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Evolution of Mutualistic Symbiosis without Vertical Transmission

Motomi Genkai-Kato and Norio Yamamura
Center for Ecological Research, Kyoto University, Kyoto 606-8502, Japan

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Mutualistic symbioses are considered to evolve from parasitic relationships. Vertical transmission, defined as the direct transfer of infection from a parent organism to its progeny, has been suggested as a key factor causing reduction of symbiont virulence and evolution of mutualism. On the other hand, there are several mutualistic associations without vertical transmission, such as those between plants and mycorrhizal fungi, legumes and rhizobia, and some corals and dinoflagellates. It is expected that all mutualisms evolve perfect vertical transmission if the relationship is really mutualistic, because hosts may fail to acquire symbionts if they do not transmit the symbionts by vertical transmission. We have developed a mathematical model to clarify the conditions under which mutualistic symbiosis without vertical transmission should evolve. The evolution may occur when and only when (i) vertical transmission involves some costs in the host, (ii) the symbiont suffers direct negative effects if it exploits the host too intensively, (iii) the host establishes the ability to make use of waste products from the symbiont, and (iv) the mechanism of vertical transmission is controlled by the host. We also clarify the conditions under which mutualistic symbiosis with vertical transmission evolves. © 1999 Academic Press

Key Words: **mutualistic symbiosis; vertical transmission; differential equation; free-living state; utilization of waste products.**

1. INTRODUCTION

Parasites rely on their hosts as their habitats and sources of energy supply. So they may suffer some negative effects owing to inactivity or even death of their hosts if they intensively exploit their hosts. It is, therefore, believed that parasites do not harm their hosts as much as they could (Roughgarden, 1975). Ishikawa (1988) stated that it is a natural process to evolve from parasitism to mutualism through commensalism and expressed this process in a phrase: an enemy today is a friend tomorrow. Ewald (1987) also claimed that parasitism should eventually evolve toward commensalism, and a commensal relationship is viewed as a raw material for the evolution of mutualism. Indeed the time course of the reduction of parasite virulence has been documented in various parasites and diseases. An example of the myxoma virus which was introduced in Australia to kill agriculturally harmful rabbits is well known (Fenner, 1965). However, it is also a fact that many parasites remain virulent to their hosts (Ewald, 1994). Thus, some parasites continue to be virulent, while others have reduced their virulence to become mutualistic symbionts for the host.

According to the theory of natural selection, a selfish organism exploiting other organisms has a reproductive advantage over a non-selfish organism in general. It is, therefore, a big mystery why such a mutualistic relationship can evolve where an organism contributes to another organism and sacrifices its own reproduction. The primary question is under what conditions mutualism evolves from parasitism. Ewald (1987) suggested that vertical transmission, defined as the direct transfer of a symbiont from a parent host to its progeny,

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is a key factor for reduction of symbiont virulence and the evolution of mutualism. When the parasite owes its reproduction to vertical transmission, it should reduce virulence to increase productivity of the host. Actually, the symptoms of diseases which mainly infect other hosts by vertical transmission are relatively light, while those of diseases which randomly spread are relatively heavy. The examples where symbionts are transmitted perfectly by vertical transmission are mycetocyte bacteria and yeasts in cockroaches, homopterans and many beetles (Douglas, 1989), and endophytic fungi in various grasses and sedges (Clay, 1990a). In such cases, symbionts are considered to be really mutualistic to their hosts.

The evolution of reduced virulence has been analyzed by various mathematical models (May and Anderson, 1983; Nowak, 1991; Lenski and May, 1994), but there are few theoretical studies to explain the evolution of mutualism (but see Frank, 1995). Yamamura (1993, 1996) developed a mathematical model, showing that there is a critical level on the vertical transmission rate, below which natural selection in the parasite would increase the rate while that in the host would not, and above which both sides would simultaneously increase the rate. Therefore, once the parasite dominates the evolutionary race so as to overcome the critical level of vertical transmission, a highly mutualistic relationship with a high vertical transmission rate evolves. This critical level is reduced when either the host or the parasite develops the ability to use waste products of the other, which can initiate the evolution of mutualistic symbiosis with a high vertical transmission rate.

There exist many cases, however, where two partners seem to help each other in a surprisingly intimate manner but symbionts are not transmitted by vertical transmission (Law and Lewis, 1983; Douglas, 1995). Mycorrhizal fungi are not vertically transmitted through the seed of plants, nor are the dinoflagellates of about half coral species through the egg. Rhizobia, nitrogen-fixing bacteria symbiotic to legumes, and luminescent bacteria in various teleost fish and cephalopod molluscs are not also vertically transmitted. In such examples of symbioses without vertical transmission, symbionts have a free-living state, independent of their hosts. If a symbiont is beneficial to a host, the host that harbors the symbiont in its body should be favored by natural selection. If the host transfers the symbiont to its offspring by vertical transmission, the acquisition of the symbiont is reliably assured, while if the host does not, it has the possibility of failing to acquire the symbiont. A critical question is why all mutualisms do not evolve perfect vertical transmission. Although several answers to the question may be considered, one of those would be that there are some costs in the host when the symbiont is vertically transmitted (Yamamura *et al.*, 1995; Yamamura, 1997). Carrying the symbiont may cause energy costs in immature hosts, or other parasites may infect by utilizing the vertical transmission mechanism of the symbiont.

Incorporating the costs in vertical transmission, we develop a simple mathematical model to identify the conditions under which evolution of mutualism without vertical transmission may occur. We deal with a facultative symbiosis where symbionts can survive and reproduce outside the hosts, rather than an obligate symbiosis where they cannot reproduce anywhere but inside their hosts as modeled by Yamamura (1993, 1996). Because symbionts that are not vertically transmitted actually reproduce outside their hosts (e.g., mycorrhizal fungi, rhizobia, and some dinoflagellates), we assume that symbionts at the beginning stages of symbiosis were able to reproduce in the environment. The model is constructed under a hierarchy of three separate timescales: a microscopic timescale on which the population dynamics determining abundance occurs, a mesoscopic timescale on which the symbionts change virulence to the hosts, and a macroscopic timescale on which changes in the vertical transmission rate and other parameters take place (Dieckmann and Law, 1996; Marrow *et al.*, 1996). The difference between the mesoscopic and macroscopic timescales is assumed from the fact that rapid changes in symbiont virulence have been often reported (e.g., Fenner, 1965), while we are aware of no examples which report so rapid changes in the vertical transmission rate or other parameters.

2. THE MODEL

We consider the host and the symbiont populations as overlapping ones such that the epidemiological dynamics is described by the differential equations

$$\frac{dU}{dt}=b_n U-f(U,I)\cdot U+(1-r)\,bI-cUS, \qquad (1)$$

$$\frac{dI}{dt}=prbI-f(U,I)\cdot I+cUS, \qquad (2)$$

$$\frac{dS}{dt}=\beta S-g(S)\cdot S+aI-cUS, \qquad (3)$$

where U, I, and S refer to the numbers of uninfected hosts, infected hosts, and symbionts in a free-living state, respectively (see Fig. 1). The uninfected host, infected

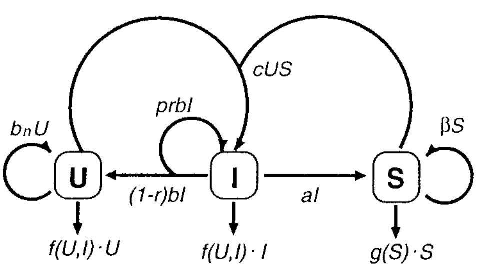

FIG. 1. A scheme of dynamics represented by Eqs. (1)–(3). Uninfected (U) and infected (I) hosts reproduce at different rates, b and b_n, respectively, but have the same death rate $f(U, I)$. Symbionts in a free-living state (S) reproduce at a rate β and have a death rate $g(S)$. Offspring of the infected host are vertically infected at a rate r. Only a fraction p of the vertically infected offspring are able to become adult because of some costs involved in vertical transmission. The number of symbionts released from an infected host into the free-living state is a. The uninfected host is infected by the symbiont in the free-living state at a rate cS.

host, and symbiont in the free-living state reproduce their offspring at rates, b_n, b, and β, respectively. The terms $f(U, I)$ and $g(S)$ refer to the death rates of the host and the symbiont, respectively. While all offspring of the uninfected host are uninfected, only a fraction r of offspring of the infected host is infected from birth by vertical transmission and the remaining fraction $1-r$ of offspring is uninfected. We call here r the vertical transmission rate, taking a value between 0 and 1. We assume that there exist some costs when a symbiont is vertically transmitted. The costs are incorporated into the model as follows: only a fraction p of vertically infected host offspring can survive to become adults, where p takes a value between 0 and 1. One of the reasons for the costs may be existence of harmful intruders which ride together in the mechanism of vertical transmission of symbionts. Another may be a heavy burden of having the symbiont for immature hosts so that a part of them could not grow up to the adult stage. The infection rate from the symbiont in the free-living state to the uninfected host is assumed to be proportional to the product of numbers of the uninfected hosts and the symbionts in the free-living state. The proportional coefficient is c. In our model, direct horizontal transmission from the infected host to the uninfected host is not involved. The symbionts reproduced inside the host are released into the free-living state. The number of released symbionts from one host per unit time is a.

