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Diversity and Evolution of Symbiotic Interactions

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Introduction

In ecological time scales and local spatial scales, biodiversity is the issue of coexistence of different species. However, in evolutionary time scales and global spatial scales, biodiversity is a result of the balance of speciation and extinction of species. In geological history, rapid speciation, called adaptive radiation, has occurred repeatedly. The origins of such newly developing taxa often evolved from the symbiosis of two different species (Price 1991). Thus, symbiosis can be considered an important source of the Earth's current biodiversity, and in this context symbiosis can be called evolutionary innovation (Margulis 1993).

In this chapter, I touch on several examples of symbiosis as a source of evolutionary innovation that was followed by adaptive radiation. Mutualistic symbioses are generally considered to evolve from parasitic relationships (Ewald 1987; Price 1991). I introduce here a mathematical model that identifies the conditions for the evolution of mutualism from parasitism, in which vertical transmission, defined as the direct transfer of infection from parent host to its progeny, is a key factor (Yamamura 1993). Finally, I discuss the evolutionary factors of mutualism without vertical transmission.

Symbiosis Followed by Adaptive Radiation

Most biologists now accept that the evolution of eukaryotes resulted from the symbiotic union of several independent ancestors (a host cell, an ancestor of mitochondria, an ancestor of the chloroplast), although the origins of other cellular organs such as the undulipodia, microtubules, centrioles, spindle, and microbody remain controversial (Maynard Smith 1989; Margulis 1993). There is no doubt that the evolution of eukaryotes provided the important source for the Earth's current biodiversity.

After the evolution of eukaryotes, there were probably several epoch-making instances in which the evolution of symbiosis was followed by adaptive radiation (Price 1991). Terrestrial plants might have evolved through the symbiosis of

aquatic algae and fungi. Large terrestrial plants such as trees might also have evolved through the symbiosis of small terrestrial plants and fungi, the mycorrhizae. It is said that insects became able to use low-nutrition food through symbiosis with microorganisms that aid in digestion. The adaptive radiation of parasitic wasps is suggested to have occurred through symbiosis with a virus. Large herbivorous mammals would also have evolved through symbiosis with microorganisms that aid in digestion. According to Price (1991), the number of species originating from such symbioses constitutes 54% of all the current species on Earth.

Coral, through its acquisition of photosynthetic symbionts, brought about adaptive radiation in geological history several times (Stanley 1981). Some fish use light organs to assist vision and to give signals, and the light is generated by luminous bacteria. The adaptive radiation of fish having such light organs occurred within different taxa of euteleostei (McFall-Ngai 1991). Termite species have established a decomposer niche in tropical forests and tropical savanna, and the prosperity of termites probably results from symbiosis with microorganisms such as protozoa, bacteria, and fungi.

Evolution of Mutualistic Symbiosis

In symbiosis that results in adaptive radiation, both interacting species help each other in a surprisingly intimate manner, and this can be termed mutualistic symbiosis. How could such neat mutualism have evolved in the first place? Many authors have suggested the evolution of mutualism from parasitism. Roughgarden (1975) stated that parasites do not harm their hosts as much as they could because parasites owe their habitats and energy resources to their hosts. Ishikawa (1988) stated that parasitism naturally evolves into mutualism and described the process in a phrase: an enemy today is a friend tomorrow. Ewald (1987) also claimed that parasitism should eventually evolve toward commensalism, and commensal relationships are viewed as the raw material for evolution of mutualism.

The origin of some symbioses may be predation of a larger organism on a smaller organism. When the smaller organism evolves such that it can survive inside the larger organism, we can say that endosymbiosis has evolved. The first phase, when the smaller organism establishes a part of its life cycle in the larger organism, would result in some degree of deleterious effect on the host as the result of resource competition or simple occupation of some space inside the host. In my definition as used here, interaction with such deleterious effects on the fitness of the host is classified as parasitism. Evolution of mutualism from an origin of this type is thus included in the case of evolution from parasitism to mutualism.

The time-course of the evolution of reduced virulence has been documented in various parasites and diseases, among which the myxoma virus in Australian rabbits is well known (Fenner 1965). Jeon (1972) made a more exact observation: a virulent bacterium that infected an ameba changed into a mutualistic symbiont of the ameba by artificial selection of the surviving ameba. However, many parasites

and diseases clearly continue to be virulent to their hosts (Ewald 1994). In conclusion, the reality would be that some parasites persist in antagonistic relationships with their hosts, while others have evolved into mutualistic relationships through reduction of their virulence.

Vertical Transmission

Many authors have suggested that vertical transmission, defined as the direct transfer of infection from a parent organism to its progeny, is a key factor for the evolution of mutualism that is highly beneficial to both organisms. For example, Ewald (1987) cited mutualism described by Buchner (1965), mainly between insect hosts and bacteria symbionts, and found that all of these accompany vertical transmission, such as transovarial transmission. Protozoa in termite guts are transferred among individuals through direct feces feeding (Breznak 1975). Colony-founding queens of some ants accompany their mutualistic partner, the mealy bug (Klein et al. 1992). Some parasitic wasps inject symbiotic virus into insect larvae when ovipositing (Stolts and Vinson 1979). This virus helps the parasitic wasp to defeat the defense mechanism of the host larvae. Surprisingly, the genome of the virus seems to be incorporated into the genome of the wasp (Fleming and Summers 1991).

