



Stochastic tunneling in the colonization of mutualistic organisms: Primary succession by mycorrhizal plants

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ABSTRACT

In mutualism under spatial structure, asynchrony between the dispersions of the interacting species can be a key determinant of their dynamics. We focused on the plant–mycorrhizal fungi system to theoretically analyze the colonization process by calculating the probability of colony establishment under environmental fluctuation. This can be considered a joint process of two sub-processes before and after the association between the host plant and the mycorrhizal fungi in a novel habitat. When colony growth undergoes environmental fluctuation, the dynamics of colony size can be considered a combination of the two stochastic sub-processes that mediated the association event between the plant and the fungi. Therefore, properties of whole system are influenced by five parameters, means and variances of colony growth rates of two sub-systems, and a rate of association of plant and fungi. For the successful establishment of a colony, the second sub-process must start before the first sub-process finishes (i.e., extinction), which we refer to as “stochastic tunneling.” Our analysis of the establishment probability of a plant colony based on this concept revealed that (1) the mean colony growth rates of the host alone and the symbiotic association affect establishment probability in different ways, (2) the variance of colony growth rate of the symbiotic association reduces the establishment probability, although the variance of growth rate of the host alone facilitates the establishment probability when the mean growth rate of the host alone is negative, and (3) a trade-off between the mean colony growth rates of the host alone and the symbiotic association could result in the evolution of either a symbiotic or parasitic relationship, based on a host decision. The model we present is widely applicable to the colonization processes of both positive and negative species relationships, where the interacting species disperse independently.

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1. Introduction

Mutualisms between species play a fundamental role in ecosystems (Bronstein, 1994), influencing not only population, but also community dynamics. In studies of plant community, mutualistic relationship with their pollinators was originally investigated well (Ehrlich and Raven, 1964; Feinsinger, 1978), although increasing knowledge of roles of microorganisms has also highlighted mutualism between plant and mycorrhizal fungi. Such mutualisms are considered an important factor in plant community succession processes (Janos, 1980; Allen, 1991), as fungi modify plant performance by various mechanisms (reviewed by Newsham et al., 1995; Smith and Read, 1997; Gupta and Kumar, 2000). Especially in primary succession, which is the

first step in the organization of ecological communities (Glenn-Lewin and van der Maarel, 1992; Peet, 1992), assists from mycorrhizal fungi can be essential for plant colonization. When plants colonize barren areas (e.g., volcanic deserts), their growth and reproductive performance in general are notably reduced, due to the lack of nutrients and/or water stress. When plants cannot persist alone in such unfavorable conditions, an association with mutualistic symbionts can enable the plant population to grow, thus facilitating colonization (Nara et al., 2003a, b; Nara, 2006a, b).

Despite the significance of mycorrhizal fungi, their effects may be substantially restricted by dispersal processes. Plants generally disperse into a new habitat via seeds, whereas mycorrhizal fungi disperse over long distances via spores (Smith and Read, 1997), resulting in their independent arrival in a habitat. Thus, the encounter and reassociation between plant and fungus must limit the efficiency of facilitating the colonization process. In the volcanic deserts of Mt. Fuji, Japan, the spore density of arbuscular mycorrhizal fungi in soil varies among locations (Wu et al., 2004), which implies that the encounter and association between plants

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and mycorrhizal fungi may be restricted, depending on the location. Accordingly, to understand the primary succession process, we should focus on the encounter and association events that follow the independent dispersions. The colonization process involving the reassociation of the organisms is divided into two phases: before and after reassociation. Since association can modify host performance, we must discriminate between the two phases to investigate the process of mutualistic colonization between plants and mycorrhizal fungi. A similar consideration is also important in investigating the colonization of organisms with a negative relationship, such as a host–parasite interaction.

Several theoretical studies of the population and evolutionary dynamics of species interactions have considered the independent behaviors of interacting species within a spatial structure. Yamamura et al. (2004) used a dual-lattice model to study the evolutionary aspects of mutualism in two-dimensional space. Travis et al. (2005, 2006) extended this concept by analyzing the dynamics of mutualists and non-mutualists across an environmental gradient. On the other hand, Amarasekare (2004) investigated spatial dynamics in a patchy landscape by looking at differences in dispersal processes and illustrating plant–pollinator or plant–disperser interactions. These approaches illuminated the meta-population and evolutionary dynamics of mutualism but did not examine the details of the colonization process in a novel habitat. To fully understand the dynamics of mutualistic species, we must focus on each colonization process in detail.

The colonization process of the mutualistic association consists of several steps, of which process is schematically illustrated in Fig. 1. First, one species arrives at a novel habitat and then sustains a colony for some period without a symbiont. If the growth rate is low and the environment harsh, the species may go extinct. Second, the remaining colony encounters and is able to associate with a symbiont before extinction, thus beginning to attain a higher growth rate. Third, these colonies often fail to establish because of environmental fluctuation, but some colonies finally establishes successfully via the escape from extinction.

In the process of an initial colonization into a novel habitat, colony maintenance can be influenced by stochasticity because of the small colony size. Hence, we considered stochastic effects in the colonization process. These dynamics can be formulated using diffusion approximation. As mentioned above, we considered two sub-processes of the full colonization process: before and after the association between two organisms. When the organism without mutualistic association tends to decrease its population size, extinction is a stable state in the first sub-process. On the other hand, when the association facilitates population growth, establishment of colony can be a stable state in the second sub-process.