We assume that the mortality terms include a density effect: the organisms suffer negative effects when the numbers become large, because of a lack of habitats or energy resources. For simplicity, we make an assumption with regard to the mortality term of the symbiont in the free-living state, $g(S)$, that the density dependency outside the host is so strong that the population in the free-living state has a carrying capacity S_0 and the deviation in the equilibrium value of S from the carrying capacity S_0 is negligible even if parameters in Eqs. (1)–(3) change. This is assumed also because symbionts are usually microorganisms such that the reproduction rate and, thus, the density outside the host is determined mainly by environmental conditions in their habitats. At equilibrium, the population of the symbiont in the free-living state is, therefore, always equal to S_0. As for the mortality term of the host, we assume that $f(U, I)$ is an increasing function of U and I, and that $f(0, 0)$ is smaller than a certain value so that positive equilibrium values of U and I exist.

At equilibrium, the right-hand sides of Eqs. (1)–(3) are equal to zero,

$$b_n U^* - f(U^*, I^*)\cdot U^* + (1-r)\,bI^* - cU^*S_0 = 0, \tag{4}$$

$$prbI^* - f(U^*, I^*)\cdot I^* + cU^*S_0 = 0, \tag{5}$$

$$\beta S_0 - g(S_0)\cdot S_0 + aI^* - cU^*S_0 = 0, \tag{6}$$

where U^*, I^*, and S_0 refer to the equilibrium values of U, I, and S, respectively. Adding Eqs. (4) and (5), we have

$$b_n U^* + \{(1-r) + pr\}\; bI^* - f(U^*, I^*)\cdot(U^* + I^*) = 0. \tag{7}$$

This leads to an equation at equilibrium for the death rate of the host,

$$f(U^*, I^*) = \frac{b_n U^* + \{(1-r) + pr\}\; bI^*}{H^*}, \tag{8}$$

where $H^* = U^* + I^*$, the equilibrium value of the total number of the hosts. Inserting Eq. (8) and $U^* = H^* - I^*$ into Eq. (5), and dividing it by H^*, we have

$$\begin{aligned} &cS_0 + (prb - b_n - cS_0)\,\xi^* \\ &\quad - [\{(1-r) + pr\}\; b - b_n]\,\xi^{*2} = 0, \end{aligned} \tag{9}$$

where $\xi^* = I^*/H^*$, the proportion of the infected host. Since the left-hand side is positive at $\xi^* = 0$ and negative at $\xi^* = 1$ when $r < 1$, the equation has only one solution for ξ^* between 0 and 1:

$$\xi^* = \frac{prb - b_n - cS_0 + \sqrt{D}}{2[\{(1-r) + pr\}\; b - b_n]} \tag{10}$$

$$D = (prb - b_n - cS_0)^2 + 4cS_0[\{(1-r) + pr\}\; b - b_n].$$

We can also show the uniqueness of U^* and I^* (see Appendix 1). This equilibrium point is stable provided that $f(U, I)$ is an increasing function of U and I, and that $f(0, 0)$ is smaller than a certain value. When $f(0, 0)$ is larger than the critical value, there is no positive equilibrium and $(U, I) = (0, 0)$ is the unique stable equilibrium (Appendix 1).

Next, we consider evolution of symbiont virulence where other parameters are constant. Equilibrium values of the populations are set by the current virulence, but gradually change as the virulence evolves. Afterward we analyze evolution of other parameters because the evolutionary rate of virulence is assumed to be rather faster than that of the other parameters.

3. EVOLUTION OF THE DEGREE OF EXPLOITATION BY SYMBIONTS

If a symbiont exploits its host more intensively, it can reproduce more inside the host while it damages the host and decreases the host reproduction rate. We assume that a and b are functions of the symbiont strategy, x, i.e., $a(x)$ and $b(x)$. The strategy, x, is the degree of exploitation of its host per unit time, for example, in energy units. Though $a(x)$ is basically an increasing function of x (Type I in Fig. 2), we also analyze the case where at large values of x, it is a decreasing function of x due to some negative effect from the host (Type II in Fig. 2). In other words, the host's value to the symbiont diminishes if the symbiont intensively exploits its host. This negative effect is, for example, caused by degradation of the environment inside the host owing to poor health conditions of the host or an increase in the host's defense level. The reproduction rate of the infected host, $b(x)$, is naturally a decreasing function of x as shown in Fig. 2.

In order to obtain an evolutionary stable strategy (ESS; Maynard-Smith, 1974) of the symbiont, we calculate the fitness of mutants adopting a strategy x in the population with most symbionts having strategy x^*. As in most ESS models (Maynard-Smith, 1982; Yamamura, 1987), we assume that the number of the mutant symbionts is so small that the equilibrium numbers of the infected and uninfected hosts in this case are almost the same as those in the case where all symbionts have the same strategy x^*.

Under these assumptions, the relative fitness of a mutant symbiont is given as

$$W_S(x, x^*) = prb(x) + \frac{cU^*S_0}{a(x^*)\,I^*} \cdot a(x). \qquad (11)$$

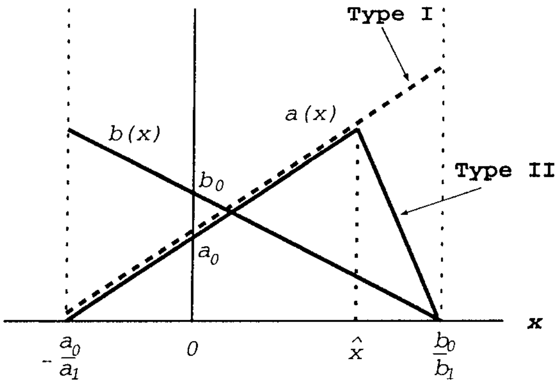

FIG. 2. The number of symbionts released from one infected host per unit time $a(x)$ and the reproduction rate of the infected host $b(x)$ as functions of the degree of exploitation x. Negative values of x mean that the symbiont assists its host at some sacrifice to its own reproduction. A function $a(x)$ can be separated into two types. Type I is a monotonically increasing function of x (broken line) and takes a form $a(x) = a_0 + a_1 x$. In Type II, there is a critical value, $\hat{x}$, below which $a(x)$ is an increasing function of x and takes the same form as Type I, and above which it is a decreasing function of x and takes a form $a(x) = [(a_0 + a_1\hat{x})/(b_0 - b_1\hat{x})] \cdot (b_0 - b_1 x)$. As for $b(x)$, it is a monotonically decreasing function of x and takes a form $b(x) = b_0 - b_1 x$. For $a(x)$ and $b(x)$ to be positive, the value of x is limited in the interval $-a_0/a_1 \leqslant x \leqslant b_0/b_1$.

This fitness function is derived from the dynamics of the mutant symbionts which adopt a slightly different strategy x from the wild-type strategy x^* (see Appendix 2). We can give an intuitive interpretation for Eq. (11). The first term means the fitness of a mutant symbiont through the reproduction of an infected host by vertical transmission. The second term means the fitness through the route passing the free-living state: the number of free symbionts released from a host, $a(x)$, is weighted by the equilibria ratio of the flow from the free-living state to the symbiotic state to the flow in the opposite direction.

If x^* is an ESS, Eq. (11) must take the maximum value at $x = x^*$ as a function of x. The necessary condition is

$$\left.\frac{\partial W_S(x, x^*)}{\partial x}\right|_{x=x^*} = pr\left.\frac{db(x)}{dx}\right|_{x=x^*} + \frac{cU^*S_0}{a(x^*)\,I^*} \cdot \left.\frac{da(x)}{dx}\right|_{x=x^*} = 0. \qquad (12)$$

If there is no vertical transmission (i.e., $r = 0$), the ESS x^* is the value at which $a(x)$ takes the maximum value.

