

Evolution of mutualism through spatial effects

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Abstract

Mutualism among species is ubiquitous in natural ecosystems but its evolution is not well understood. We provided a simple lattice model to clarify the importance of spatial structure for the evolution of mutualism. We assumed reproductive rates of two species are modified through interaction between species and examine conditions where mutualists of both species, that give some benefit to the other species with their own cost, invade non-mutualists populations. When dispersal of offspring is unlimited, we verified the evolution of mutualism is impossible under any condition. On the other hand, when the dispersal is limited to neighboring lattice sites, mutualists can invade if the ratio of cost to benefit is low and the intrinsic reproductive rate is low in case where the parameter values are symmetric between species. Under the same conditions, non-mutualists cannot invade mutualist populations, that is, the latter are evolutionarily stable. In case of asymmetric parameters, mutualists tend to invade if the average value of costs to two species is low or that of benefits is high, and if the intrinsic reproductive rate is low for one of the two species. A mechanistic explanation of why mutualists increase when the dispersal is limited is given by showing that mutualist pairs of the two species at the same lattice site rapidly increase at the initial phase of the invasion.

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1. Introduction

Species interact constantly in diverse ways in ecosystems. In mutualistic interaction, one of the species provides some kind of “service” that its partner species cannot provide for itself and receives some kind of “reward” in return. The two mutualistic species survive and reproduce by helping each other. Such mutualism plays a fundamental role in all ecosystems (Boucher, 1985; Smith and Douglas, 1987; Bronstein, 1994). Evolution of mutualism has been studied as one of the most important problems in ecology (Doebeli and Knowlton, 1998; Herre et al., 1999; Hoeksema and Bruna, 2000; de Mazancourt et al., 2001; van Baalen and Jansen, 2001).

One important factor to promote the evolution of mutualism has been suggested to be vertical transmis-

sion of symbionts through hosts, which assures a long relationship between offspring of the interacting individuals of the two species over generations (Maynard-Smith, 1991; Yamamura, 1993, 1996; Genkai-Kato and Yamamura, 1999). If offspring of the symbiont interact with offspring of the host, the symbiont could drive a greater advantage by helping rather than exploiting their hosts. Even without vertical transmission, the interaction between individuals of two species will continue over generations if dispersal of the two species is spatially limited. Doebeli and Knowlton (1998) showed the importance of spatial structure for mutualism to evolve in their Iterated Prisoner's Dilemma (IPD) game model.

The IPD was proposed (Axelrod and Hamilton, 1981) and had been analysed (Nowak and May, 1992; Nakamaru et al., 1997; Wakano and Yamamura 2001) as a theoretical method to investigate the phenomena of cooperation in a single species, mainly by simulating higher animals' or human's cognitive processes. Here, in order to clarify the effect of spatial structure, per se, on the evolution of mutualism between different species, we apply a simpler spatial model of cost and benefit, used for the analysis of the evolution of altruism (Matsuda,

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1987; Taylor, 1992; Wilson et al., 1992), without any complex interaction between partners, as assumed in the IPD game. It is a new challenge that we apply the mutual altruistic behavior for interaction of different species, although evolution of altruism within a single species has intensively been studied (for recent studies, see Irwin and Taylor, 2001; Le Galliard et al., 2003).

Our model includes several independent parameters: benefit to one species from another species, cost to each species, and intrinsic reproductive rates that are the primary determinants of population densities of both species. First, we show analytically that the evolution of mutualism is impossible in this simple model when dispersal is unlimited; that is, when there is no spatial structure. Next, we investigate numerically the conditions of parameter values under which mutualism can evolve when dispersal is limited, where both symmetric and asymmetric parameter values between species are examined.

2. The model

We assume a two-dimensional lattice space where species A and B inhabit; only one individual can occupy one lattice site for each species. Individuals of different species can coexist at the same lattice site and then interact with each other. The individuals of two species are divided into two classes each. A_M and A_{NM} are frequencies of mutualists and non-mutualists of species A, respectively. Similarly, B_M and B_{NM} are frequencies of mutualists and non-mutualists of species B, respectively. A_E and B_E are frequencies of empty sites for species A and B, respectively. One can imagine a lattice habitat populated by species A and another lattice parallel to it, called as its “dual”, which is inhabited by species B. Doebeli and Knowlton (1998) proposed this dual-lattice description, but did not assume empty sites in their model. We have the following identities for the two lattices:

