when the aid increases the partner's vigor and the total level of reciprocation.

Current models of cooperative symbiosis start with the assumption that each species donates a fraction of its energy to aid partners. For example, hypercycle models assume mutual enhancement of replication by separate species of replicators and then study

the conditions under which complex genomes can evolve (Eigen & Schuster, 1979; Maynard Smith & Szathmáry, 1995). Models for the origin of chromosomes start with the assumption of positive synergism between separate replicators and then ask when selection favors those separate replicators to become biochemically linked on chromosomes (Maynard Smith & Szathmáry, 1993).

In this paper I study the prior step in the evolution of cooperative symbiosis: How do different species first evolve to aid partner species? This step must be passed before one can invoke synergism to study hypercycles, genomic integration, and the evolution of chromosomes. I emphasize the early evolution of genetic systems, but the models apply to any kind of cooperative mutualism with behaviorally inflexible traits (e.g. biochemical mutualism).

The processes that influence the origin of synergistic traits can be guessed fairly easily by analogy with the Prisoner's Dilemma and from a prior study on the genetics of mutualism. First, both species must have a minimal level of expression for their mutualistic trait. Second, pairs that develop positive synergism must be associated in space so that benefits conferred to one species are returned to the initial donor. These spatial associations have two components. Between species, selection creates spatial association in trait values among symbiotic partners (Frank, 1994*a*). Within species, the benefits of cooperation, returned from partner species, must be provided to relatives of the original donor (Hamilton, 1972; Wilson, 1980).

This past work suggests the following conjecture: The initial level of trait expression and the spatial associations determine threshold trait values that are required for the origin and evolution of synergistic symbiosis. The conjecture is described by the heuristic model in Fig. 1(a). Species 1 has a trait, T_1, that enhances the reproductive rate of species 2 but reduces its own fitness. Likewise, species 2 has a trait, T_2, that enhances the reproduction of species 1 at a cost to itself. Larger values of T provide more benefit to the partner at a higher cost to the donor. When both species have low trait values, as would be expected when two species first meet, selection pressure continually pushes the traits to lower values. If, however, the pair of traits is above a threshold when the species first meet, then cooperation can increase because of synergistic feedback between species. The analysis below shows the assumptions needed to make this model work, and the particular conditions that define the cooperative threshold.

An example of how particular conditions affect cooperative evolution is shown in Fig. 1(b). The benefit:cost ratio defines a scaling for the positive effect a species has on its partner relative to its own cost. In this example, both species start with the same trait value, T. If the benefit:cost ratio is low, then selection reduces trait values from any starting point. As benefits increase relative to costs the potential for positive feedback increases: lower trait values are needed to get over the initial threshold, and the traits evolve to higher equilibrium values.

This threshold is a key step in the origin of synergistic traits and cooperative symbiosis. Therefore it is useful to formalize the qualitative arguments given here and to quantify the factors that influence the threshold. I present a model in which two species interact according to modified Lotka–Volterra dynamics, where the interaction depends on a genetically variable trait in each species.

The Model

To study symbiotic evolution one has to make specific assumptions. How often do individuals interact? When an individual provides benefits to a partner species, who receives returns from that partner? How do the cooperative traits affect reproductive rate and ecological dynamics?

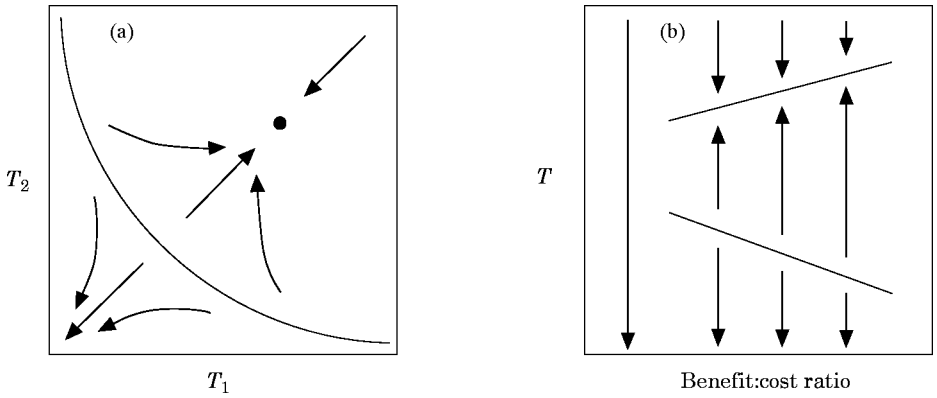

FIG. 1. The threshold model for the evolution of cooperative symbiosis.