In order to calculate x^* in Eq. (12) explicitly, we give simple functions for $a(x)$ and $b(x)$ as follows. We assume

$$a(x) = \begin{cases} a_0 + a_1 x & \text{for} \quad x \leqslant \hat{x} \\ \text{a decreasing function of } x & \text{for} \quad x \geqslant \hat{x}, \end{cases} \tag{13}$$

where $\hat{x}$ is a critical value of exploitation below which the symbiont can raise $a(x)$ as x increases, and above which the symbiont reduces $a(x)$ by exploiting its host too intensively. The value of a_1 is always positive, while the value of a_0 is zero when the symbiont is unable to reproduce without exploiting its host. When it can reproduce some without exploitation, a_0 is positive. We assume that the vertical transmission rate is independent of the symbiont strategy, x, and that the number of symbionts released from an infected host, $a(x)$, does not reduce at the cost of vertical transmission. This is because we imagine a case where the vertical transmission rate is determined not by the number of the symbionts inside the host but by the efficiency of some mechanistic method of transmission. As for $b(x)$, we assume the simplest linear function

$$b(x) = b_0 - b_1 x, \tag{14}$$

where b_1 is positive. The value of b_0 is naturally positive because the reproduction rate of hosts is positive when nothing is exploited (i.e., $x = 0$). We discriminate b_0 from b_n which is the reproduction rate of the uninfected host, because we will consider an evolutionary change in b_0 later. For the moment, we assume that b_0 is not smaller than b_n (i.e., $b_0 \geqslant b_n$).

Although the expression "exploitation" implies x to be positive, we also extend x to negative values, which means that the symbiont assists its host at some sacrifice to its own reproduction. Since the number of symbionts released from one host per unit time, $a(x)$, and the reproduction rate of the infected host, $b(x)$, must be zero or positive, the value of x is restricted in the interval $-a_0/a_1 \leqslant x \leqslant b_0/b_1$. Negative values of x are admissible only when a_0 takes positive values. The critical value $\hat{x}$ in Eq. (13), above which $a(x)$ is a decreasing function, should take a value between 0 and b_0/b_1. Putting $\hat{x} = b_0/b_1$, we can also analyze the case where $a(x)$ does not have any decreasing parts. We call this case Type I while the former case where $a(\hat{x})$ takes a maximum value is called Type II. The functions of $a(x)$ and $b(x)$ are illustrated in Fig. 2.

We can show that the ESS value x^* is never larger than $\hat{x}$ ($-a_0/a_1 \leqslant x^* \leqslant \hat{x}$). If x^* took a value between $\hat{x}$ and b_0/b_1 ($\hat{x} < x^* \leqslant b_0/b_1$), the right-hand side of Eq. (12) should be always negative because $a(x)$ and $b(x)$ are deceasing functions of x in the interval. Therefore, symbionts should evolve to decrease x^* to $\hat{x}$. Inserting Eq. (13) for $x \leqslant \hat{x}$ and Eq. (14) into Eq. (12), we have

$$-prb_1 + a_1 \cdot \frac{cU^* S_0}{(a_0 + a_1 x^*)\, I^*} = 0. \tag{15}$$

From Eq. (15), we have the ESS x^* when $x^* \leqslant \hat{x}$,

$$x^* = -\frac{a_0}{a_1} + \frac{1 - r}{p^2 h r^2 - a_1\{pb_n + (1-p)\, cS_0\}\, r + a_1 cS_0} \times \frac{hcS_0}{b_1}, \tag{16}$$

where $h = a_0 b_1 + a_1 b_0$ (see Appendix 3). Note that in Eq. (16) $x^* = b_0/b_1$ when $r = 0$ and $x^* = -a_0/a_1$ when $r = 1$. The denominator of the second term must be positive, because, if negative, the second term becomes negative so that x^* becomes smaller than $-a_0/a_1$. Thus, x^* in Eq. (16) is a decreasing function of r. As previously shown, however, the ESS cannot be larger than $\hat{x}$. Therefore, the ESS is $\hat{x}$ when the left-hand side of Eq. (16) is larger than $\hat{x}$ as shown in Fig. 3. If $a(x)$ takes Type I instead of Type II, $\hat{x} = b_0/b_1$.

The relationship between x^* and r can be classified into several cases according to the values of parameters p and cS_0 as shown in Fig. 3 (see Appendix 3). The ESS value of x^* is a non-increasing function of r, which is similar to that in an obligate symbiosis model (Yamamura 1996). It is reasonable that the higher the vertical transmission rate, the more the symbiont should reduce the degree of exploitation on the host because its reproduction owes the reproduction of the host. There is a critical vertical transmission rate $\hat{r}$ such that $x^*(\hat{r}) = \hat{x}$ in Eq. (16). The degree of exploitation decreases with increasing r when $r > \hat{r}$, and $x^* = \hat{x}$ when $r < \hat{r}$. We can see from Fig. 3 that the constant range ($x^* = \hat{x}$) becomes larger as cS_0 becomes smaller. When the value cS_0 is lower than b_n, there exists a critical value of p below which the ESS x^* is always $\hat{x}$ and is independent of r. This means that even if the vertical transmission rate is high, the symbiont would never help its host at some sacrifice to its reproduction when the costs involved in vertical transmission are large. When pr is low, the reproduction of the symbiont is not closely coupled to the reproduction of its host, so the symbiont need not reduce its virulence to the host.

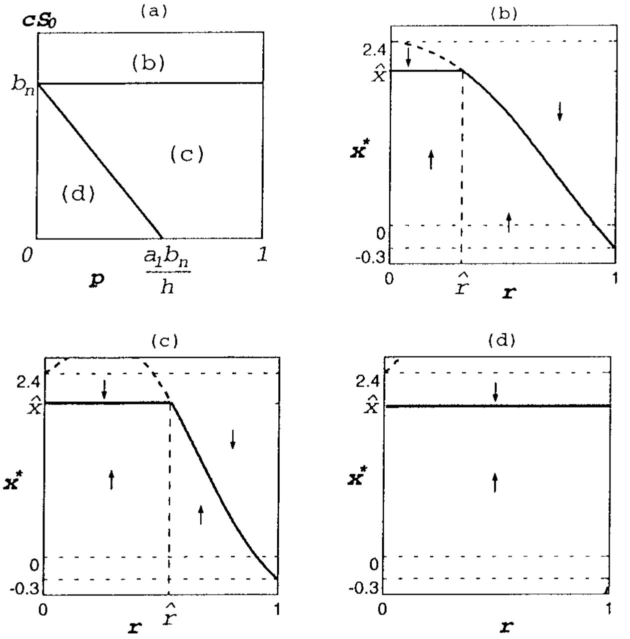

FIG. 3. Relationship between the ESS degree of exploitation x^* and the vertical transmission rate r. (a) The relationship between x^* and r in Eq. (16) can be classified into three cases according to the values of parameters cS_0 and p. An oblique line is $ph = a_1(b_n - cS_0)$. (b)–(d) Relationship between x^* and r in Eq. (16): (b) monotonically decreasing function, (c) non-monotonic function, and (d) monotonically increasing function in Eq. (16) but in practice a constant function independent of r. There is a critical vertical transmission rate $\hat{r}$ in (b) and (c), below which $x^* = \hat{x}$ and above which x^* is a decreasing function of r. Arrows in (b)–(d) stand for the directions of evolution: in areas where the arrow points upward the right-hand side of Eq. (12) is positive, and in areas where the arrow points downward it is negative. In these graphs, the values of parameters are $a_0 = 0.3$, $a_1 = 1.0$, $b_n = 1.0$, $b_0 = 1.2$, and $b_1 = 0.5$, which are common in (b)–(d); (b) $cS_0 = 1.2$, $p = 0.8$; (c) $cS_0 = 0.5$, $p = 0.8$; (d) $cS_0 = 0.3$, $p = 0.4$. With these values of parameters, the degree of exploitation is restricted in the interval $-0.3 \leqslant x \leqslant 2.4$. If a function $a(x)$ takes Type I in Fig. 2, a critical value $\hat{x}$ is equal to b_0/b_1 (i.e., 2.4).