$$A_M + A_{NM} + A_E = 1 \quad (1a)$$

and

$$B_M + B_{NM} + B_E = 1. \quad (1b)$$

In our model, mutualists of A and B species reproduce by helping each other. A cost to a reference species (measured in terms of the reduction of reproductive rate) is always associated with the benefit it provides to the partner species. Let r_A , d_A , b_A and c_A denote intrinsic reproductive rate, death rate, benefit of mutualism and cost of mutualism for species A, respectively. Let r_B , d_B , b_B and c_B denote the corresponding parameters for species B, respectively. We assume, for simplicity, that the reproductive rates are modified through species interaction, but that death

rates are not. When a lattice site is occupied by a mutualist of species A and the corresponding site in the “dual” lattice also has a mutualist of species B, their reproductive rates are $r_A + b_A - c_A$ and $r_B + b_B - c_B$. If the site in the dual site is occupied by a non-mutualist of species B, their reproductive rates are $r_A - c_A$ and $r_B + b_B$. Those for the contrary case are $r_A + b_A$ and $r_B - c_B$. That is, a mutualist pays a cost without discrimination whether the opponent is a mutualist or non-mutualist. If a mutualist is associated with an empty site, the reproductive rate of the mutualist is $r_A - c_A$ for species A and $r_B - c_B$ for species B when mutualists pay costs before assuring whether there is an opponent at the dual lattice site or not (Case I). They are r_A and r_B when mutualists do not pay any costs when the dual lattice site is empty (Case II). The reproductive rates of non-mutualists remain r_A and r_B when they are associated with empty sites or non-mutualists of the other species. The reproduction is successful only when offspring can enter empty sites for each species.

3. Unlimited dispersal

When dispersal of reproduced offspring is unlimited and they randomly reach any site, the changes in frequencies of A_M , A_{NM} , B_M and B_{NM} for Case I can be written as differential equations:

$$\begin{aligned} \frac{dA_M}{dt} = & (r_A - c_A)A_E A_M (B_E + B_{NM}) \\ & + (r_A - c_A + b_A)A_E A_M B_M - d_A A_M, \end{aligned} \quad (2a)$$

$$\begin{aligned} \frac{dA_{NM}}{dt} = & r_A A_E A_{NM} (B_E + B_{NM}) \\ & + (r_A + b_A)A_E A_{NM} B_M - d_A A_{NM}, \end{aligned} \quad (2b)$$

$$\begin{aligned} \frac{dB_M}{dt} = & (r_B - c_B)B_E B_M (A_E + A_{NM}) \\ & + (r_B - c_B + b_B)B_E B_M A_M - d_B B_M, \end{aligned} \quad (2c)$$

$$\begin{aligned} \frac{dB_{NM}}{dt} = & r_B B_E B_{NM} (A_E + A_{NM}) \\ & + (r_B + b_B)B_E B_{NM} A_M - d_B B_{NM}. \end{aligned} \quad (2d)$$

These equations are derived from the assumptions of the model. For example, the first term of the right-hand side of (2a) represents the condition that mutualists of species A (the frequency is A_M) reproduce $r_A - c_A$ offspring when they are associated with empty sites or non-mutualists of species B (the frequency is $B_E + B_{NM}$) and the offspring survives only when they reach empty sites (the frequency is A_E). We omit the explanation of the other terms and the other equations because they are straightforward.

From Eqs. (2a) and (2b), we have

$$\frac{1}{A_M} \frac{dA_M}{dt} - \frac{1}{A_{NM}} \frac{dA_{NM}}{dt} = -c_A A_E (B_E + B_{NM} + B_M) = -c_A A_E < -\varepsilon < 0, \quad (3)$$

where ε is a positive value, because empty sites are always produced due to the death of mutualists and non-mutualists. That is, the specific increasing rate of A_M is always smaller than that of A_{NM} . This equation can be rewritten as

$$\frac{d}{dt} \log \left(\frac{A_M}{A_{NM}} \right) < -\varepsilon. \quad (4)$$

Integrating this in time interval from 0 to t , we have

$$\frac{A_M(t)}{A_{NM}(t)} < \frac{A_M(0)}{A_{NM}(0)} \exp(-\varepsilon t). \quad (5)$$

As $A_{NM}(t)$ is bounded under 1, $A_M(t)$ must approach zero as t goes to infinity. Similarly, since

$$\frac{1}{B_M} \frac{dB_M}{dt} - \frac{1}{B_{NM}} \frac{dB_{NM}}{dt} = -c_B B_E (A_E + A_{NM} + A_M) = -c_B B_E < -\varepsilon < 0, \quad (6)$$

B_M must approach zero. Therefore, mutualists cannot increase for any parameter values under the conditions of Case I.