Stochasticities in two sub-processes could result in transition between those two states, i.e., extinction and establishment. Such a shift between stable states by stochastic dynamics can be referred to as “stochastic tunneling.” The role of stochastic tunneling has been investigated in evolutionary studies. In particular, it has been recently formulated and analyzed well in the evolutionary dynamics of the canceration process (Nowak et al., 2002; Komarova et al., 2003; Iwasa et al., 2004, 2005). In these studies, mutations are considered to result in the transition of the cell state $0 \rightarrow 1 \rightarrow 2$, where cell fitness is low at state 1, but high at state 2. Researchers investigating the frequency dynamics of mutant cells have focused on demographic stochasticity in cellular reproduction. The cell cycle is possibly more sensitive to demographic stochasticity, because its internal condition is maintained by homeostasis. However, in ecological processes, individual success can be highly influenced by environmental fluctuations, resulting in environmental stochasticity in population dynamics. Accordingly, we focused on environmental stochasticity in our analysis.

In this study, we aimed to reveal general features of invasion and colonization processes of organisms with a tight interspecific relationship, by focusing on plant–mycorrhizal fungi interactions. We calculated a probability of successful colonization, introducing the “stochastic tunneling” effect into population dynamics based on the ecological context. The probability significantly depends on properties of population dynamics, i.e., means and variances of population growth rates in the absence and presence of symbiotic partner, and an association rate between plant and symbiont. In the plant–mycorrhizal fungi symbiosis, trade-offs could exist among those properties. Comparable studies among forb species showed negative correlations between survivorships with and without mycorrhizal fungi (Smith and Read, 1997, Chapter 15), which may suggest the trade-off between colony growth rate of the host alone and that with the symbiont. It is also known that plants promoted the germination of mycorrhizal spores and hyphal growth by exuding some materials (Siqueira et al., 1991; Anderson, 1992; Smith and Read, 1997; Bais et al., 2006), which suggested a cost to promote association, implying a trade-off between growth rate without symbiotic fungi and association rate. Based on our analysis, we can also discuss evolution of symbiotic relationship under those trade-offs among symbiotic properties, by considering a fitness landscape with trade-off (Levins, 1968).

In the present paper, we constructed a theoretical model of the colonization process in a symbiotic, not parasitic, relationship, although a parameter modification allows the formulation to cover various processes. Accordingly, the model provides a basic framework for understanding a colonization process by species

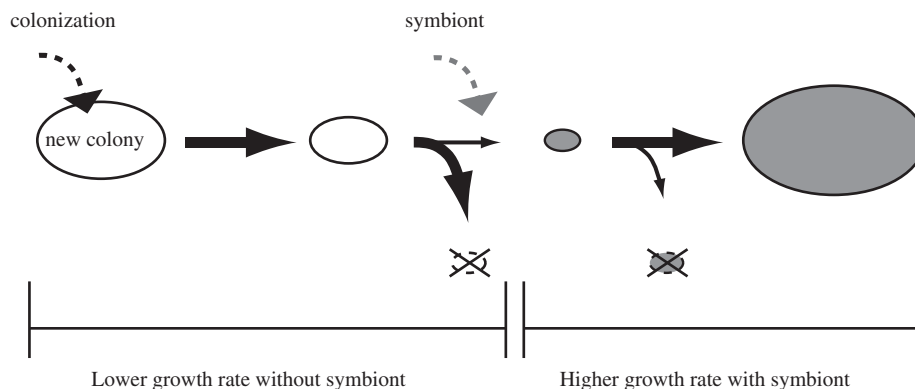


Fig. 1. A scheme of colonization dynamics of the mutualistic association. Before an encounter to mutualistic partner, the focal species tends to reduce colony size, and then often becomes extinct. After an encounter, the colony is likely to expand, suppressing extinction.

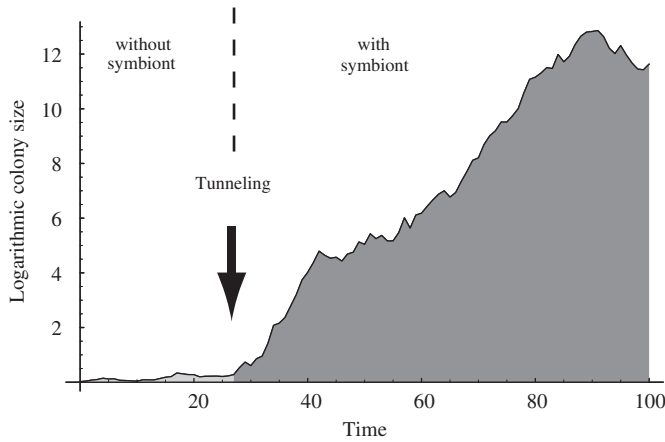


Fig. 2. Example of the colonization process. In the absence of symbionts, the mean growth rate of the host is relatively low, and the host colony tends to go extinct. However, once the host obtains a symbiont, the colony may increase because of its higher mean growth rate. The two processes are connected by the association event with the symbiont.

sharing any type of interspecific relationship without synchronous dispersal.