4. EVOLUTION OF THE VERTICAL TRANSMISSION RATE

We consider evolution of r from the viewpoint of the symbiont where the degree of exploitation is settled as a corresponding ESS x^* to the current value of r^*. The relative fitness of a mutant symbiont with a vertical transmission rate r in the wild-type symbionts with r^* is given as

$$W_S(r, r^*) = prb(x^*(r^*)) + \frac{cU^*S_0}{a(x^*(r^*))\, I^*} \cdot a(x^*(r^*)), \tag{17}$$

where the number of the mutant symbionts is assumed to be small as in Eq. (11). This fitness function is derived from the dynamics of the mutant symbionts, adopting a slightly different strategy r from the wild-type strategy r^* (see Appendix 2). Reflecting the assumption that the number of symbionts released from the host per unit time, $a(x^*(r^*))$, is not reduced at the cost of vertical transmission, the mutant fitness always increases as r increases. If this trait is controlled only by the symbiont, the highest possible rate would evolve so that mutualism without vertical transmission never evolves.

Next, we consider the evolution of r from the viewpoint of the host. The relative fitness of a mutant host with r in the wild-type hosts with r^* is calculated as

$$W_H(r, r^*) = [\,p(1-r^*)\, b(x^*)\, I^* - cU^*S_0\,]\; r + \text{constant}. \tag{18}$$

This fitness function is derived from the dynamics of the mutant hosts, adopting a slightly different strategy r from the wild-type strategy r^* (see Appendix 2). The "constant" term does not include the mutant strategy r. The sign of the coefficient of r in Eq. (18) determines evolution of the vertical transmission rate: natural selection in the host would increase r if the sign is positive, while it would decrease r if negative.

First, we consider the case where the current value of r^* is larger than the value $\hat{r}$ which has been defined by $x^*(\hat{r}) = \hat{x}$ in Eq. (16). In this case, the ESS x^* satisfies Eq. (16), a decreasing function of r^* as shown in Fig. 3. Using Eqs. (15) and (16), the coefficient of r in Eq. (18) can he rewritten as

$$\frac{hI^*pr^*(1-r^*)[\,p^2hr^* - a_1\{pb_n + (1-p)\, cS_0\}\,]}{a_1[\,p^2hr^{*2} - a_1\{pb_n + (1-p)\, cS_0\}\, r^* + a_1 cS_0\,]}. \tag{19}$$

As previously shown in Eq. (16), the denominator of (19) is positive when $r^* > \hat{r}$. There exists a critical vertical transmission rate which makes the numerator of (19) equal to zero. The critical value is

$$r_H = \frac{1}{p} \cdot \frac{a_1 b_n}{h} + \frac{1-p}{p^2} \cdot \frac{a_1 cS_0}{h}, \tag{20}$$

where $h = a_0 b_1 + a_1 b_0$. When the current vertical transmission rate is larger than r_H, (19) is positive (i.e., the mutant host with greater r is selected when $r^* > r_H$, while that with smaller r is selected when $r^* < r_H$). At the beginning stage of symbiosis, it would be natural that a symbiont could not reproduce inside its host without exploiting the host ($a_0 = 0$) and that an infected host reproduces at the same rate as an uninfected host if it was not exploited by its symbiont at all ($b_0 = b_n$). Since $h = a_1 b_n$, the critical value r_H is larger than 1, which means that the host should decrease the vertical transmission rate because r^* is always smaller than r_H. As a_0 or b_0 increases, r_H decreases so that it may take a smaller value than 1, which we will analyze in detail later.

Next, we consider the case where current r^* is smaller than $\hat{r}$. In this case, $x^* = \hat{x}$ and the condition under which the coefficient of r in Eq. (18) is positive is

$$D_H \equiv b_0 - b_1 \hat{x} - \frac{p b_n + (1-p)\, c S_0}{p^2} > 0 \qquad (21)$$

(see Appendix 4). The condition (21) does not include r^* so that the coefficient of r in Eq. (18) is positive irrespective of r^* in the interval $0 \leqslant r^* < \hat{r}$, when $D_H > 0$; otherwise, it is negative irrespective of r^*. At the beginning stage of symbiosis where $b_0 = b_n$, we can easily show that $D_H < 0$. Therefore, natural selection in the host would cause r^* to decrease. As b_0 increases, D_H may be positive. When $D_H = 0$, r_H in Eq. (20) corresponds to $\hat{r}$ (see Appendix 4), and therefore when $D_H > 0$, r^* increases to 1.

5. THE CONDITION FOR MUTUALISM

We first assume that the symbiont always obtains a profit from its host by means of symbiosis, because, otherwise, the symbiont avoids infecting the host so that symbiosis between the two species does not occur. In order to determine the relationship between the host and the symbiont, let us introduce the function

$$W_H = \{(1 - r^*) + p r^*\}(b_0 - b_1 x^*) - b_n. \qquad (22)$$

The first and the second terms are the net reproduction rate of the infected host and that of the uninfected host, respectively. We can call the relationship as parasitic when $W_H < 0$, and as mutualistic when $W_H > 0$. Using Eqs. (4) and (8) for Eq. (18), we can see that the sign of the coefficient of r in Eq. (18) exactly corresponds to that of W_H when $p = 1$. This implies that when there are no costs in vertical transmission, the host would increase the vertical transmission rate if the symbiont is beneficial, and vice versa.

When $r^* > \hat{r}$, W_H can be rewritten by using Eq. (16) as

$$W_H \propto p h r^* - a_1 b_n, \qquad (23)$$

where the symbol "$\propto$" implies that both sides are equal in their signs. There exists a critical vertical transmission rate above which $W_H > 0$ and below which $W_H < 0$. The critical value is

$$r_1 = \frac{1}{p} \cdot \frac{a_1 b_n}{h}. \qquad (24)$$

When $r^* < \hat{r}$ where $x^* = \hat{x}$, W_H is a monotonically decreasing function of r^*. There exists a critical vertical transmission rate above which $W_H < 0$ and below which $W_H > 0$. The critical value is

$$r_0 = \frac{1}{1-p}\left(1 - \frac{b_n}{b_0 - b_1 \hat{x}}\right). \qquad (25)$$

At the beginning stage of symbiosis where $a_0 = 0$ and $b_0 = b_n$, $r_1 > 1$ and $r_0 < 0$ for $p < 1$, so that the relationship between the host and the symbiont is parasitic at any vertical transmission rate.

6. UTILIZATION OF PARTNER'S WASTE PRODUCTS AND FINALLY EVOLVING SYSTEM

Although we have dealt with the evolution of strategies x and r so far, other parameters could also evolve. Listed in Table I are the evolutionary trends which the symbiont or the host would slowly develop during a long interaction with parasitism. A symbiont may increase a_0 by evolving to utilize some metabolic or digestive waste products excreted by the host. It may increase a_1 by improving the translation efficiency of exploiting matters

TABLE I

Evolutionary Trends of Changes in Parameters and Their Effects on r_H in Eq. (20), D_H in Eq. (21), r_1 in Eq. (24), and r_0 in Eq. (25).

		Evolutionary trends	Does it make:			
			$r_H < 1$?	$D_H > 0$?	$r_1 < 1$?	$r_0 > 0$?
Symbiont strategy	a_0	↗	Yes	No	Yes	No
	a_1	↗	No	No	No	No
Host strategy	b_0	↗	Yes	Yes	Yes	Yes
	b_1	↘	No	(Yes)	No	(Yes)

Note. Some parameters reduce the values r_H and r_1 to possibly make them smaller than 1, while others do not. Some parameters increase the values D_H and r_0 to possibly make them positive, while others do not.

to its fitness. It is also probable that a host evolves to be able to utilize waste products excreted by the symbiont (increase in b_0), or to reduce the fitness effect of exploitation by the symbiont (decrease in b_1). According to such a slow change in a_0, a_1, b_0, or b_1, evolutionary dynamics of r changes, resulting in changes in the relationship between the host and the symbiont. We can analyze the transition of dynamics by examining the parameter dependence of r_H, D_H, r_1, and r_0 given in the previous sections.

An increase in a_0 makes $r_H < 1$ or $r_1 < 1$. An increase in b_0 makes $r_H < 1$, $r_1 < 1$, $D_H > 0$, or $r_0 > 0$. Although a decrease in b_1 makes $D_H > 0$ or $r_0 > 0$, the increase in b_0 is more crucial than the decrease in b_1. This is because, even if b_1 decreases to take an infinitely small value, $D_H < 0$ and $r_0 < 0$ so far as the value of b_0 remains at b_n. The effects of these parameters on the critical values are summarized in Table I.