The changes in the frequencies of A_M , A_{NM} , B_M and B_{NM} for Case II can be written as the following differential equations:

$$\begin{aligned} \frac{dA_M}{dt} &= r_A A_E A_M B_E + (r_A - c_A) A_E A_M B_{NM} \\ &+ (r_A - c_A + b_A) A_E A_M B_M - d_A A_M, \end{aligned} \quad (7a)$$

$$\begin{aligned} \frac{dA_{NM}}{dt} &= r_A A_E A_{NM} (B_E + B_{NM}) \\ &+ (r_A + b_A) A_E A_{NM} B_M - d_A A_{NM}, \end{aligned} \quad (7b)$$

$$\begin{aligned} \frac{dB_M}{dt} &= r_B B_E B_M A_E + (r_B - c_B) B_E B_M A_{NM} \\ &+ (r_B - c_B + b_B) B_E B_M A_M - d_B B_M, \end{aligned} \quad (7c)$$

$$\begin{aligned} \frac{dB_{NM}}{dt} &= r_B B_E B_{NM} (A_E + A_{NM}) \\ &+ (r_B + b_B) B_E B_{NM} A_M - d_B B_{NM}. \end{aligned} \quad (7d)$$

These equations are derived from the assumptions, noting that mutualists do not pay costs when they are associated with empty sites.

In this case,

$$\frac{1}{A_M} \frac{dA_M}{dt} - \frac{1}{A_{NM}} \frac{dA_{NM}}{dt} = -c_A A_E (B_{NM} + B_M) < 0, \quad (8)$$

that is, the specific increasing rate of A_M is always smaller than that of A_{NM} . By the same procedure as in Case I, we can show that A_M must approach zero. Similarly, B_M must approach zero.

We conclude that mutualists cannot survive under existence of non-mutualists for any case when dispersal is unlimited. It is reasonable that mutualists, which pay some costs, are less advantageous than non-mutualists, which pay no costs, if association between mutualists of different species is random due to unlimited dispersal.

4. Computer simulation for limited dispersal

We now investigate the evolution of mutualism, i.e., invasibility of mutant mutualists against non-mutualists in the lattice model by means of computer simulation. The evolution of mutualism is more difficult for Case I, where mutualists pay a cost even when the corresponding site of species B is empty, than for Case II. Thus, we examine Case I in order to clarify whether or not the evolution of mutualism can be realized through spatial effects. A lattice of size 25×25 is modeled and the periodic boundary conditions of a torus are applied. The lattice is dual, composed of lattice A and lattice B. Each lattice site can be in one of the three possible states: empty, non-mutualist or mutualist.

First, the model parameters are assumed to be symmetric between species, i.e., $r_A = r_B = r$, $c_A = c_B = c$, $b_A = b_B = b$ and $d_A = d_B = d$. In order to study the invasion condition, the initial frequencies of mutualists of both species are chosen with low frequencies. Our aim is to see if mutualists can invade the population of non-mutualists.

The following loop is repeated 625 times in one generation; this number is the number of sites in the lattice. (i) A lattice site X is chosen at random. (ii) If there is an individual at site X on lattice A, the average number of offspring β is calculated, depending on the state of the corresponding site of lattice B. For example, $\beta = r - c + b$ when both the site X on lattice A and the site X on lattice B are inhabited by mutualists (see Case I in the model section). (iii) At each neighboring site on lattice A (four neighbor assumption adopted), the offspring is produced at probability $\beta/4$ when the site is empty. (iv) The same reproductive process is repeated around the site X on lattice B. (v) Individual at site X on lattice A is killed at probability d . (vi) Individual at site X on lattice B is killed at probability d .

In order to study invasibility, we put “wild-type” individuals on all sites on lattice A and B, and ran simulations for 1000 generations to obtain the equilibrium state. Then we introduced mutants by placing mutant individuals at random sites on lattice A and B at frequency 0.04 (25 individuals). After 1000 generations, the average mutant frequencies on lattice A and B were

calculated. The invasion was defined to be successful when both of the average frequencies are higher than 0.04 (the initial frequencies). We also calculated invasibility of non-mutualists in wild-type populations of mutualists by the similar procedure.

In order to examine effects of the lattice size on the invasibility of mutualists and non-mutualists, we practiced similar computer simulation on 50×50 and 100×100 lattices.

Time series of the numbers of mutualist pairs on the same site of lattice A and B, and neighboring mutualist pairs on the same lattice were also calculated and plotted in order to illustrate how mutualist mutants increase their frequencies. Finally, we investigated invasibility of mutualists in case of asymmetric parameter values between two species.