A model that made detailed assumptions about each aspect of a potential symbiosis would be too complex to analyze. On the other hand, a model that failed to specify rules for the movements of individuals, competition for resources between potential partners, and other basic processes would provide little insight into the evolution of cooperative symbiosis.

To balance this tradeoff between realism and generality, I chose a specific biological problem and then simplified the life history. The problem is how replicative strands (RNA or DNA) in early protocells evolved cooperative genomes with a high degree of metabolic synergism. I provide an outline of the model in the remainder of this section. I then turn to the details in the following sections.

Each protocell contains copies of genetic material. I call each strand of genetic material a chromosome. The population of protocells has a life cycle with discrete generations. At the end of each generation protocells are chosen for reproduction with a probability (fitness) proportional to the total growth of their chromosomes within the cell.

The reproducing cell produces one progeny, which contains a fixed number of copies of the parental chromosomes. Each chromosome transmitted to the progeny is chosen stochastically in proportion to its abundance within the parental cell. I refer to the sampling of parental chromosomes as segregation. The chromosome may mutate during transmission.

At the reproductive stage parental cells may fuse with each other before producing a progeny. The chromosomes of fused cells are mixed and then segregate to form one offspring.

The cells of one-half of the initial population contain chromosomes of species 1, the remaining cells contain chromosomes of species 2. The species mix within cells when parents fuse before reproduction. Each chromosome has an associated trait that reduces its own reproductive rate—the larger the trait value the greater the fitness cost. The trait of species 1 enhances the growth rate of species 2, and species 2's trait enhances the growth of species 1. Larger trait values have greater beneficial effects on partners. I present equations for the dynamics of growth within cells in the next section.

This protocell model highlights biochemical synergism and the importance of spatial interaction. Without physical linkage of species or other processes that force codispersal, stochastic sampling in segregation may cause the loss of one partner species from a cell (Maynard Smith & Szathmáry, 1993). I will discuss later the important interactions between synergism and linkage. The model here focuses on the synergism stage in the evolution of cooperative symbiosis.

DYNAMICS OF GROWTH

I use the standard Lotka–Volterra equations to describe the growth dynamics of chromosomes within cells. A more detailed description of the equations is given in the Appendix. Here I summarize the simplified, non-dimensional equations.

Each chromosome is either of species 1 or species 2. Within each species there is genetic variability for the symbiotic trait. Thus, in a cell, the abundance of chromosomes of species 1 with genotype j is X_{1j}. These chromosomes have trait value y_{1j}. There can be several different genotypes of each species within a cell, that is, j can vary. Thus the dynamical system requires one equation for each genotype of each species

$$\Delta X_{1j} = X_{1j}\left[h_{1j} - \sum_k h_{1k}X_{1k} - \sum_k h_{2k}X_{2k} \right]\Delta\tau$$

$$\Delta X_{2j} = X_{2j}\left[h_{2j} - \sum_k h_{1k}X_{1k} - \sum_k h_{2k}X_{2k} \right]\Delta\tau \qquad (1)$$

where

$$h_{1j} = 1 - y_{1j} + a\sum_k y_{2k}^d X_{2k}$$

$$h_{2j} = 1 - y_{2j} + a\sum_k y_{1k}^d X_{1k} \qquad (2)$$

The carrying capacity of the cell is standardized to one (see Appendix for scaling relations). The character values y are given as the fractional reduction in the maximal growth rate, that is, the cost of the symbiotic trait. The parameter a is the benefit a partner species obtains from the trait value y relative to the cost to the donor's reproductive rate (see Appendix). The trait values, y, can increase in spite of cost to the donor because a high trait value increases the abundance of the partner species, which in turn enhances the return benefit from the partner. The parameter $0 < d \leqslant 1$ determines the shape of the relationship between the trait value and the benefit to the partner species.