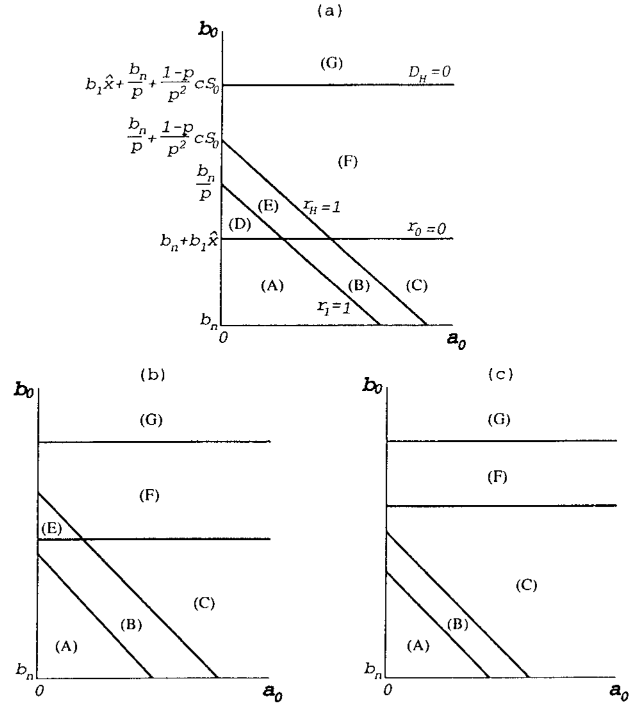

FIG. 4. Diagrams describing effects of changes in a_0 and b_0 on evolution of vertical transmission under the control of the host and on the relationship between the host and the symbiont. (a) $b_n + b_1\hat{x} < b_n/p$; (b) $b_n/p < b_n + b_1\hat{x} < b_n/p + (1-p)\,cS_0/p^2$; (c) $b_n/p + (1-p)\,cS_0/p^2 < b_n + b_1\hat{x}$. Lines parallel to the a_0-axis are $b_0 = b_1\hat{x} + b_n/p + (1-p)\,cS_0/p^2$, which is obtained from $D_H = 0$ given in (21) (above), and $b_0 = b_n + b_1\hat{x}$ obtained from $r_0 = 0$ in Eq. (25) (below). Oblique lines are $p(a_0b_1 + a_1b_0) = a_1b_n + (1-p)\,a_1cS_0/p$ obtained from $r_H = 1$ in Eq. (20) (above), and $p(a_0b_1 + a_1b_0) = a_1b_n$ obtained from $r_1 = 1$ in Eq. (26) (below). In an evolutionary sense, the values of a_0 and b_0 tend to increase from the point $(a_0, b_0) = (0, b_n)$.

Since the change in a_1 never has effects on the dynamics of r and the change in b_1 has only small effects on its dynamics, we consider only changes in a_0 and b_0 in the following. According to values of a_0 and b_0, the relationship between the host and the symbiont is classified into several cases as shown in Fig. 4. The lines $D_H = 0$ and $r_0 = 0$ are horizontal in the space (a_0, b_0) where the origin is $(0, b_n)$. The former line is always above the latter line. The oblique lines $r_H = 1$ and $r_1 = 1$ are also parallel, and the former is always above the latter. The line $D_H = 0$ is always above the line $r_H = 1$ but there are three cases depending on whether $r_0 = 0$ intersects $r_H = 1$ and $r_1 = 1$. The evolutionary dynamics of r in each case and the relationship in each region, which is divided by the lines in Fig. 4, are shown in Fig. 5.

In the region (A) where $r_H > 1$, $D_H < 0$, $r_1 > 1$, and $r_0 < 0$, the relationship is parasitic and these is always selection for lower r in the host, irrespective of r^*. In (B) where $r_1 < 1$, the relationship is parasitic when $r^* < r_1$ while it is mutualistic when $r^* > r_1$, and there is always selection for lower r in the host. In (C) where $r_1 < 1$ and $r_H < 1$, the relationship is parasitic when $r^* < r_1$ while it is mutualistic when $r^* > r_1$, and selection on the host favors lower r when $r^* < r_H$ while it favors greater r when $r^* > r_H$. In (D) where $r_0 > 0$, the relationship is mutualistic when $r^* < r_0$ while it is parasitic when $r^* > r_0$, and there is always selection for lower r in the host. In (E) where $r_1 < 1$ and $r_0 > 0$, the relationship is mutualistic when $r^* < r_0$ and $r^* > r_1$ while it is parasitic when $r_0 < r^* < r_1$, and there is always selection for lower

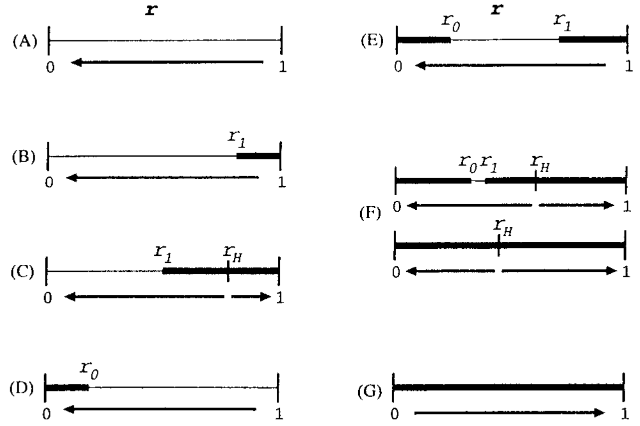

FIG. 5. Diagrams describing evolution of vertical transmission controlled by the host and the relationship between the host and the symbiont. Arrows show directions of evolution of the vertical transmission. Thick parts mean "mutualistic" and thin parts "parasitic." Letters (A)–(G) correspond to the letters (A)–(G) in Fig. 4.

r in the host. In (F) where $r_1 < 1$, $r_H < 1$, and $r_0 > 0$, the relationship is mutualistic when $r^* < r_0$ and $r^* > r_1$ while it is parasitic when $r_0 < r^* < r_1$, and selection on the host favors lower r when $r^* < r_H$ while it favors greater r when $r^* > r_H$. The parasitic part can disappear if b_0 increases enough so that r_0 and r_1 meet together at $\hat{r}$ (see Appendix 4). In (G) where $D_H > 0$, the relationship is mutualistic and there is always selection for greater r in the host, irrespective of r^*.

We can see from Fig. 5 that mutualism without vertical transmission evolves for the regions (D)–(F) in Fig. 4 if the mechanism of vertical transmission is controlled by the host. The combined region of (D)–(F) is specified as the following condition for b_0:

$$b_1\hat{x} + b_n < b_0 < b_1\hat{x} + \frac{b_n}{p} + \frac{1-p}{p^2}\, cS_0. \tag{26}$$

When $p = 1$, there are no values of b_0 which satisfy (26). In other words, mutualism without vertical transmission never evolves if there are no costs for vertical transmission. This is because the signs of the coefficient of r in Eq. (18) and W_H correspond to each other when $p = 1$ so that the condition under which there is selection for greater r in the host is exactly the same as that when the relationship is mutualistic (i.e., the regions (D)–(F), as well as (B), in Fig. 4 disappear). Moreover, the regions (D)–(F) become larger as p becomes smaller.

We can see from (26) that the higher cS_0, the wider the interval of b_0 in which mutualism without vertical transmission evolves. When the host can easily acquire the symbiont in a free-living state, it does not require vertical transmission. A decrease in b_1 makes the interval to move to smaller values but it does not increase the width.

When the function $a(x)$ takes Type I in Fig. 2, mutualism without vertical transmission would never evolve even if the host can make sufficient use of waste products excreted by its symbiont. This is because Type I does not have the critical value $\hat{x}$ at which $a(x)$ has a maximum value, so that r_0 given in Eq. (25) does not become positive. It is necessary for the evolution without vertical transmission that the symbiont has to suffer some negative effects if it exploits its host too severely (i.e., Type II in Fig. 2).

We can also see from Figs. 5C and 5F that if a symbiont happened to increase r to a value larger than r_H where there is selection for greater r in the host, mutualism with perfect vertical transmission should evolve even if the control of r was transferred afterward. Adding the case (G), mutualism with vertical transmission may evolve when

$$b_0 + \frac{a_0}{a_1} b_1 > \frac{b_n}{p} + \frac{1-p}{p^2}\, cS_0. \tag{27}$$

This condition is satisfied when either b_0 or a_0 increases, while (26) is satisfied only when b_0 increases. Thus, we can say that utilization of waste products from the symbiont by the host, instead of the reversed utilization, is important for evolution of mutualism without vertical transmission.