2. Mathematical model

A state of plant colony can be categorized into two phases; colonies with and without mycorrhizal fungi, of which growth rates are high and low, respectively. Fig. 2 illustrates an example of this colonization process into harsh habitat. For simplicity, we assumed no carrying capacity for the plant colony, thus implying negligible intraspecific competition in the initial process of colonization. As illustrated in Fig. 2, the establishment of the plant colony is represented by a combination of two stochastic sub-processes: the dynamics of the plant alone and that with a mycorrhizal association. These two processes are connected by a random event, i.e., the encounter and association between the plant and the mycorrhizal fungus.

The probability that a new plant colony ultimately and successfully establishes can be considered as

$$P = [\text{encounter rate between host and symbiont before extinction of the host}] \times [\text{probability of the association of host and symbiont escaping extinction}].$$

This process can be formulated using diffusion approximation. Below, we describe the analysis of the stochastic dynamics.

2.1. Diffusion approximation

We considered the dynamics of colony size as a stochastic process with environmental fluctuation. When the density effect is negligible, we can easily formulate and analyze such a system (Lande and Orzack, 1988; Lande, 1993). In the model, the colony size is denoted by N . We defined the extinction threshold of colony size as \hat{N} , below which the colony is assumed to be extinct. For the analysis, we considered the logarithm of relative colony size as $x = \ln(N/\hat{N})$. Thus, the colony is extinct when $x = 0$.

2.1.1. Dynamics of colony size distribution before association

We denoted the mean and variance of the colony growth rate of the host alone, with no symbiont, as r_1 and σ_1^2 , respectively. In the studies of stochastic population dynamics r_1 is known as the long-run growth rate of the population (Tuljapurkar, 1982; Lande

and Orzack, 1988; Lande, 1993). We assumed that a host colony encounters and associates with the symbiont at rate p , independently of its colony size. Denoting the initial logarithmic relative colony size as x_0 , we can formulate the dynamics of the probability distribution of colony size x without the symbiont at time t , $u(x, t)$ as

$$\frac{\partial u(x, t)}{\partial t} = \frac{\sigma_1^2}{2} \frac{\partial^2 u}{\partial x^2} - r_1 \frac{\partial u}{\partial x} - pu, \quad (1a)$$

$$u(x_0, 0) = \delta(x), \quad (1b)$$

$$u(0, t) = 0, \quad (1c)$$

by diffusion approximation. Eq. (1a) indicates that the colony size increases with growth rate r_1 , although the size distribution diffuses by the variance σ_1^2 . In addition, a colony with no symbiont transforms to one with a symbiont at rate p . Eq. (1b) represents an initial condition, where $\delta(x)$ is the delta function. Eq. (1c) is the boundary condition for extinction at $x = 0$. The total probability of the size distribution decreases with time, due to colony extinction and association with the symbiont. These equations can be solved analytically as

$$u(x, t|x_0, 0) = \frac{\exp[-pt]}{\sqrt{2\pi\sigma_1^2 t}} \left\{ \exp\left[-\frac{(x - r_1 t - x_0)^2}{2\sigma_1^2 t}\right] - \exp\left[-\frac{2r_1 x_0}{\sigma_1^2} - \frac{(x - r_1 t + x_0)^2}{2\sigma_1^2 t}\right] \right\}. \quad (2)$$

2.1.2. Dynamics of colony size distribution after association

The mean and variance of the growth of the host colony with a symbiont are defined by r_2 (long-run growth rate) and σ_2^2 , respectively. To avoid confusion, the logarithm of the relative size of a colony with the symbiont is defined by y , instead of x . Denoting the initial y value at $t = 0$ (i.e., initial time of association) by y_0 , the dynamics of the probability distribution of the host colony size y at time t , $v(y, t)$, is

$$\frac{\partial v(y, t)}{\partial t} = \frac{\sigma_2^2}{2} \frac{\partial^2 v}{\partial y^2} - r_2 \frac{\partial v}{\partial y}, \quad (3a)$$

$$v(y_0, 0) = \delta(y), \quad (3b)$$

$$v(0, t) = 0. \quad (3c)$$

Compared to Eq. (1), this dynamic does not include the association term with rate p in Eq. (3a). This dynamic can be solved as

$$v(y, t|y_0, 0) = \frac{1}{\sqrt{2\pi\sigma_2^2 t}} \left\{ \exp\left[-\frac{(y - r_2 t - y_0)^2}{2\sigma_2^2 t}\right] - \exp\left[-\frac{2r_2 y_0}{\sigma_2^2} - \frac{(y - r_2 t + y_0)^2}{2\sigma_2^2 t}\right] \right\}. \quad (4)$$

According to this equation, if the mean growth rate r_2 is positive, the colony can escape extinction with the probability

$$ES(y_0) = \lim_{t \rightarrow \infty} \int_0^{\infty} v(y, t|y_0, 0) dy = 1 - \exp\left[-\frac{2r_2 y_0}{\sigma_2^2}\right], \quad (5)$$

which can be regarded as the establishment probability of the host colony that associates with a symbiont. On the other hand, if r_2 is negative, the population ultimately becomes extinct with probability 1, i.e., $ES(y_0) = 0$.

2.1.3. Formulation of the establishment probability of a colony

Based on the above formulations, the probability that a newly colonizing colony ultimately establishes successfully is

$$P = \int_0^{\infty} \int_0^{\infty} pu(x, t | x_0, 0) ES(x) dx dt, \quad (6)$$

which can be considered as “tunneling rate” between two stable state, i.e., extinction and establishment of the colony. The integration can be solved analytically with respect to x , but not t . Hence, Eq. (6) is analyzed numerically to reveal the properties of the colonization process by the host–symbiont system.