5. Results of the simulation

Fig. 1 shows invasibility of mutualists in the parameter space of cost (c) and benefit (b) in case of symmetric parameter values between two species. Death rate and intrinsic reproductive rate were fixed ($d = 0.25$ and $r = 0.4$ in Fig. 1a). Mutualist mutants could successfully invade wild-type populations of non-mutualists when c was low and b was high (represented by horizontal segments “-”). Generally, only mutualists remained after 1000 generations when the invasion was successful and only non-mutualists remained when unsuccessful, although mutualists and non-mutualists continued to coexist in some cases owing to stochastic effects. The invasion of non-mutualists in wild-type populations of mutualists was successful when c was high and b was low (represented by vertical segments “|”), while unsuccessful in the opposite case, implying the mutualist population was evolutionarily stable. The region occupied mainly by “-” signs and that by “|” signs were almost separated by a straight line (nearly $c = 0.13b$ in this case). The results near the boundary line were not constant, due to stochasticity of the model, especially depending on the initial spatial distribution of mutants. Generally speaking, a necessary condition for mutualists to invade or for non-mutualists not to invade is that the ratio of cost of mutualists to benefit to the individual of other species is lower than a constant value. As the intrinsic reproductive rate is increased ($r = 0.5$ in Fig. 1b), the critical ratio of cost to benefit becomes lower (nearly $c = 0.075b$). In other words, the evolution of mutualism becomes more difficult with increasing reproductive rate.

Fig. 2 shows effects of the lattice size on the invasibility of mutualists and non-mutualists. The parameter values are the same as in Fig. 1a ($d = 0.25$ and $r = 0.4$), where the initial frequencies of mutants are also the same (0.04). The critical boundaries of

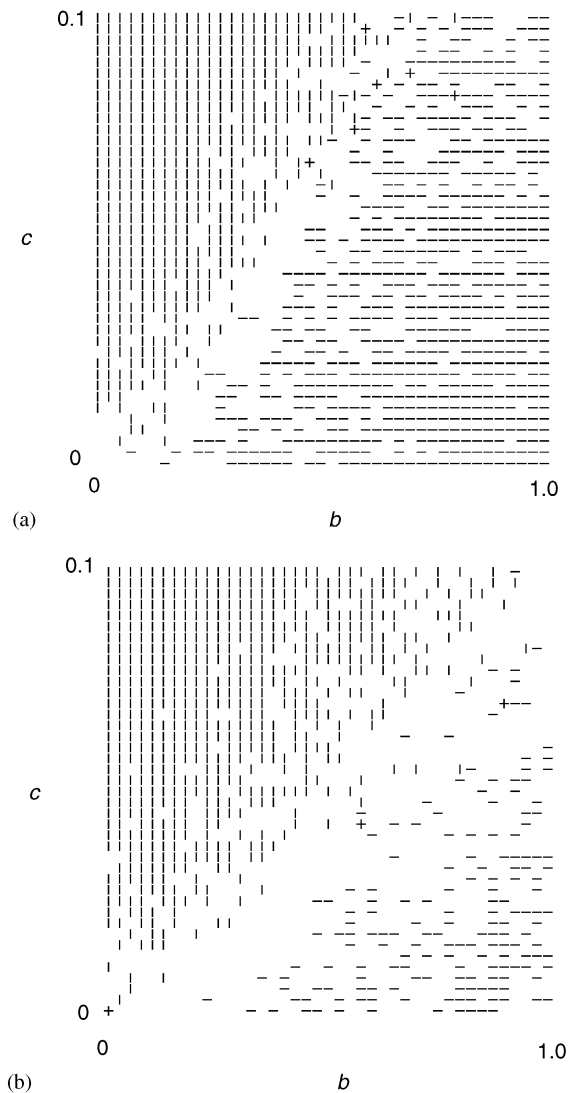


Fig. 1. Invasibility of mutants in the space of benefit (b) and cost (c). One run was conducted at each point of combination of b (0, 0.025, 0.05, ..., 1.0) and c (0, 0.0025, 0.005, ..., 0.1). A horizontal bar means that mutualists invaded non-mutualist populations. A vertical bar means that non-mutualists invaded mutualist populations. We set death rate as $d = 0.25$, and intrinsic reproductive rate as (a) $r = 0.4$ and (b) $r = 0.5$. The region for successful invasion of mutualists is smaller for higher reproductive rate.

successful mutualists invasion in cases of (a) 50×50 lattice and (b) 100×100 lattice were almost the same as in the 25×25 lattice, but the boundaries became clearer as the lattice size increased. We could confirm the results on the critical cost–benefit ratio are robust even in a rather small lattice such as 25×25 . In Fig. 2b with less stochasticity, we can see small region, at an upper part of the boundary, where both mutualists and non-mutualists invade and another small region, at lower part, where neither mutualists nor non-mutualists invades. Therefore, there may exist the region of coexistence between mutualists and non-mutualists at