The degree of exploitation x^* evolves to the negative minimum value $-a_0/a_1$ when r^* evolves to 1 (see Eq. (16)). On the other hand, x^* evolves to the possible maximum value $\hat{x}$ when r^* evolves to 0. The modes of mutualism between the two cases are completely different. In the former case, the symbiont comes to sacrifice its reproduction ($a(x^*) = 0$), while in the latter case the symbiont exploits the host but the host utilizes waste products from the symbiont so that the symbiont is beneficial to the host in the total balance (i.e., $b_0 - b_1\hat{x} > b_n$).

7. DISCUSSION

Using a simple model where the symbiont can reproduce outside the host, we have shown that a mutualistic relationship without vertical transmission may evolve from parasitism under the following conditions: (i) some costs are involved when a symbiont is vertically transmitted, (ii) a symbiont suffers some negative effects if it exploits its host too intensively, (iii) a host evolves such that it can utilize waste products excreted by its partner, and (iv) the mechanism of vertical transmission is controlled by the host. We have also clarified the conditions under which a mutualistic relationship with perfect vertical transmission evolves: (v) either partner evolves such that it can utilize waste products excreted by the other partner, and (vi) the mechanism of vertical transmission is controlled by the symbiont, or a symbiont happened to increase the vertical transmission rate larger than a certain value (i.e., r_H in Eq. (20)). We can say that characteristic conditions for evolution of the mutualistic symbiosis without vertical transmission, which are never required for that with vertical transmission, are conditions (i) and (ii). Since the conditions for evolution of the mutualistic symbiosis with vertical transmission are the same as those in the obligate symbiosis case analyzed by Yamamura (1993, 1996) and were already discussed in various aspects, we discuss here only the evolution of mutualistic symbiosis without vertical transmission.

We have assumed that there exist some costs when a symbiont is vertically transmitted. In mycorrhizas, it is conceivable that a transportation of the symbiont from the root to the parts in which seeds are produced involves a great cost, especially in tall trees, although some grasses transfer symbionts through seeds (Clay, 1990b). Another reason why we have introduced the costs involved in vertical transmission is a possibility of a burden for immature hosts. Since resources for growth are more or less exploited by the symbiont, a part of the hosts carrying the symbiont could not grow up to the adult stage. Actually, under low phosphorus conditions, the effectiveness of mycorrhizal fungi changes from parasitic to mutualistic with host growth (Bethlenfalvay *et al.*, 1982; Koide, 1985). Some marine invertebrates acquire symbionts through ingestion at a certain growth stage (Trench, 1979), suggesting that the symbiont may be beneficial for the adult stage of the host while it may be harmful for the immature stage. Another reason may be the disadvantage of having symbionts with a single strain through generations compared with hosts changing symbionts among various strains under a fluctuating environment. Since the symbionts reproduce asexually inside the hosts, the strain of the symbionts inside the offspring of the hosts never changes if the symbionts are vertically transmitted. There may be symbionts with various strains in a free-living state, each adapting to its local environments. Without vertical transmission, the host establishing a new habitat can acquire a proper symbiont from the environment. The effectiveness of mycorrhizal symbionts is likely to vary with environmental conditions (Newsham *et al.*, 1994), and corals actually have an ability to cope with environmental change through changes in symbiont community composition (Rowan *et al.*, 1997). If there were no costs in vertical transmission, mutualistic partners should evolve a mechanism of vertical transmission because it is the most reliable method for the host to obtain the mutualistic symbiont.

We have shown that mutualism without vertical transmission never evolves if the number of symbionts released from one infected host, $a(x)$, is a monotonically increasing function of the degree of exploitation (Type I in Fig. 2): the form like Type II in Fig. 2 contributes to preventing the symbiont from exploiting its host too severely. There are some implications that trees defend by lignification, deposition of tannins, or lysis of hyphae when they are invaded by incompatible fungi (Molina and Trappe, 1982; Malajczuk *et al.*, 1984). The critical value on the degree of exploitation, $\hat{x}$, can result from inactivity, as well as defense systems on the host side, owing to severe exploitation. If the critical value is caused by inactivity of the host, $\hat{x}$ seems to take relatively large positive values. If it is caused by a defense system of the host such as an immune system, $\hat{x}$ seems to take relatively small positive values. Since r_0 in Eq. (25) is a decreasing function of $\hat{x}$, a smaller $\hat{x}$ can more easily cause evolution of mutualism without vertical transmission. When the defense system in the host has a keen sensitivity to exploitation from its symbiont, the symbiont has to keep virulence low, where mutualism without vertical transmission would easily evolve if the host can make use of waste products excreted by its symbiont. When the defense system is not so sensitive to exploitation and therefore inactivity of the host owing to symbiont exploitation reflects the symbiont behavior, the symbiont can exploit to a considerable extent, where mutualism without vertical transmission would not easily evolve even if the host can make use of waste products excreted by its symbiont.

We may also regard the negative effects to the symbiont fitness under severe exploitation as a result from suppression of host growth. If high exploitation by the symbiont restrains growth of the host, the release rate of symbionts from the host would become lower because the release rate may be proportional to the host size. Thus, mutualism without vertical transmission is likely to evolve in host organisms that can grow into a large size. Symbioses in trees and mycorrhizal fungi or in many corals and dinoflagellates seem to satisfy this condition.

We have assumed that a host is infected by one symbiont, but S can also be interpreted as the number of infective doses of symbionts in the case where the host is infected by more than one. We have shown that mutualism without vertical transmission is more likely to evolve when the number of (infective doses of) symbionts in the free-living state (S_0) is large (see condition (26)). It is actually considered a most intuitive and an acceptable reason that trees and many corals do not vertically transmit the symbionts because the symbionts are available, at least, before the hosts become adults. However, we stress here that such easy availability alone cannot give the full explanation for evolution of mutualism without vertical transmission. As shown in condition (26), the evolution is easily realized when b_1 is small or b_0 is large. In the symbioses between plants and mycorrhizal fungi, and legumes and rhizobia, the symbionts exploit carbon as a resource from the hosts, but the damage on the host side seems small (b_1 is small) when the light condition is good enough to produce much carbon. On the other hand, the symbionts aid the hosts by giving nitrogen and phosphorus (b_0 is large) which seem sufficient for themselves. These characters result in easy evolution of mutualism without vertical transmission.

As in the previous model with an obligate symbiont that has no free-living state (Yamamura, 1996), mutualism with perfect vertical transmission may evolve in the present model with a facultative symbiont. This implies that it is not surprising that some corals vertically transmit their symbionts while others do not. We will have to examine carefully whether corals and other symbioses without vertical transmission have trends suggested here as the evolutionary condition.

APPENDIX 1

Existence of Unique Positive I^* and Its Stability

Since $\xi^* = I^*/(U^* + I^*)$, $U^* = (1/\xi^* - 1)\, I^*$. Equation (8) in the text can be rewritten as

$$f\left(\left(\frac{1}{\xi^*} - 1\right) I^*, I^*\right) = b_n + A\xi^*, \tag{A1}$$

where $A = \{(1-r) + pr\}\, b - b_n$. As ξ^* described in Eq. (10) takes a value between 0 and 1, $b_n + A\xi^* > 0$. Because the left-hand side of (A1) is a monotonically increasing function of I^*, a positive solution of I^* uniquely exists if and only if $f(0, 0) < b_n + A\xi^*$. Due to the uniqueness of ξ^* and I^*, U^* is also unique.

We demonstrate that the condition $f(0, 0) < b_n + A\xi^*$ is equivalent to the condition that the origin (0, 0) is unstable. From Eqs. (1) and (2), we can see that the origin is also a stationary point. Linearizing Eqs. (1) and (2) at the origin, we have

$$\frac{d}{dt}\begin{bmatrix} \delta U \\ \delta I \end{bmatrix} = \begin{bmatrix} b_n - f_0 - cS_0 & (1-r)\, b \\ cS_0 & prb - f_0 \end{bmatrix} \begin{bmatrix} \delta U \\ \delta I \end{bmatrix} = M_0 \begin{bmatrix} \delta U \\ \delta I \end{bmatrix}, \tag{A2}$$

where $f_0 = f(0, 0)$, and δU and δI are sufficiently small displacements from the origin. From Eq. (A2), the necessary and sufficient condition that the origin is stable is $\operatorname{tr} M_0 < 0$ and $\det M_0 > 0$. Then, the condition is

$$\operatorname{tr} M_0 = prb + b_n - cS_0 - 2f_0 < 0, \tag{A3}$$

and

$$\det M_0 = f_0^2 - (prb + b_n - cS_0)\, f_0 - \{(1-r) + pr\}\, bcS_0 + prbb_n > 0. \tag{A4}$$

Inequality (A3) leads to

$$f_0 > \tfrac{1}{2}(prb + b_n - cS_0), \tag{A5}$$

and inequality (A4) leads to

$$f_0 < \tfrac{1}{2}(prb + b_n - cS_0 - \sqrt{D'})$$

or,

$$f_0 > \tfrac{1}{2}(prb + b_n - cS_0 + \sqrt{D'}), \tag{A6}$$

where $D' = (prb + b_n - cS_0)^2 + 4[\{(1-r) + pr\}\, bcS_0 - prbb_n]$. Combination of inequalities (A5) and (A6), which is the condition that the origin is stable, is equivalent to

$$f_0 > \tfrac{1}{2}(prb + b_n - cS_0 + \sqrt{D'}). \tag{A7}$$

Using Eq. (10), the right-hand side of (A7) is equal to $b_n + A\xi^*$. This means that I^* does not take a positive equilibrium value when the origin is stable and that there is one positive equilibrium value when the origin is unstable.