3. Results

3.1. Establishment probability (tunneling rate)

Fig. 3 illustrates the probability that a new host plant colony ultimately establishes in the novel habitat, which is plotted against the mean growth rates of the host alone (r_1) and with a symbiotic association (r_2). If the mean growth rate of the host alone is small, the mean growth rate of symbiotic association is less effective at increasing the establishment probability. Otherwise, the mean growth rate of symbiotic association notably promotes the establishment probability, although it tends to saturate rapidly.

Fig. 4 illustrates the establishment probabilities with alternative variance of growth rates in either the host alone or in symbiotic association. Figs. 4a and c indicate the absolute establishment probabilities, whereas Figs. 4b and d show the probabilities relative to the results of Fig. 3. As seen in Figs. 4a and b, the fluctuation of the growth rate of the host alone can variously affect the establishment probability. This fluctuation is likely to decrease the establishment probability when the mean growth rate of the host alone is high (typically positive), whereas

the opposite tendency appears when the rate is low (typically negative). This is because environmental stochasticity is likely to enhance extinction when the mean growth rate is positive, but tends to suppress it when the rate is negative. On the other hand, the fluctuation of the symbiotic association growth rate tends to reduce the establishment probability generally (Figs. 4c and d). However, the reduction is relatively small when both the growth rate of the host alone and that of the symbiotic association are high.

3.2. Optimal strategy under a trade-off between two parameters

Based on these analyzes, we can consider the optimal strategy of the host species that maximizes the probability of establishment in colonizing a novel habitat under the given trade-off by considering fitness landscape (Levins, 1968). The establishment probability can be a criterion of evolution if short-living colonies with small size do not sufficiently contribute to colony reproduction in comparison to establishing colonies.

3.2.1. Trade-off between the growth rate of the plant alone (r_1) and that with the symbiont (r_2)

First, we consider a trade-off between the mean growth rate of the host alone (r_1) and that with the symbiont (r_2). Raina et al. (2000) described the three basic functional components of the mycorrhizal symbiosis as (i) fungal mycelium that explores large volumes of soil and helps to retrieve mineral nutrients, (ii) fungus–plant interface where nutrient transfer occurs, and (iii) plant tissues that produce and store carbohydrate. The special physiological mechanisms needed for (ii) and (iii) may require additional investments by the plant, especially one without mycorrhizal fungi. The mechanism of (ii) could result in plant vulnerability to parasites or pathogens when mycorrhizal fungi are absent. These factors may cause a trade-off between the mean growth rate of the host alone and that with the symbiotic association, in that the performance of the host species in association with a symbiont (higher r_2) is promoted by some physiological mechanism that reduces performance in the absence of the symbiont (lower r_1). Indeed, comparable studies among forb species indicated a negative correlations between survivorships with and without mycorrhizal fungi (Smith and Read, 1997, Chapter 15; we confirmed its statistical significance), which may suggest the trade-off between colony growth rate of the host alone and that with the symbiont. However, a clear correlation did not appear between with and without the fungi in production and survivorship \times production (Grime et al., 1987; Smith and Read, 1997, Chapter 15), which may results from a variation of basal productions among forb species.

Fig. 5a illustrates the contour plots of establishment probability in relation to the mean growth rates of the host alone (r_1) and with the symbiont (r_2). In Fig. 5b, three virtual trade-off lines are illustrated on the establishment probability contour plot, with the circle indicating the optimal set of parameters to maximize establishment probability. The shaded area in Fig. 5b represents a region where the symbiont is harmful to the host, because it induces a growth rate reduction ($r_1 > r_2$). In the r_2 – r_1 space, the contour curves of establishment probability tend to decline rapidly at very low r_2 , although the slope becomes more moderate with increasing r_2 . According to this contour curve form, the optimal set of mean growth rates (r_1 and r_2) that maximizes the establishment probability with trade-off tends to locate in the high r_1 , low r_2 region (circles on the broken and dotted lines in Fig. 5b), except when the slope of the trade-off line is less steep (circle on the dotted-dashed line in Fig. 5b). These tendencies can be applied to some degree on non-linear trade-off