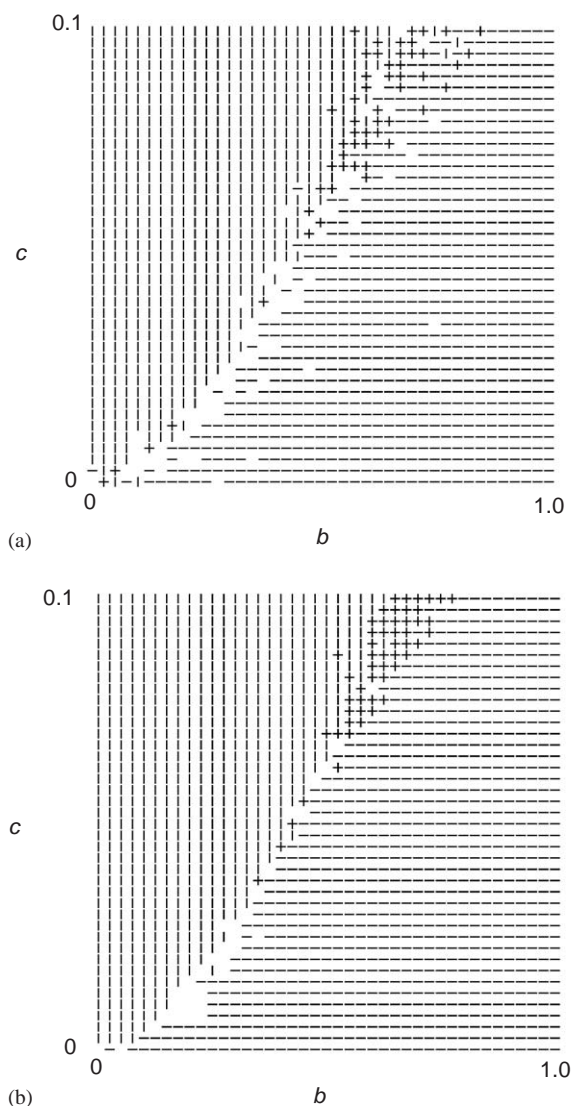


Fig. 2. Effects of the lattice size on the invisibility of mutualists and non-mutualists. The meaning of horizontal and vertical bars are the same as in Fig. 1, and the parameter values are the same as in Fig. 1a ($d = 0.25$, $r = 0.4$). As the lattice size increases ((a) 50×50 and (b) 100×100), the critical boundary for successful invasion of mutualists becomes clearer.

the former part, and the region of bistability at the latter part. If so, such regions are small and most of the parameter space will be filled with the two regions where mutualists can invade and are stable, and where non-mutualists can invade and are stable.

Fig. 3a shows an example of time series of the numbers of mutualists on lattice A and lattice B, where mutualist mutants invaded the populations dominated by non-mutualists ($r = 0.4$, $b = 0.7$, $c = 0.01$ and $d = 0.25$; see also Fig. 1a). The mutualists of the two species seem to increase in an approximately corresponding manner. Time series of the numbers of mutualist pairs on the same site of lattice A and B and neighboring

mutualist pairs on the lattice A and B were also calculated. Fig. 3b shows the ratios of the numbers to their expected values if the mutualists were randomly distributed on the two lattices. At the initial phase when the numbers of mutualists were low, the relative numbers of neighboring mutualist pairs took considerably high values, implying the mutualists increased to make clusters by reproducing in neighboring lattice sites. The high value of the relative number of pairs between different species during the same phase implies that the mutualists could increase by pairing with each other at a high probability. Fig. 3c shows an example of time series of the numbers of non-mutualists on lattice A and lattice B, where non-mutualist mutants invaded the populations dominated by mutualists ($r = 0.5$, $b = 0.2$, $c = 0.05$ and $d = 0.25$; see Fig. 1b). The non-mutualists seem to increase independently. As shown in Fig. 3d, during the initial phase when the numbers of non-mutualists were low, the relative numbers of neighboring non-mutualist pairs also took high values, but not as high as in case of the mutualists invasion, implying the degree of clustering of non-mutualists was weaker. The relative number of pairs between different species during the same phase was remarkably low and became less than one, implying that the non-mutualists of different species kept away from each other. This may be because non-mutualist mutants could increase by exploiting mutualists of the other species.