Next, we will show that the equilibrium point is stable provided that I^* has a positive equilibrium value. Linearizing Eqs. (1) and (2) at the equilibrium point (U^*, I^*), we have

$$\frac{d}{dt}\begin{bmatrix} \delta U \\ \delta I \end{bmatrix} = \begin{bmatrix} b_n - f^*_U \cdot U^* - f^* - cS_0 & -f^*_I \cdot U^* + (1-r)\, b \\ -f^*_U \cdot I^* + cS_0 & prb - f^*_I \cdot I^* - f^* \end{bmatrix} \begin{bmatrix} \delta U \\ \delta I \end{bmatrix} = M \begin{bmatrix} \delta U \\ \delta I \end{bmatrix}, \tag{A8}$$

where

$$f^*_U = \partial f(U, I)/\partial U|_{U = U^*, I = I^*},$$

$$f^*_I = \partial f(U, I)/\partial I|_{U = U^*, I = I^*},$$

and

$$f^* = f(U^*, I^*).$$

Using Eqs. (4) and (5), we have

$$M = \begin{bmatrix} -f_U^* \cdot U^* - \dfrac{(1-r)\,bI^*}{U^*} & -f_I^* \cdot U^* + (1-r)\,b \\ -f_U^* \cdot I^* + cS_0 & -f_I^* \cdot I^* - \dfrac{cU^*S_0}{I^*} \end{bmatrix}. \tag{A9}$$

The condition that the equilibrium point (U^*, I^*) is stable is $\operatorname{tr} M < 0$ and $\det M > 0$. We have $\operatorname{tr} M$ and $\det M$ from (A9):

$$\operatorname{tr} M = -f_U^* \cdot U^* - f_I^* \cdot I^* - \frac{(1-r)\,bI^*}{U^*} - \frac{cU^*S_0}{I^*}, \tag{A10}$$

$$\det M = \left(\frac{(1-r)\,bI^*}{U^*} + \frac{cU^*S_0}{I^*} \right) \cdot (f_U^* \cdot U^* + f_I^* \cdot I^*). \tag{A11}$$

It is obvious that $\operatorname{tr} M < 0$ and $\det M > 0$, because $f(U, I)$ is an increasing function of U and I (i.e., $f_U > 0$ and $f_I > 0$).

APPENDIX 2

Derivation of Mutant Fitness $W_S(x, x^*)$ in Eq. (11)

The dynamics of mutant symbionts adopting a strategy x' in the population with most symbionts having a strategy x is given by

$$\frac{dI'}{dt} = prb'I' - f(U^*, I^*) \cdot I' + cU^*S', \tag{B1}$$

$$\frac{dS'}{dt} = \beta S' - g(S_0) \cdot S' + a'I' - cU^*S', \tag{B2}$$

where U^* and I^* are the equilibrium values in the text. The symbol "′" denotes "mutant." In these equations, "I'" means the number of hosts infected by the mutant symbionts. We have assumed that the number of mutant symbionts is so small that U^* and I^* are almost the same as those in the case where all symbionts have the same strategy x^*. Using Eqs. (5) and (6) for $f(U^*, I^*)$ and $g(S_0)$, we have

$$\begin{aligned} \frac{d}{dt} \begin{bmatrix} I' \\ S' \end{bmatrix} &= \begin{bmatrix} pr(b'-b) - \dfrac{cU^*S_0}{I^*} & cU^* \\ a' & -\dfrac{aI^*}{S_0} \end{bmatrix} \begin{bmatrix} I' \\ S' \end{bmatrix} \\ &= M_S^x \begin{bmatrix} I' \\ S' \end{bmatrix}. \end{aligned} \tag{B3}$$

The characteristic equation of M_S^x is given by

$$\lambda'^2 - (\operatorname{tr} M_S^x)\,\lambda' + \det M_S^x = 0. \tag{B4}$$

We assume that the difference between x' and x is so small that λ' is also sufficiently small. Neglecting λ'^2 in Eq. (B4), we have

$$\begin{aligned} \lambda' &\simeq \frac{\det M_S^x}{\operatorname{tr} M_S^x} \\ &= \frac{-(aI^*/S_0)\{pr(b'-b) - (cU^*S_0/I^*)\} - a'cU^*}{pr(b'-b) - (cU^*S_0/I^*) - (aI^*/S_0)}. \end{aligned} \tag{B5}$$

In the denominator, $pr(b'-b)$ is sufficiently small in comparison with the other terms. Neglecting $pr(b'-b)$, we have

$$\begin{aligned} \lambda' &\simeq \frac{aI^{*2}}{cU^*S_0^2 + aI^{*2}} \left\{ pr(b'-b) + \frac{cU^*S_0}{aI^*}\,(a'-a) \right\} \\ &\propto pr(b'-b) + \frac{cU^*S_0}{aI^*}\,(a'-a). \end{aligned} \tag{B6}$$

If the right-hand side is negative, the mutant symbionts cannot invade the system because the eigenvalue is negative ($\lambda' < 0$). On the other hand, the mutant symbionts can invade the system if the right-hand side of (B6) is positive. Since the eigenvalue λ in the case where all symbionts have the same strategy x is zero, we can describe (B6) by

$$\Delta\lambda \propto pr\,\Delta b + \frac{cU^*S_0}{aI^*}\,\Delta a, \tag{B7}$$

where $\Delta\lambda = \lambda' - \lambda$, $\Delta a = a' - a$, and $\Delta b = b' - b$. We define $x' - x$ as Δx. Dividing (B7) by Δx and then taking the limit $\Delta x \to 0$, we have

$$\frac{d\lambda}{dx} \propto pr\,\frac{db(x)}{dx} + \frac{cU^*S_0}{aI^*}\,\frac{da(x)}{dx}. \tag{B8}$$

Here, we introduce a function

$$W_S(x', x) = prb(x') + \frac{cU^*S_0}{a(x)\,I^*}\,a(x'). \tag{B9}$$

In (B6) and Eq. (B9), "λ' takes a maximum value 0 at an ESS x" is equivalent to "$W_S(x', x)$ takes a maximum value at the ESS x." Replacing x' and x with x and x^*, respectively, we have the function given in Eq. (11) in the text.

Derivation of Mutant Fitness $W_S(r, r^*)$ in Eq. (17)

The dynamics of mutant symbionts adopting a strategy r' in the population with most symbionts having a strategy r is given by

$$\frac{dI'}{dt} = pr'bI' - f(U^*, I^*)\cdot I' + cU^*S', \tag{B10}$$

$$\frac{dS'}{dt} = \beta S' - g(S_0)\cdot S' + aI' - cU^*S', \tag{B11}$$

where the symbol "$'$" denotes "mutant." Handling Eqs. (B10) and (B11) with the same procedure as that in $W_S(x^*, x)$, we have $W_S(r^*, r)$ in Eq. (17).

Derivation of Mutant Fitness $W_H(r, r^*)$ in Eq. (18)

The dynamics of mutant hosts adopting a strategy r' in the population with most hosts having a strategy r is given by

$$\frac{dU'}{dt} = b_n U' - f(U^*, I^*)\cdot U' + (1 - r')\,bI' - cU'S_0, \tag{B12}$$

$$\frac{dI'}{dt} = pr'bI' - f(U^*, I^*)\cdot I' + cU'S_0, \tag{B13}$$

where the symbol "$'$" denotes "mutant." In these equations, "I'" means the number of mutant hosts. We have the function $W_H(r^*, r)$ in Eq. (18) from Eqs. (B12) and (B13).