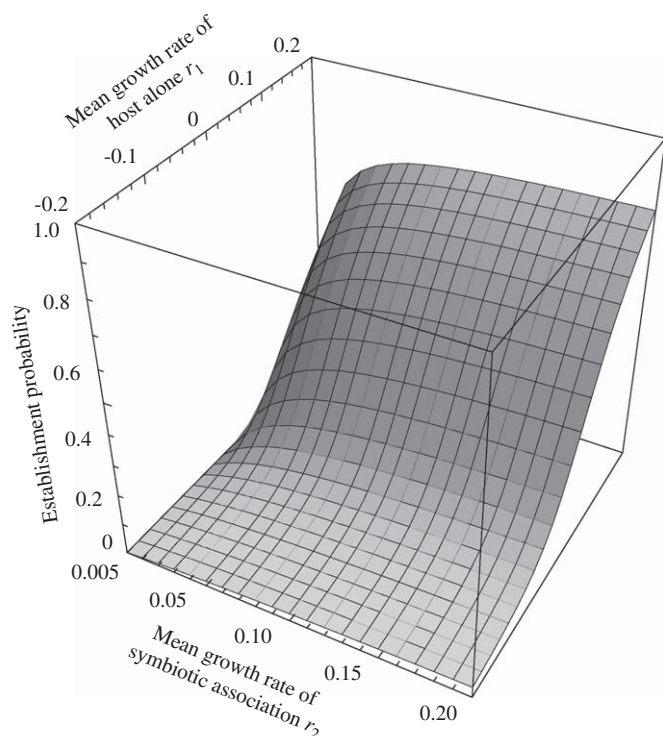


Fig. 3. Establishment probability of a colony in relation to the mean growth rate of the host alone and in a symbiotic association. The parameters are $\sigma_1^2 = \sigma_2^2 = 0.25$, $p = 0.01$ and $x_0 = 1$ ($N_0 \approx 2.718$).

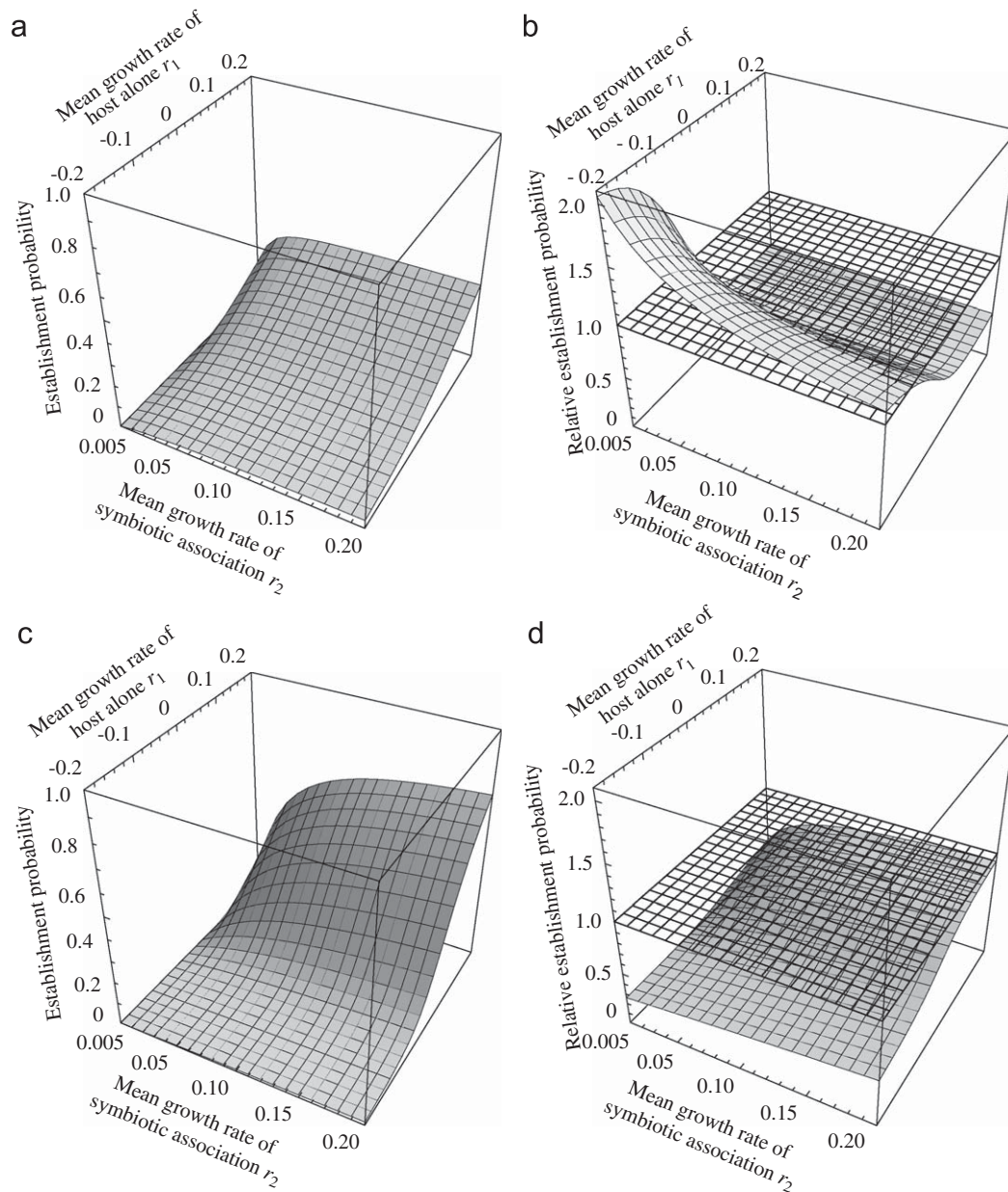


Fig. 4. Effects of the magnitude of environmental fluctuation on the establishment probability of a colony. (a) and (c) illustrate the establishment probabilities at $\sigma_1^2 = 1.0$ and $\sigma_2^2 = 1.0$, respectively, with the other parameters the same as in Fig. 3. (b) and (d) illustrate relative establishment probabilities compared to the results of Fig. 3. The frame surface indicates a relative probability of 1, where the establishment probability is the same as that in Fig. 3. Above and below the surface, the probability is greater and smaller, respectively, than the results shown in Fig. 3.

functions that are decreasing functions in the r_2 – r_1 space. Interestingly, the mean growth rate of the host alone (r_1) may be greater than that of the symbiotic association (r_2) at the optimal point (see broken and dotted lines in Fig. 5b), implying that the symbiont confers a substantial disadvantage upon the host, i.e., it is parasitic. This is because an enhanced growth rate of the host alone is effective at increasing the establishment probability of the host, even if it reduces the performance of the symbiotic association. Accordingly, the host could prefer a parasitic relationship with the symbiont and give up a mutualistic interaction.