SUMMARY OF LIFE CYCLE AND PARAMETERS

I now describe the model formally and summarize the key parameters. To start each computer run I initialized a population of 1000 cells, each with Kz chromosomes, where $0 < z < 1$ is a fraction of the cellular carrying capacity. The initial abundance of each chromosome is $1/K$. In this first generation

one-half of the cells have chromosomes of species 1, the other one-half of the cells have chromosomes of species 2. The initial trait value, y, for all chromosomes is chosen from a uniform distribution centered at v and ranging over $\pm 0.005v$.

The growth equations describe the change in abundance of each chromosome in the cell. In each generation all cells go through $S = 10$ iterations of the growth described in eqn (1). The size of the time steps, $\Delta\tau$, is adjusted in each generation so that $hS\Delta\tau \to 1$, where h is the average growth rate from equation (2).

After growth, 1000 new cells are formed to create the offspring generation. The parental cells are then destroyed. To form a new cell, a parental cell is chosen (with replacement) from the population; the relative fitnesses of cells are proportional to the total abundance of chromosomes in each cell. A second parental cell is chosen with probability m, the fusion rate. If fusion occurs, the two parental cells come together and their chromosomes mix randomly to form a single parental cell. From the parent, Kz chromosomes are chosen stochastically, with the relative fitnesses of chromosomes determined by their abundances in the cell. Each chromosome transmitted to the offspring has initial abundance $1/K$. No distinction between chromosomes of different species is made during segregation.

The symbiotic trait y mutates during transmission with probability μ. The trait value is changed up or down with equal probability by an amount $y\lambda$, subject to the constraints that $y = 0$ if mutation reduces y below zero, and the amount of change in trait values is λ if $y < 1$. Thus $0 < \lambda < 1$ is a fractional change in the trait value if $y > 1$ and an absolute change if $y < 1$.

I present results in the next section to show how key processes determine the course of symbiotic evolution. The processes are controlled by the following parameters: the benefit:cost scaling for cooperative traits, a, the initial trait values, v, the shape of the benefit returns as a function of trait values, d, the rate of mixing caused by cellular fusions, m, the mutation rate μ and mutation scaling λ, the total initial abundance of chromosomes in offspring cells, z, and the number of chromosomes that segregate into a progeny cell, Kz.

SIMULATION RESULTS

The results shown in Fig. 2 confirm the threshold model for the evolution of cooperative symbiosis [see Fig. 1(a)]. The lower curve in Fig. 2 shows the threshold for initial trait values, v, required to favor cooperation. Below the threshold, cooperative traits are lost quickly. Above the threshold, traits evolve toward an equilibrium shown in the upper curve. The trait values

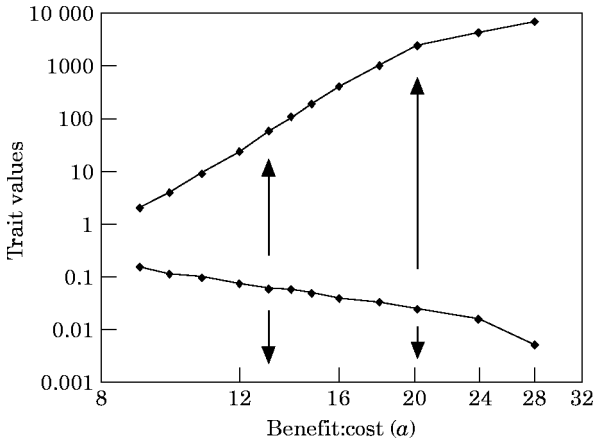

FIG. 2. Quantitative analysis of the threshold model for symbiotic evolution. The parameter a is a benefit:cost scaling. The other parameters for these computer runs are: the rate of cellular fusions, $m = 0.1$; the mutation rate, $\mu = 0.1$, and the effect of each mutation, $\lambda = 0.01$; initial abundance in each cell, $z = 0.25$; the number of chromosomes that segregate into each progeny cell, $Kz = 12$; and the exponent for the benefit returns, $d = 0.9$. The lower threshold was determined by running three replicates for each parameter value of a and initial trait value. Holding it constant, the initial trait values were increased until cooperation was favored in at least two of three of the replicates. The trait values were increased in steps of 0.01 or 0.005. The upper curve was obtained by using initial trait values just above the threshold and running for 20000 generations.