APPENDIX 3

Derivation of the ESS x^*

We define the left-hand side of Eq. (15) as L_{15}. Using Eq. (5), L_{15} can be rewritten as

$$\begin{aligned} L_{15} &= -prb_1 + \frac{a_1\{f(U^*, I^*) - prb(x^*)\}}{a_0 + a_1x^*} \\ &= -\frac{1}{a_0 + a_1x^*}\{prh - a_1 f(U^*, I^*)\}, \end{aligned} \tag{C1}$$

where $h = a_0b_1 + a_1b_0$. Inserting Eq. (8) into Eq. (C1), we have

$$\begin{aligned} L_{15} = -&\frac{1}{a(x^*)} \\ &\times (prh - a_1b_n - a_1[\{(1-r) + pr\}\, b(x^*) - b_n]\,\xi^*), \end{aligned} \tag{C2}$$

where $\xi^* = I^*/H^*$ and we replaced $a_0 + a_1x^*$ with $a(x^*)$. Inserting Eq. (10) into Eq. (C2), we have

$$\begin{aligned} L_{15} = -&\frac{1}{2a(x^*)} \\ &\times \{2prh - pra_1b(x^*) - a_1b_n + a_1cS_0 - a_1\sqrt{D}\}. \end{aligned} \tag{C3}$$

Setting Eq. (C3) to zero and solving with regard to x^*, we have the ESS x^* given in Eq. (16) in the text.

Relationship between x^* and r

Differentiating Eq. (16) with regard to r in order to see the dependency of x^* on r, we have

$$\frac{\partial x^*}{\partial r} \propto p^2h(1-r)^2 - p\{ph - a_1(b_n - cS_0)\}, \tag{C4}$$

where the symbol "$\propto$" implies that both sides are equal in their signs. The right-hand side, which we define as $R(r)$, is a monotonically decreasing function of r in the interval, $0 \leqslant r \leqslant 1$. According to parameters such as p and cS_0, the dependency of x^* in Eq. (16) on r takes various forms: x^* is a monotonically decreasing function of r irrespective of p if $R(0) < 0$ (i.e., $cS_0 > b_n$), and it is a monotonically increasing function of r if $R(1) > 0$ (i.e., $ph < a_1(b_n - cS_0)$). As for the latter case where x^* given in Eq. (16) is a monotonically increasing function of r, the ESS x^* is, however, a constant ($x^* = \hat{x}$) independent of r, because the right-hand side of Eq. (12) is always positive in the region $0 < r < 1$ and $-a_0/a_1 < x < \hat{x}$. When $ph > a_1(b_n - cS_0) > 0$, x^* is not a monotonic function of r.

APPENDIX 4

Host's Behavior at Large Values of b_0 When $r^* < \hat{r}$

We consider the case where the vertical transmission rate is smaller than the critical value $\hat{r}$ which satisfies $x^*(\hat{r}) = \hat{x}$ in Eq. (16) in the text. The degree of exploitation is, therefore, a constant ($x^* = \hat{x}$). Using Eq. (4) for cU^*S_0 and Eq. (8), Eq. (18) can be rewritten as

$$W_H(r, r^*) \propto ([\{(1-r^*) + pr^*\}\, b(x^*(r^*)) - b_n]\, \eta^* - (1-p)(1-r^*)\, b(x^*(r^*)))\, r + \text{constant}, \tag{D1}$$

where $\eta^* = 1 - \xi^*$ or $\eta^* = U^*/H^*$, the proportion of the uninfected lost. We define the coefficient of r in (D1) as C_{D1}. Inserting Eq. (10) into C_{D1} and replacing x^* with $\hat{x}$ to deal with the case $r^* < \hat{r}$, we have

$$C_{D1} = \tfrac{1}{2}\{2pb(\hat{x}) - pb(\hat{x})\, r^* - b_n + cS_0 - \sqrt{D}\}. \tag{D2}$$

It is obvious that C_{D1} is negative if $2pb(\hat{x}) - pb(\hat{x})\, r^* - b_n + cS_0 < 0$, where there is always selection for lower r in the host.

We will consider the sign of C_{D1} under the condition that $2pb(\hat{x}) - pb(\hat{x})\, r^* - b_n + cS_0 > 0$. We can rewrite Eq. (D2) as

$$\begin{aligned} C_{D1} &= \frac{1}{2}\, \frac{(2pb(\hat{x}) - pb(\hat{x})\, r^* - b_n + cS_0)^2 - D}{2pb(\hat{x}) - pb(\hat{x})\, r^* - b_n + cS_0 + \sqrt{D}} \\ &= \frac{1}{8b(\hat{x})}\, \frac{(1-r^*)\{p^2 b(\hat{x}) - pb_n - (1-p)\, cS_0\}}{2pb(\hat{x}) - pb(\hat{x})\, r^* - b_n + cS_0 + \sqrt{D}}. \end{aligned} \tag{D3}$$

Selection on the host favors greater r if $p^2 b(\hat{x}) - pb_n - (1-p)\, cS_0 > 0$, while it favors lower r if $p^2 b(\hat{x}) - pb_n - (1-p)\, cS_0 < 0$.

The condition that there is selection for greater r in the host ($C_{D1} > 0$) is

$$2pb(\hat{x}) - pb(\hat{x})\, r^* - b_n + cS_0 > 0, \tag{D4}$$

and

$$p^2 b(\hat{x}) - pb_n - (1-p)\, cS_0 > 0. \tag{D5}$$

Using Eq. (14), (D4) can be rewritten as

$$b_0 - b_1 \hat{x} - \frac{1}{2-r^*}\, \frac{b_n - cS_0}{p} > 0, \tag{D6}$$

and (D5) can be rewritten as

$$b_0 - b_1 \hat{x} - \frac{pb_n + (1-p)\, cS_0}{p^2} > 0. \tag{D7}$$

Since (D6) is a necessary condition of (D7), the condition under which $C_{D1} > 0$ is equivalent to (D7). Here, we define the left-hand side of (D7) as D_H. To the contrary, there is selection for lower r in the host if $D_H < 0$. Note that D_H does not include r^*. This means that selection on the host favors lower r if $D_H < 0$, and it favors greater r if $D_H > 0$ in the interval $0 \leqslant r^* \leqslant \hat{r}$.

When the host evolves to increase b_0 such that $D_H = 0$, the coefficient of (D1) becomes equal to zero in the interval $0 \leqslant r^* \leqslant \hat{r}$. We can show that $D_H = 0$ is the condition under which r_H given in Eq. (20) becomes $\hat{r}$. This condition is equivalent to the condition

$$x^*(r_H) = \hat{x}. \tag{D8}$$

Inserting Eq. (20) into Eq. (16), we have

$$x^*(r_H) = \frac{b_0}{b_1} - \frac{pb_n + (1-p)\, cS_0}{p^2 b_1}. \tag{D9}$$

Inserting Eq. (D9) into Eq. (D8) and solving with regard to b_0, we have

$$b_0 - b_1 \hat{x} - \frac{pb_n + (1-p)\, cS_0}{p^2} = 0. \tag{D10}$$

Thus, when b_0 increases such that $D_H = 0$, the critical value r_H reaches $\hat{r}$. Then, there is selection for greater r in the host irrespective of the current r^* if the host evolves to increase b_0 such that $D_H > 0$.

Correspondence of r_1 to r_0 at $\hat{r}$

The critical value r_1 in Eq. (24) and the critical value r_0 in Eq. (25) should meet together if the parameter b_0 continues to increase, because r_1 and r_0 are monotonically decreasing and increasing functions, respectively, and $r_1 \to 0$ and $r_0 \to 1/(1-p)$ in the limit $b_0 \to \infty$. We will show that these two critical values meet together at $\hat{r}$.

The two critical values are obtained from setting W_H given in Eq. (22) to zero. The value r_1 is given by

$$\{(1-r^*) + pr^*\}(b_0 - b_1 x^*) = b_n, \tag{D11}$$

where x^* is given in Eq. (16) and $r^* \geqslant \hat{r}$. The value r_0 is given by

$$\{(1-r^*)+pr^*\}(b_0-b_1\hat{x})=b_n, \tag{D12}$$

where $\hat{x}$ is independent of the vertical transmission rate or other parameters, and $r^* \leqslant \hat{r}$. It is obvious that Eqs. (D11) and (D12) are exactly the same if $r^*=\hat{r}$, because $\hat{r}$ has been defined by $x^*(\hat{r})=\hat{x}$. This means that if b_0 continues to increase, r_1 decreases while r_0 increases so that they meet together at $\hat{r}$.

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