Ewald (1987) pointed out that among other various modes of transmission, vertical transmission is the most remarkable characteristic of intimate mutualism between a symbiont and its host. Perhaps what occurred in the evolutionary history was a conflict in the vertical transmission rate between a host and a parasite. In the evolutionary sense, a host would not want its parasite to infect its progeny, while the parasite would want to infect the progeny. If the host continues to dominate this evolutionary race, the antagonistic relationship between the host and the parasite will also continue. If the parasite, however, wins the race and attains a higher vertical transmission rate, it could not continue to exploit the host so severely, because its progeny owe their lives mainly to the progeny of the host.

A Mathematical Model for the Evolution of Mutualism

I have made a simple mathematical model, based on Darwinian fitness, to identify the conditions under which evolution of mutualism from parasitism may actually occur (Yamamura 1993). The model also clarifies whether or not a long interrelationship between different species necessarily develops into evolution of mutualism, that is, whether or not an enemy today is a friend tomorrow, as Ishikawa (1988) stated.

The model is constructed as follows. An infecting parasite reproduces $a(x)$ offspring, where x is a parasite strategy that is the degree of exploitation on its host, for example, in energy units. Because the parasite can reproduce more offspring if

exploiting the host more severely, $a(x)$ is an increasing function of x:

$$a(x) = a_0 + a_1 x \tag{1}$$

On the other hand, an infected host reproduces $b(x)$ offspring, where $b(x)$ is a decreasing function of x:

$$b(x) = b_0 - b_1 x \tag{2}$$

The values of a_1, b_0, and b_1 are naturally positive, but a_0 may be zero or even negative because parasites may be unable to reproduce without exploiting a host resource more than some critical amount. I extended x to negative values, which means that the parasite gives the host some positive effects in the sacrifice of its own fitness. For the negative values of x, the parasite is not parasitic but is actually beneficial to the host. Therefore, I will use "symbiont" hereafter to refer to both parasitic and beneficial cases. Because the numbers of offspring, $a(x)$ and $b(x)$, should be positive, the value of x is restricted in the interval, $-a_0/a_1 < x < b_0/b_1$. Therefore, negative values of x are admissible only when a_0 is positive.

An uninfected host reproduces b_n offspring. I discriminated b_n from b_0, the number of offspring of an infected host when $x = 0$, because I consider an evolutionary change in b_0 later. The vertical transmission rate r is defined as the proportion of offspring directly infected from their parent among $b(x)$ offspring. Offspring escaping from vertical transmission are exposed to infection by the parasites from other infected hosts along with offspring of uninfected hosts.

I have calculated, as the parasite strategy, the evolutionarily stable degree of exploitation, which is finally reached through evolution when the parameters involved remain constant. The solution x^* is a decreasing function of the vertical transmission rate r, as shown in Figure 5.1. It is easily realized that the parasite should reduce its virulence as r increases, and it should become a mutualist when r is larger than a critical value r_1 because x^* is negative in this range.

Next, I calculated the evolutionary direction of r from the point of view of both the symbiont and the host (see Fig. 5.1). When the vertical transmission rate r is controlled only by the symbiont, its value always increases. On the other hand, if it is controlled only by the host, its value decreases when r is smaller than a critical value r_2, and increases otherwise. The critical value of vertical transmission is represented as

$$r_2 = \frac{a_1 b_n}{a_1 b_0 + a_0 b_1} \tag{3}$$

This evolutionary pattern implies that there is a conflict between the symbiont and the host for smaller values of r and that there is no conflict for larger values of r. Suppose that r starts from a value in the conflict region. Once the symbiont wins the vertical transmission conflict and r increases to a value larger than r_2, one-way evolution begins toward a higher vertical transmission rate and highly mutualistic
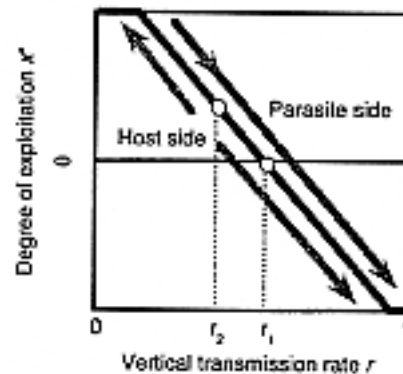
FIGURE 5.1. The evolutionary stable degree of exploitation x^* is a decreasing function of the vertical transmission rate r. There is a critical value r_1 above which the value of x^* is negative. There is another critical value, r_2, represented by Eq. 3, below which the evolutionary directions of r for the parasite and the host are conflicting, and above which they correspond to each other. When r exceeds r_2, one-way evolution begins toward a higher vertical transmission rate and highly mutualistic corporation.

cooperation because x^* is negative. Finally, the value of r reaches to 1, which indicates a perfect vertical transmission.