are shown as the fractional cost to maximal growth rate. Thus a threshold value of 0.1 implies that each species must, before meeting its partner, carry a symbiotic trait with a 10% fitness cost, a very unlikely situation. Thus Fig. 2 shows that high benefit:cost ratios (the parameter a) are required for symbiosis to get started.

The upper equilibria in Fig. 2 are all above a cost of one. The high cost implies that, once symbiotic evolution has occurred, the species become obligate partners that can no longer grow alone (contingent irreversibility, Maynard Smith & Szathmáry, 1995). The evolution of mutual dependence can be seen in the time-series plot of Fig. 3. Initially, each species can grow alone at a standardized rate near one. The initial trait values were chosen to be just above the symbiotic threshold, so at first the cooperative traits increase slowly. After a few thousand generations the growth rate of each species when alone is less than zero, and the interaction has become obligate. A period of rapid cooperative evolution then follows until the upper equilibrium shown in Fig. 2 is obtained ($y \approx 25$ and $1 - y \approx -24$). Trait values fluctuate around the equilibrium, showing a tension between, on the one hand, greater cooperative tendencies (higher y) and greater cellular success in competition with other cells and, on the other hand, greater competitive tendencies (lower y) and greater success against partners within cells.

The average trait values for both species are plotted in Fig. 3. The values can hardly be distinguished in spite of fluctuations, implying a strong stabilizing pressure that maintains nearly equal reproductive rates for the two species. Disparity in reproductive rates would cause one species to outcompete the other within a cellular lineage, leaving the fast species without a partner. However, when cooperative symbiosis is favored, cellular lineages that maintain both species have a large efficiency advantage over unispecies lineages. Thus any force that caused a disparity in reproductive rates between species would be detrimental to cooperative symbiosis and would further increase the benefit of physical linkage between the species. Linkage prevents competition within cells and the loss of a partner species during segregation (Maynard Smith & Szathmáry, 1993).

The remainder of the simulation results provide details about how various parameters affect the height of the threshold and upper equilibria. I describe the effects of changing each parameter relative to the results shown in Fig. 2. The parameter values used in Fig. 2 are listed in the caption.

The rate of cellular fusion (or migration among lineages) has three effects. First, reduced fusion increases the relatedness within cells among members of the same species. Increased relatedness improves the chances of success for cooperation between species because return benefits of cooperation are conferred on genotypes that are more closely correlated to the donor's. Second, reduced fusion can increase the genetic correlation between species that is created by selection (Frank, 1994*a*). This correlation between species describes the spatial association of relatively high trait values. The third effect is the relative magnitude of fusion (migration) and drift. When cellular fusions are rare, cells containing both species may be lost from the population by sampling processes. Thus low fusion rates enhance the probability of successful symbiosis by increasing relatedness, but if fusion is too rare then the species mixtures may be lost by drift.