Fig. 4 shows invisibility of mutualists in case of asymmetric parameter values between two species where the invisibility is represented as frequency isoclines of invading cases among 100 trials. Although the isoclines are unsteady due to highly stochastic nature of the model, the following tendency is clearly recognized. When reproductive rates of species A (r_A) and species B (r_B) were different but cost and benefit were the same (Fig. 4a), the invading probability was higher if the reproductive rate of either species was higher, corresponding to the result of symmetric parameter cases (compare Fig. 1a and b, having different r values). An interesting fact is that the isoclines tend to be convex downwards, which implies that mutualism may evolve even when the reproductive rate of only one species is low. Fig. 4b shows the case of asymmetric costs between species while reproductive rates and benefits are the same. The invasion probability was higher if the cost of either species was higher, corresponding to the result of symmetric parameter cases (Fig. 1). The frequency isoclines seem to be weakly convex, but close to a straight line. Fig. 3c illustrates the case of asymmetric benefits between species, while reproductive rates and costs are the same. The frequency isoclines also seem to be near a straight line. We can say that in the case of asymmetric values of cost or benefit, the probability of mutualism evolution is determined by the average value between different species.

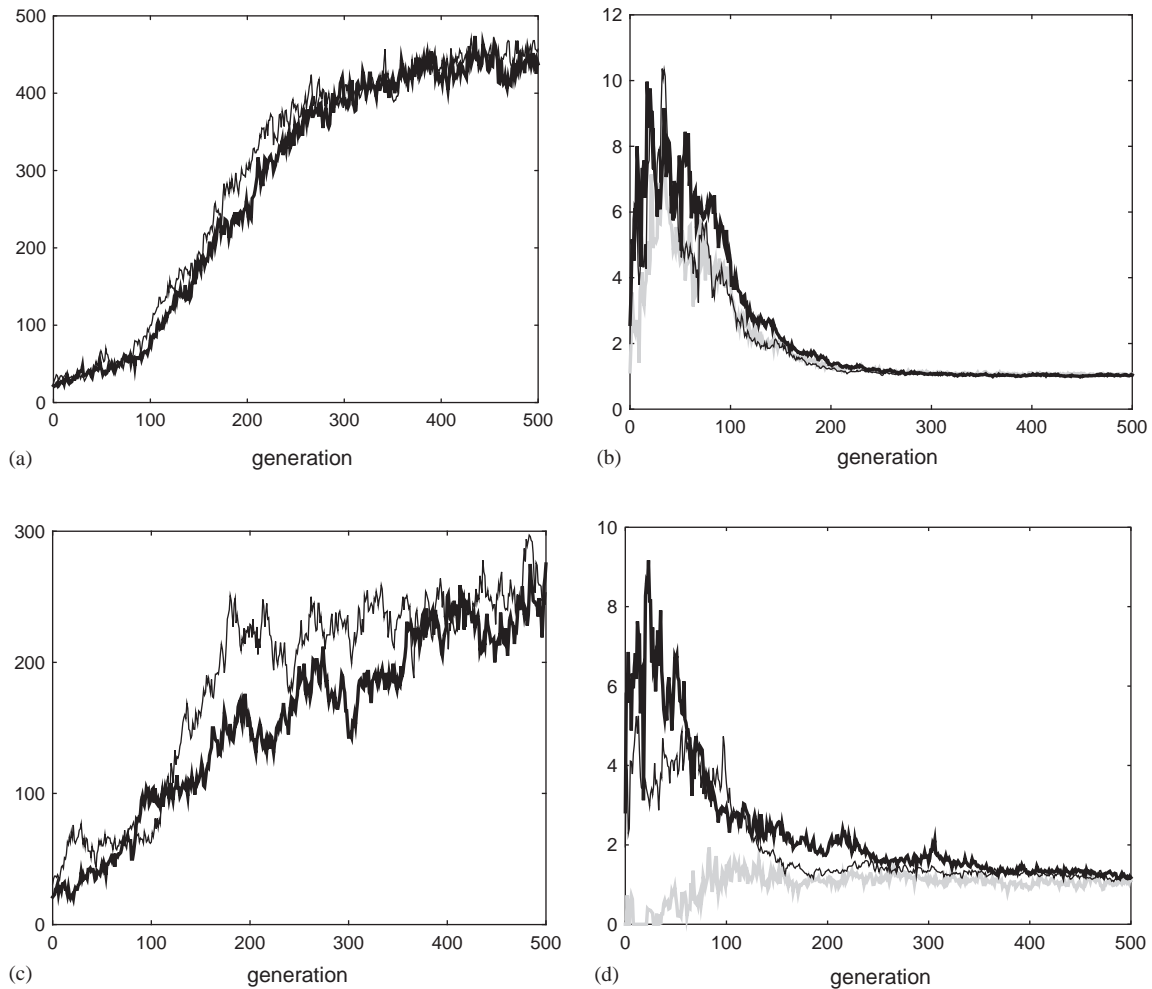


Fig. 3. When mutualists invade populations of non-mutualists ($d = 0.25, r = 0.4, b = 0.7, c = 0.01$), (a) the numbers of mutualists in lattice A (thick line) and in lattice B (thin line) increase rather correspondingly, and (b) the ratio of the number of pairs of neighboring mutants in lattice A to the number expected from random distribution (thick line), the same index in lattice B (thin line) and the ratio of the number of pairs of mutants across the lattices to the expected number (gray line) took high values during the initial phase. When non-mutualists invade populations of mutualists ($d = 0.25, r = 0.5, b = 0.2, c = 0.05$), (c) the numbers of non-mutualists in lattice A (thick line) and in lattice B (thin line) increase independently, and (d) the ratio of the number of pairs of neighboring mutants in lattice A to the expected number (thick line) and the same index in lattice B (solid line) took high values but the ratio of the number of pairs of mutants across the lattices to the expected number (gray line) took low values during the initial phase.

6. Discussion

We provided a simple lattice model to clarify the importance of spatial structure for the evolution of mutualism. When dispersal of offspring is unlimited, we verified analytically that the evolution of mutualism is impossible under any condition. On the other hand, when the dispersal is limited to neighboring lattice sites, mutualists can invade non-mutualists if the ratio of cost to benefit is low and the intrinsic reproductive rate is also low. Although our model is very simple, these results do suggest that the evolution of mutualism between species is more likely in organisms that have low dispersal abilities.

We can regard the mechanism of mutualism evolution in our model as mutual “altruism” between different

species. Altruism has been investigated as a behavior of an individual that give benefit to another individual, with its own cost, in the same species (Hamilton, 1964; Yamamura and Higashi, 1992). Apparent altruism may evolve when the ratio of cost to benefit is low and genetic relatedness between the interacting individuals is high. Yet even when individuals cannot discriminate whether or not their opponents are relatives, altruism can evolve if dispersal is limited, because there is a high probability that the interacting individuals are relatives to each other (Matsuda, 1987). In our model, the interacting individuals are of different species and thus are not clearly relatives. However, a mutualistic individual which facilitates reproduction of a mutualistic individual of the other species may nevertheless obtain returns if the dispersal is limited for both species:

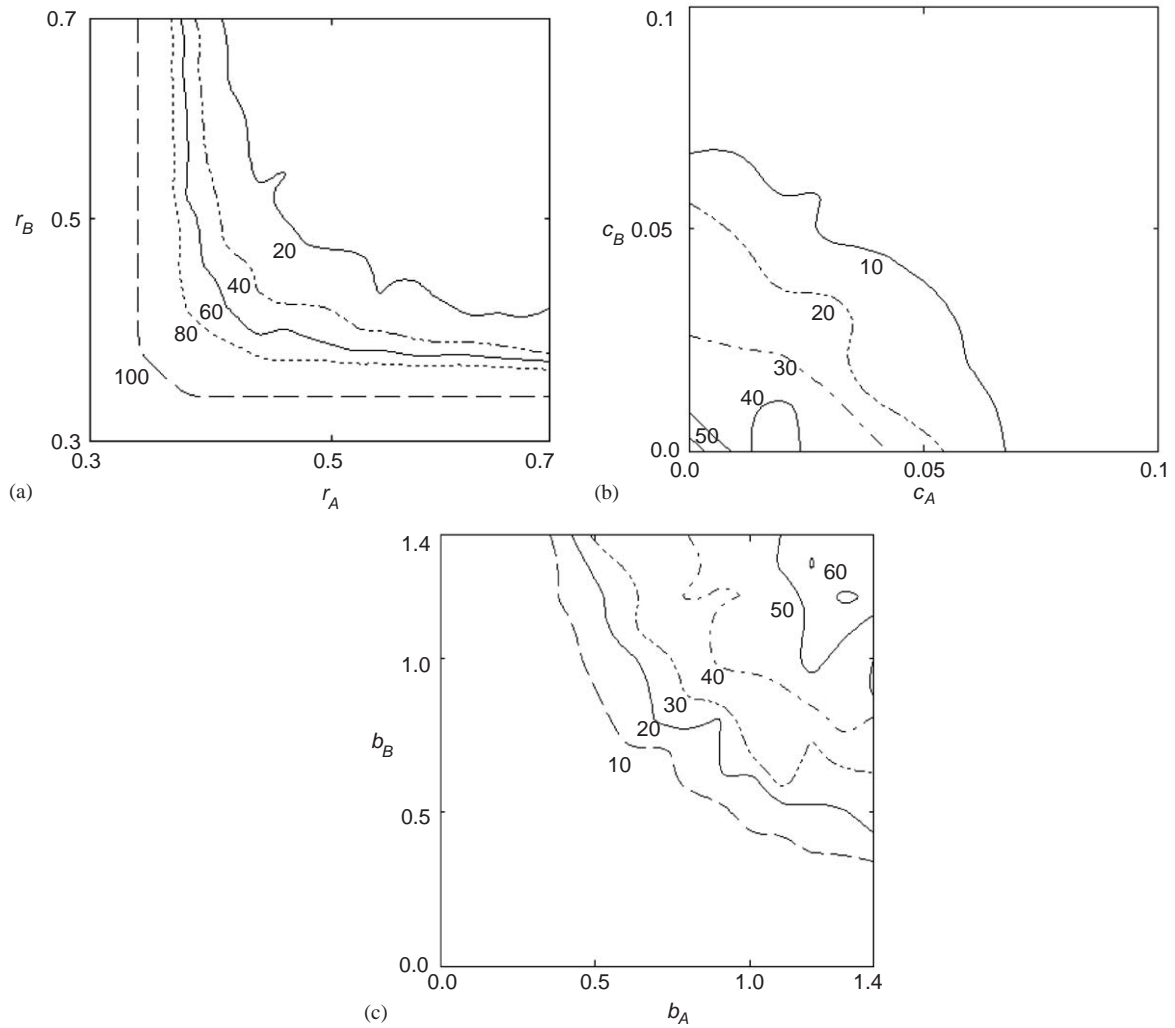


Fig. 4. Invasibility of mutualists are represented as isoclines of probabilities of the successful invasion when parameters are asymmetric between species. Parameters are set as $r = 0.5$, $d = 0.25$, $b = 0.7$, $c = 0.03$ unless they are not changed. (a) Intrinsic reproductive rates (r_A, r_B) are changed within $(0.3, 0.3)–(0.7, 0.7)$ at 0.02 intervals. (b) Costs of mutualism (c_A, c_B) are changed within $(0, 0)–(0.1, 0.1)$ at 0.01 intervals. (c) Benefits of mutualism (b_A, b_B) are changed within $(0, 0)–(1, 1)$ by at 0.1 intervals. At each data point, the invasion probability was calculated, based on 100 trials, from which the probability isoclines were interpolated.

offspring of the former individual is likely to be helped by offspring of the latter individual. As shown in Fig. 2b, the high values of the number of pairs of mutualists during the initial phase of mutualists invasion suggests that the mechanism stated above really can operate. The high probability of mutualist pairs of different species functions as the primary role for the evolution of mutualism and the high probability of neighboring mutualist pairs of the same species is the result of the process, while the latter directly contributes to the altruism evolution in a single species.

Mutualism in our model may evolve under the same condition as in the evolution of altruism, where the ratio of cost to benefit is low. This condition would be more feasible in the evolution of mutualism because different species require different resources for reproduction and thus it is likely that a small cost for one species becomes

a large benefit for the other species (Yamamura, 1993). Therefore, values of the critical cost–benefit ratio such as 0.13 or 0.075 in Fig. 1 do not seem to be unrealistic.