Even if r itself does not change, one-way evolution still begins when the critical value r_2 is reduced to a value smaller than r. The conditions whereby r_2 decreases can easily be identified from Eq. 3. The parameters a_0, a_1, b_0, and b_1 are coefficients of $a(x)$ and $b(x)$ in Eqs. 1 and 2, which may change through evolution during a long interaction of symbiosis. It is probable that a parasite increases a_0 by evolving toward use of some metabolic or digestive wastes excreted by the host. The parasite may increase a_1 by improving the conversion efficiency of exploiting resources to its fitness. A host may also evolve toward use of resources excreted by the parasite, leading to some increase in b_0, or to reduce the fitness effect of exploitation by the parasite, leading to some decrease in b_1. All the probable changes in parameters do not necessarily lead to the evolution of mutualism. It is certain that improvement of a_0 and b_0 (an effective use of the partner's disuse) favors the evolution of mutualism because r_2 is a decreasing function of a_0 and b_0. However, improvement of a_1 (the efficiency of resource usage) conversely reduces the possibility of mutualism because r_2 is an increasing function of a_1. Improvement of b_1 also has the same effect on r_2 as a_1.

The mathematical model here suggests that the vertical transmission rate is the most important factor for reduction of parasite virulence, and that initiation of the one-way evolutionary process from parasitism to mutualism may occur when the symbiont wins the conflict against the host on vertical transmission rate or when either side utilizes wastes of the partner. In the latter case, the attained mutualistic interaction can be regarded as a miniecosystem because matter circulation across different species is maintained.

Mutualism Without Vertical Transmission

In the model, vertical transmission is defined as the transfer of symbionts from generation to generation. The same effect as vertical transmission can be expected when symbionts reproduce in a host growing to a large size. For example, mycorrhizae reproduce following the growth of the roots of a tree. Because the model predicts that mutualism evolves under a high vertical transmission rate, it is likely to evolve when the host grows to a large size and lives a long life. Coral and a large colony of social insects can be categorized as such hosts with a long life span.

However, true vertical transmission is not common among this type of mutualism. Why are mycorrhizae not transmitted vertically through the seeds of the tree? More generally, why do not all mutualisms evolve into perfect vertical transmission? Mutualism without vertical transmission necessarily requires that symbionts have a free-living stage, independent of their hosts. Otherwise, newly born host individuals rarely could gain the symbionts. I discuss here three factors to explain the evolution of mutualism without vertical transmission.

The first possibility is that the apparent mutualism may actually be a parasitism or a manipulation. Leguminous bacteria might be parasitic on bean plants. The plants obtain nitrogen from bacteria, while giving sugar to the bacteria. The total effect on the plant might be negative. On the contrary, plants might manipulate bacteria and use them as tools for preparing nutrients. In this case, there is no benefit for the bacteria. When only one side gains, the other side should disturb the evolution of vertical transmission.

The second possibility is that the symbiotic association is beneficial for both partners under restricted conditions. In the phenomenon called bleaching, which is well known in coral, the photosynthetic symbionts depart from the host coral at high water temperatures (Brown and Ogden 1993). It is unclear in bleaching whether symbionts escape by themselves or the coral drives out the symbionts. In the case in which the benefits of symbiosis are temporarily changing, vertical transmission may not pay for its cost, and therefore it is less likely to evolve.

The last possibility, which I think is the most important, is that the symbiont adopts a bet-hedging strategy in which it uses the host as a refuge. Luminous bacteria can reproduce by themselves in seawater (McFall-Ngai 1991), but conditions for reproduction in seawater may fluctuate greatly. The inside of fish must be a stable environment for luminous bacteria, and it may serve like a dormant seed bank of weed grasses where a grass population can recover by germination of the dormant seeds even after a complete destruction. The host need not evolve vertical transmission in the case in which free-living symbionts are common in the habitat of the host, although the density of the free-living symbionts may fluctuate.

In conclusion, the full life cycles of most symbionts with a free-living stage have not been sufficiently investigated. In particular, studies on the mechanism of encounter and departure between the symbiont and its host are greatly lacking. Extensive ecological studies on these organisms will clarify how symbionts with-

out vertical transmission are mutualistic to their hosts. At the same time, such studies, along with further studies of cases with vertical transmission, will give us basic biological information necessary for maintenance of biodiversity because the various symbioses involved in all ecosystems serve vital components of these ecosystems, and human activities in ignorance may disrupt parts of such important symbiotic relationships.

Summary

In geological history, rapid speciation, called adaptive radiation, has occurred repeatedly. The origins of such newly developing taxa often evolved from the symbiosis of different species. Mutualistic symbioses are generally considered to evolve from parasitic relationships. A mathematical model has suggested that the vertical transmission rate is the most important factor for reduction of parasite virulence, and that initiation of the one-way evolutionary process from parasitism to mutualism may occur when the symbiont wins the conflict against the host on vertical transmission rate, or when either side utilizes the wastes of the partner. In the latter case, the attained mutualistic interaction can be regarded as a miniecosystem because matter circulation across different species is maintained. Finally, a bet-hedging strategy of the symbiont was stressed as an evolutionary factor of mutualism without vertical transmission.

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