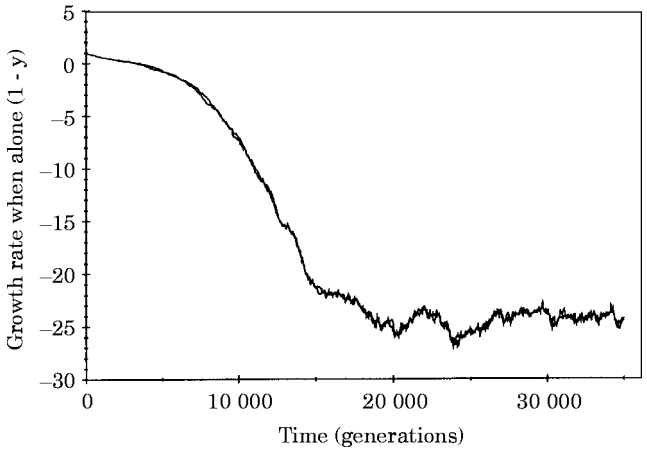

FIG. 3. Time-course of mutualistic evolution between two species. The y-axis shows the average growth rate of each species when its partner species is absent. The average trait values of both species are plotted; these values are always close. This growth rate is $1-y$, where y is the symbiotic trait that costs a fraction y of the donor's maximum growth rate and enhances the recipient's growth rate by ay^d per unit abundance (concentration) of the donor. When growth rate, $1-y$, is less than zero, then a species cannot grow without its partner and the symbiosis has become obligate. Parameters as in Fig. 2, with initial trait values of 0.1 and $a=12$.

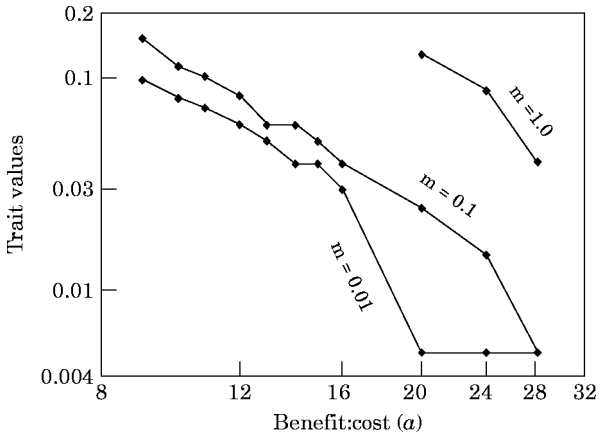

FIG. 4. The effect of cellular fusions (migration) on the threshold for cooperative symbiosis. The middle curve is the same as the lower curve in Fig. 2.

Threshold trait values are shown in Fig. 4 for different rates of cellular fusion. Lower fusion rates reduce the threshold. The relatedness within species increased as fusion rates declined. This change in relatedness is probably the main reason for the variation in threshold values. For low fusion rates of approximately one per generation ($m=0.001$ in a population of 1000) the results were erratic because the stochastic effects of drift play an important role [compare Figs 5(a) and 5(b)].

Changes in the number of chromosomes per cell, Kz, cause two opposing forces. First, an increase in Kz reduces relatedness among chromosomes and therefore reduces cooperative evolution. Second, a rise in Kz increases the probability that both species will be transmitted to progeny cells. In obligate mutualisms, loss of one species during segregation leads to the death of the progeny. In a symmetric interaction, equal abundances of each species are most favorable for cellular success (Maynard Smith & Szathmáry, 1993). The strong stabilizing selection at the cellular level for equal doses of each species causes strong selection favoring linkage and mendelian genetics.