3.2.2. Trade-off between the growth rate of the plant alone (r_1) and the association rate (p)

In Figs. 5c and d, we consider a trade-off between the mean growth rate of the host alone (r_1) and the association rate with the

symbiont (p). Since r_2 is set at 0.1 in this analysis, the relationship between the organisms is symbiotic at $r_1 < r_2 = 0.1$ and parasitic at $r_1 > r_2 = 0.1$, as represented in Fig. 5d by the white and shaded areas, respectively. In the symbiotic region ($r_1 < r_2$), the establishment probability increases with p and r_1 both increasing, whereas in the parasitic region ($r_1 > r_2$), it increases with decreasing p and increasing r_1 (see Figs. 5c and d).

In the symbiotic relationship, the host benefits by increasing encounters and the association rate (p). Indeed, plants possess physiological mechanisms that enhance associations with mycorrhizae. For example, plant root exudates include materials that promote the germination of mycorrhizal spores and hyphal growth (Siqueira et al., 1991; Anderson, 1992; Smith and Read, 1997; Bais et al., 2006). Akiyama et al. (2005) detected a chemical substance released from roots that induces hyphal branching of mycorrhizal fungi. These factors facilitate encounters and

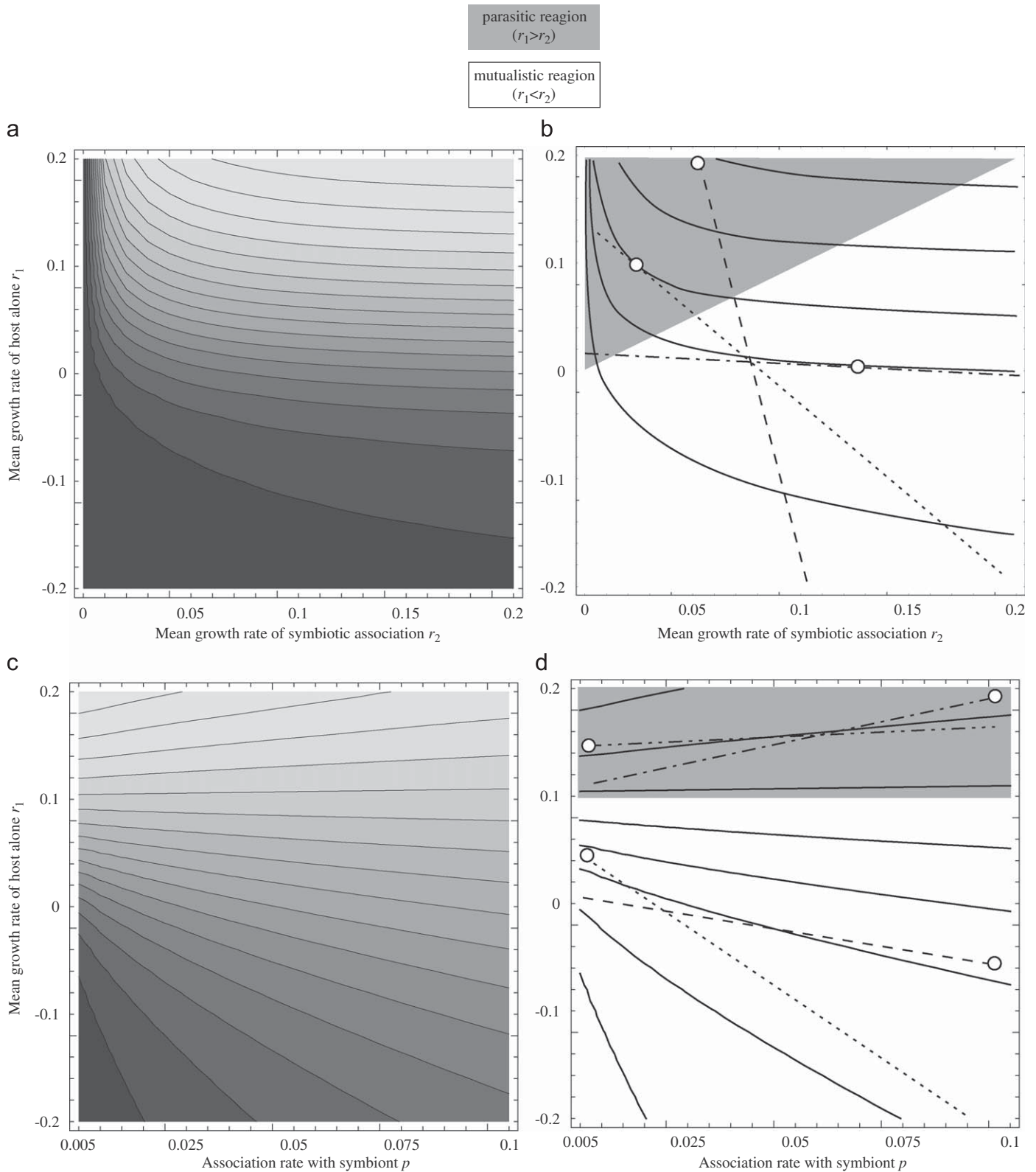


Fig. 5. Contour plots of the establishment probability of a colony. (a) Plot in the r_2 - r_1 space (same as Fig. 3); lighter colors indicate higher probability. (b) The same plot with some virtual trade-off lines; white and shaded areas represent mutualistic ($r_1 < r_2$) and parasitic ($r_1 > r_2$) regions, respectively. (c) Plot in the p - r_1 space, with $r_2 = 0.1$. (d) The same plot with some virtual trade-off lines.