Mutualism in our model may evolve more easily when intrinsic reproductive rates are small (compare Fig. 1a and b). This would be because equilibrium frequencies of wild-type non-mutualists are low under the low intrinsic reproductive rate and mutualists of different species easily make clusters together using the high frequencies of empty sites. A similar explanation was given for the evolution of altruism when the equilibrium frequency is low (Matsuda, 1987). On the other hand, in a spatial model of the evolution of altruism without empty sites, such evolution does not occur, because competition for reproductive sites cancels out any helping effect that may be conferred by neighboring altruists (Taylor, 1992; Wilson et al., 1992).

The evolution of mutualism does not hinge on the equivalent costs and benefits between interacting species because the average value of costs and that of benefits tend to determine the probability of the evolution even if the parameters are asymmetric (Fig. 3b and c). Regarding the asymmetry of intrinsic reproductive rates, the probability of the evolution is high when this parameter is low for either one of the two species (Fig. 3a). We did not examine the asymmetry of dispersal rates, with relaxing the assumption of neighborhood dispersal. However, in a special case of neighborhood dispersal for one species and random dispersal for the other species, we confirmed that mutualism could not evolve. This would be because mutualist pairs between different species are frequently lost by the random dispersal of one species.

Our study in case of limited dispersal is based on computer simulation. There are several analytical methods to investigate spatial dynamics such as pair approximation (Nakamaru et al., 1997; Le Galliard, 2003). The results that we obtained here may be reinforced by applying such analytical methods, but our computer simulation could clearly have shown the importance of spatial structure in evolution of mutualism.

Spatial effects are generally very important in dynamics and evolution of interacting species (Tilman and Kareiva, 1997; Thompson, 1999). The present study elaborates on this conclusion, and provides a robust example of the importance of spatial structure in the evolution of mutualism.

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