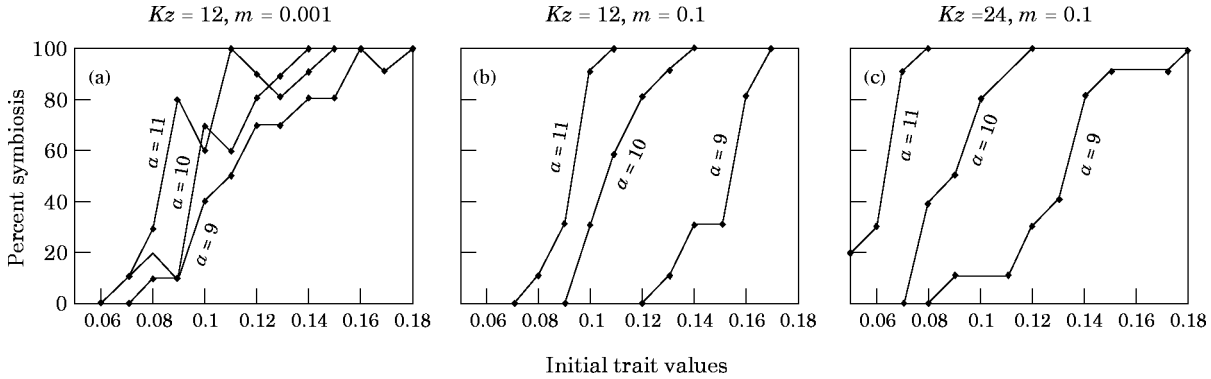

FIG. 5. Stochastic component of cooperative evolution. Each panel shows the percentage of ten replicates in which symbiotic traits increase for a given set of parameters. The middle panel (b) has the same parameters as Fig. 2. The left panel (a) shows the reduced initial trait values needed for symbiosis when the rate of cellular fusions is lowered to $m=0.001$. The irregularities in (a) show the larger effects of stochastic forces when cellular fusions are rare events. The right panel (c) shows the reduced initial trait values needed for symbiosis when the number of chromosomes per cell, Kz, is doubled relative to (b). In (c), the complete curve for $a=11$ and low initial trait values includes the points for initial trait values 0.02, 0.03, 0.04 and the respective percent symbioses 0, 10, 10.

The net effect of the two opposing forces, relatedness and segregation, is shown in Fig. 5(c). For the parameters in that figure, an increase in Kz reduces the threshold for cooperative evolution. Note that high cost:benefit ratios, a, and high initial traits (costs) are still required for cooperative evolution.

Lower mutation rate increases the threshold for cooperative evolution. The lower curve of Fig. 6 shows the threshold for the core parameter set from Fig. 2, with the mutation rate per chromosome of $\mu=0.1$. The upper curve shows the same parameter set except that the mutation rate is reduced to $\mu=0.01$. Lower mutation may increase the threshold by reducing the genetic variability available that selection uses to create genetic correlations between species. Positive genetic correlations favor increased cooperation between species (Frank, 1994*a*). If each species is considered as a different gene, then these correlations are similar to a measure of linkage disequilibrium. Opposing this advantage of mutation for cooperative symbiosis, high mutation rates reduce relatedness and increase conflict within cells (Bonhoeffer & Nowak, 1994; Frank, 1994*b*).

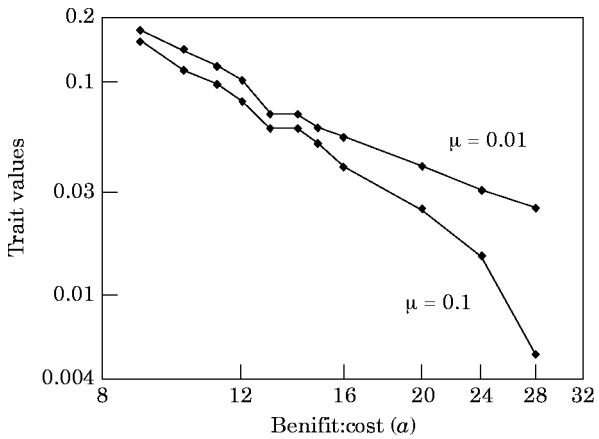

FIG. 6. The effect of mutation rate on the threshold for cooperative symbiosis. The lower curve is the same as the lower curve in Fig. 2. The upper curve is based on runs with the same parameters except that mutation was decreased to $\mu=0.01$.

The parameter z is the initial abundance of chromosomes in cells relative to the cellular carrying capacity. Lower values of z reduce benefits for partners because the benefits depend on the frequency of interaction, which in turn depends on abundance (concentration). Reducing z therefore raises the threshold trait values for the spread of cooperation. For example, the threshold in Fig. 2 for $a=15$ and $z=0.25$ is 0.05. When z is decreased to 0.125, the threshold increases to 0.16.

The final parameter, d, is the exponent that determines the shape of the benefit returns per unit cost to the donor. Linearity, with $d=1$, can cause the traits to increase without bound if the initial threshold conditions for cooperation are met. I therefore used a slightly diminishing rate of returns in Fig. 2, $d=0.9$. When d is reduced, benefits increase more rapidly for low cost and increase more slowly for high costs. Thus lower d reduces both the threshold and the upper equilibrium. The threshold in Fig. 2 for $a=15$ and $d=0.9$ is 0.05. When d is lowered to 0.8, the threshold decreases to 0.035. Note that a change in d also changes the benefit:cost ratio for a given trait value and the scaling relations for the nondimensional parameter a (see Appendix).