associations between plants and mycorrhizae, although they probably require some investments by the plant, which may decrease the growth rate (r_1). Accordingly, the trade-off curve should have a negative slope in the p - r_1 space when $r_1 < r_2$

(broken and dotted lines in Fig. 5d). On the other hand, in a parasitic relationship, the host hopes to reduce the rate of encounter and infection (p). Organisms produce various types of anti-parasite, anti-herbivore, and anti-predator defenses. For

example, plants have defensive mechanisms against pathogens and parasites (Bais et al., 2006; Tiffin and Moeller, 2006; Pieterse and Dicke, 2007), including attacks against soil microbes (Siqueira et al., 1991). If those mechanisms that reduce the infection rate (decreasing p) require a cost for the plant, the mean growth rate (r_1) may be reduced. In this case, the trade-off curve should have a positive slope in the p – r_1 space when $r_1 > r_2$ (single dotted-dashed and double dotted-dashed curves in Fig. 5d). In either case, as shown in Fig. 5d, the slopes of the trade-off lines tend to have the same sign as that of the contour curves, and it is difficult to find general tendencies in the optimal strategy of the host. Fig. 5d plots extreme cases, in which the optimal point (circle on the trade-off line) locates at the end of the trade-off line, although the optimum is also likely to locate at an intermediate point, depending on the non-linearity of the trade-off function.

4. Discussion

4.1. Applicability of the model

Various types of symbiosis, including mutualism and parasitism, are ubiquitous in nature. However, the dispersal processes of the interacting species generally occur independently. Accordingly, to understand characteristics of symbiotic systems, it is important to consider the dynamics of the interacting species, including independent dispersal. Our analysis is an initial theoretical approach to exploring symbiotic systems in terms of stochastic processes, which are especially important in mutualistic relationships in which the association with a symbiont significantly benefits the host. Our analysis is particularly applicable to the plant–mycorrhizal fungal system, where plant performance significantly decreases without fungi (Smith and Read, 1997). However, even when host performance is relatively high in the absence of a symbiont, the symbiont can be an essential partner for the host in reducing the probability of extinction. Properties of those systems can be clarified only in terms of stochastic processes, as we do here.

If the association rate (large p) were very high, our approach might be trivial. For example, in the plant–mycorrhizal fungal system, if a plant community already exists at or near the target habitat, fungal spores may be supplied to the habitat at a high probability. In this case, a colonizing plant immediately associates with the symbiont at an extremely high rate ($p \rightarrow \infty$), rendering the first sub-process of colonization without a symbiont negligible. Thus, the establishment probability of the colony is simply $P = 1 - \exp[-2r_2x_0/\sigma_2^2]$, which is equivalent to the results of Lande and Orzack (1988) and Lande (1993).

In this study, we focused on the establishment probability of a single host colony that newly colonizes a novel habitat. Using our formulation, we can also calculate the average waiting time until the initiation of a successful colonization that ultimately achieves colony establishment. Taking q as the colonization rate at which a plant disperses into a certain habitat, $q \times P$ represents the rate of colony foundation that ultimately reaches establishment and escapes extinction. Since the inverse of the rate is the average waiting time until the event, $1/qP$ is the average waiting time until the initiation of successful colonization. Using this criterion, we can evaluate a primary succession initiation process in a barren area and also that of vegetative regeneration in the disturbed habitat.

4.2. Gradient between mutualism and parasitism

Mycorrhizal associations occupy a spectrum along the mutualism to parasitism continuum (Johnson et al., 1997). Our analysis

indicates that the evolution of these associations can be considered a strategy of the host. In our analysis, we focused on two types of host species trade-offs: one between the mean growth rate of the host alone and that with the symbiont and the other between the mean growth rate of the host alone and its association rate with symbionts. In particular, the former provides an important implication on the evolution of symbiosis: hosts may evolve various levels of symbiotic associations, depending on the functional form of trade-offs.

Our results suggest that a host decision can orient the symbiotic relationship. Mutualism and parasitism are defined by the relative difference between the performance of the host with and without a symbiotic association. If the performance of the host with a symbiotic association is higher than that without, the relationship is mutualistic; otherwise, it is parasitic. When a trade-off exists between the performance with or without a symbiotic association and when the trade-off function crosses the $r_1 = r_2$ line, the interspecific relationship can be either symbiotic or parasitic, depending on the trade-off function and performance landscape. As shown in Fig. 5b, this relationship can emerge from the host strategy, rather than the symbiont strategy, which may drive the evolution of symbiosis from parasitism to mutualism. Theoretical studies of the evolution from parasitism to mutualism have tended to suggest that the symbiotic relationship is determined by the symbiont alone (e.g., Yamamura, 1993, 1996; Neuhauser and Fargione, 2004) or by a conflict between the host and symbiont (Johnstone and Bshary, 2002). In either case, the host has resisted the parasitic relationship. Contrary to those studies, we have demonstrated the possibility that the host alone makes the evolutionary choice of a parasitic relationship with the symbiont. This may explain the variation in mycorrhizal associations from facultative to obligate symbiosis (Janos, 1980).