Conclusion

The Prisoner's Dilemma is an excellent model of strategy and psychology. This strategic model also includes generic features of cooperative symbiosis,

such as the threshold effect and the role of spatial structure. However, I chose to study a simpler population dynamic model that focuses on continuous variation in a constantly expressed trait. My model of growth dynamics seems closer to the biochemical symbioses that have defined the major innovations of life: the first genomes near the origin of life, integrated prokaryotic cells, the complex symbiotic communities that evolved into modern eukaryotic cells, lichens, mycorrhizae, and so on (Maynard Smith, 1988; Maynard Smith & Szathmáry, 1995).

The origin of genetic systems has become the dominant model for biochemical symbiosis. This work began with Eigen & Schuster's (1979) hypercycle model in which mutually complementary genes evolve by coupling in a cyclic replicative system. For example, A increases B's rate of growth and B increases A's rate of growth, as in my models.

Models of hypercycles and other processes that could explain cooperative genomes assume a fixed level of altruism for each species, in other words, they assume that there is no genetic variability in the cooperative traits of each species (Szathmáry, 1989*a*, *b*; Szathmáry & Demeter, 1987; Maynard Smith & Szathmáry, 1993). These models fail to explain how cooperative traits first appeared and how obligate symbioses evolved. My model adds to this literature by analyzing the origin and genetical evolution of the cooperative traits. The model shows that the threshold for cooperative evolution is a generic feature shared by biochemical and strategic models. In biochemical models, symbionts may evolve through an irreversible stage, leading to an obligate relationship in which neither partner can live alone (Maynard Smith & Szathmáry, 1995).

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APPENDIX

Here I derive the scaling relations and nondimensional parameters that I used for the model presented in the text. The dynamical equations for the change in the abundance of the first species, X_{1j}, and the second species, X_{2j}, with varying genotype j are given by the Lotka–Volterra equations for interactions between species that compete for a common resource and have a combined carrying capacity of K

$$\Delta X_{1j} = X_{1j}\left[h_{1j} - \left(\sum_k h_{1k}X_{1k} + \sum_k h_{2k}X_{2k} \right)/K \right]\Delta t$$

$$\Delta X_{2j} = X_{2j}\left[h_{2j} - \left(\sum_k h_{1k}X_{1k} + \sum_k h_{2k}X_{2k} \right)/K \right]\Delta t$$

where

$$h_{1j} = \delta - cy_{1j} + a\sum_k y_{2k}^d X_{2k}$$

$$h_{2j} = \delta - cy_{2j} + a\sum_k y_{1k}^d X_{1k}$$

The genotypes $j = 0, 1, 2, \ldots$ vary such that the symbiotic trait values $y_{1j} = y_{2j} = j/\alpha$, where α is an arbitrary scaling factor greater than one. A large value of α provides approximate continuity of the character values. I used $\alpha = 10^4$ in my computer runs. The parameter δ is the growth rate when all trait values y are zero, c is the reproductive cost to the donor per unit of contribution to the partner species, and a is the

growth benefit received by a species from its symbiotic partner. The exponent $0 < d \leqslant 1$ determines the shape of the relationship between the trait value and the benefit to the partner species.

This dynamical system is easier to analyze when rewritten in nondimensional form (Segel, 1972; Murray, 1989). Non-dimensional analysis focuses attention on a minimal set of parameters and highlights relative magnitudes (scaling relations) among the processes that drive the dynamics. This is accomplished without altering the dynamics or interpretation because one can translate freely between the biologically motivated formulation and the non-dimensional quantities.

The system can be rewritten with the following substitutions

$$\hat{X} = X/K,\ \hat{y} = (c/\delta)y,\ \hat{a} = aK/(c^d\delta^{1-d}),\ \tau = \delta t.$$

Using these substitutions in the original system and dropping the hats yields the non-dimensional system given in eqn (1) of the main text, with the non-dimensional values of h also obtained from these substitutions. Note that as $\Delta\tau \to 0$, the dynamics are given by a system of continuous differential equations, whereas for larger $\Delta\tau$ the system is discrete with arbitrarily chosen time steps.