4.3. Implication to previous studies of interspecific mutualism

Evolution of interspecific mutualism has been studied previously on spatial structure (Yamamura et al., 2004; Travis et al., 2005, 2006), in which mutualism between two interacting species was analyzed by using dual-lattice model. In their simulations, non-mutualist forms of two species originally attained a basal growth rate r , whereas mutualism modifies the rate. The mutualist is assumed to spend a cost c for altruism (the total growth rate is $r-c$), but can obtain benefit b only when it can associate with partner species (the total growth rate becomes $r-c+b$). According to simulations, they indicated that evolution of mutualism tends to be suppressed by an increment of basal population growth rate (r).

The approach of the present analysis was significantly different from that of the previous studies because we did not involve dynamics of symbiont explicitly. Despite of such a difference, our model provided a result that corresponds with the finding of previous studies. Fig. 6 illustrates a contour plot of establishment probability that is identical with Fig. 5b with a different range of r_1 in the vertical axis. The broken line indicates $r_1 = r_2$ that represents a non-mutualist in simulations of the previous studies, of which growth rate does not vary anytime, i.e., $r_1 = r_2 = r$. On the other hand, performance of mutualist depends on an existence of partner species, which is $r-c$ and $r-c+b$ without and with the partner, respectively. In Fig. 6, those two strategies are connected by solid line for various r values. The approach of previous studies can be interpreted as a comparison of performance between two ends of each solid line, at which strategy sets are $(r_1, r_2) = (r, r)$ and $(r-c, r-c+b)$.

According to the Fig. 6, non-mutualist with (r, r) is more advantageous for large r , while mutualist with $(r-c, r-c+b)$

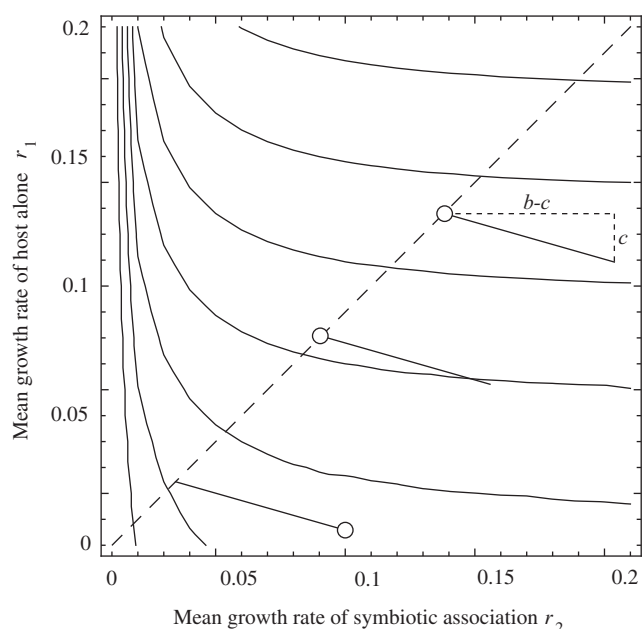


Fig. 6. Contour plots of the establishment probability of a colony, which is same as Fig. 5b with different r_1 range. A broken line represents $r_1 = r_2$, whereas solid lines connect strategy sets that correspond with of non-mutualist and mutualist in Yamamura et al. (2004) and Travis et al. (2005, 2006). Circles on the solid lines indicate the better strategy between the given set of non-mutualist and mutualist strategies, which results in higher establishment probability.

becomes more beneficial for smaller r . This result can be considered to correspond with previous consequences of dual-lattice simulations. From Fig. 6, it is expected that if slopes of contour curves on $r_1 = r_2 = r$ line are constant independently of r value, the advantageous type is not altered by varying r . Our analysis indicates that asymmetric effects of two growth rates (with and without mutualistic partner) on the total performance is essential for the correlation between lower basal growth rate and mutualism.

4.4. Some restrictions on the present model

In our model, we assumed that once the symbiont reaches a host colony, all members of the colony immediately associate with the symbiont. However, this assumption may not apply to situations in which the host colony has grown sufficiently large before the symbiont arrives. In such a case, the host colony comprises individuals simultaneously with and without symbionts, resulting in a heterogeneous host–symbiont association in the colony. Moreover, in terms of evolution, we assume that the establishment probability is maximized for a host colony that invades a novel habitat, with no density dependence considered. However, when the colony size can become relatively large, the density dependence may not be negligible. If the carrying capacity is effective in the dynamics, any populations may ultimately become extinct under fluctuating environment (Lande, 1993), by which the establishment probability is no longer a valid criterion for successful colonization. Despite this restriction, our model may be applicable to pioneer species that are adapted to the invasion of new habitats and tend to be selected at relatively low density, at which influence of carrying capacity is relatively low.

This paper is the first study that focuses on colony establishment probability in the invasion processes of organisms with a tight interspecific relationship. It clearly indicates the important role of stochasticity on the initial processes of colonization and community establishment in novel habitats.

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