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REVIEW ARTICLE

Mathematical model of colonization process of mycorrhizal plants: effect of interaction between plants with fungi

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In interspecific mutualisms, the interacting species generally disperse independently, by which the colonization must be restricted by the reassociation between them. We theoretically analyzed colonization process of mycorrhizal plant in a novel habitat, focusing on the probability of colony establishment under environmental fluctuation. The process is a joint process of two sub-processes before and after the association between the plant and the mycorrhizal fungi. Properties of whole system are influenced by five parameters, means and variances of colony growth rates of two sub-systems, and a reassociation rate. Our analysis revealed that (1) the mean colony growth rates of the host alone and the symbiotic association affect establishment probability in different ways, and (2) 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.

Keywords: symbiosis; theory; population dynamics; evolution

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, 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, 2003b; Nara 2006a, 2006b).

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.

Accordingly, the colonization process of the mutualistic association consists of several steps. 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 is 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. These processes involving the reassociation of the organisms can be divided into two phases: before and after reassociation. The association can modify host performance, therefore, we must discriminate between these two phases to investigate the process of mutualistic colonization. A similar consideration is also important in investigating the colonization of organisms with a negative relationship, such as a host-parasite interaction.

Yamauchi et al. (2009) theoretically analyzed the colonization process of mycorrhizal plants, considering the reassociation process between organisms. In the analysis, the process was formulated by using diffusion approximation, taking into account the effect of environmental stochasticity. In this paper, we shortly review the approach of Yamauchi et al. (2009). The theoretical model was constructed to study 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 sharing any type of interspecific relationship without synchronous dispersal.

Model and results

In Yamauchi et al. (2009), we considered the dynamics of colony size as a stochastic process with environmental fluctuation. For simplicity, we assumed no carrying capacity for the plant colony, thus implying negligible intraspecific competition in the initial process of colonization. Under this assumption, we can easily formulate and analyze such a system by using diffusion approximation (Lande and Orzack 1988; Lande 1993). In the mathematical model, the colony size is denoted by N. We defined the extinction threshold of colony size as $\tilde{N}$, below which the colony is assumed to be extinct. For the analysis, we considered the logarithm of relative colony size as $x = \ln(N/\tilde{N})$, indicating that the extinction threshold becomes $x = 0$ in the logarithmic scale. We also denoted the initial logarithmic relative colony size as x_0,

The mean and variance of the colony growth rate of the host alone, with no symbiont, are denoted as r_1 and σ_1^2, whereas those of the host colony with symbiont are represented by r_2 and σ_2^2, respectively. The growth rates (r_1 and r_2) correspond with 'long-run growth rate of the population' that is considered in the studies of stochastic population dynamics (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. The probability that a new plant colony ultimately and successfully establishes can be formulated as

$$P = \int_0^\infty \int_0^\infty p u(x, t \,|\, x_0, 0)$$
$$\times \left(1 - \exp\left[-\frac{2r_2 x}{\sigma_2^2}\right]\right) dx\, dt, \qquad (1a)$$

where

$$u(x, t \,|\, x_0, 0) = \frac{\exp[-pt]}{\sqrt{2\pi \sigma_1^2 t}}$$
$$\times \left\{ \exp\left[-\frac{(x - r_1 t - x_0)^2}{2\sigma_1^2 t}\right] \right.$$
$$\left. - \exp\left[-\frac{2r_1 x_0}{\sigma_1^2} - \frac{(x - r_1 t + x_0)^2}{2\sigma_1^2 t}\right] \right\} \qquad (1b)$$

(For the details of calculation, see Yamauchi et al. 2009).

Figure 1 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). The figure indicates that if the mean growth rate of the host alone is small, the mean
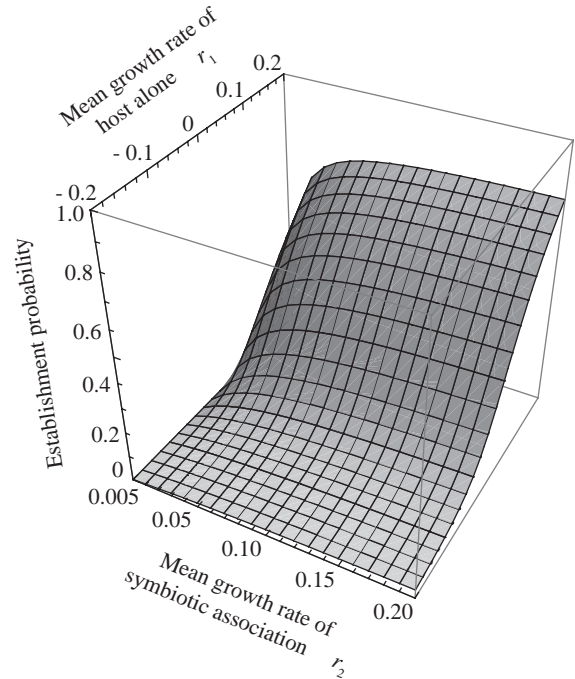

Figure 1. Establishment probability of a colony in relation to the mean growth rate of the host alone and in a symbiotic association. The parameters are $\sigma_1^2 = \sigma_2^2 = 0.25$, $p = 0.01$ and $x_0 = 1$. Reprinted from Journal of Theoretical Biology, 261(1). A. Yamauchi et al., pp. 74–82, Copyright © (2009) with permission from Elsevier.

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.

Based on this result, 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 consulting 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. We considered 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 is promoted (higher r_2) by some physiological mechanism that reduces performance in the absence of the symbiont (lower r_1). This may be possible if the special physiological mechanisms needed for mutualistic symbiosis may require additional investments by the plant, especially one without mycorrhizal fungi. Indeed, comparable studies among forb species indicated a 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. However, a clear correlation did not appear between with and without the fungi in

production and survivorship×production (Grime et al. 1987; Smith and Read 1997, Chapter 15), which may results from a variation of basal productions among forb species. Thus, we discussed evolution of symbiotic relationship under the trade-off between colony growth rates, by considering a fitness landscape (Levins 1968).

Figure 2a 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 Figure 2b, three virtual trade-off lines are illustrated on the establishment probability contour plot, with the circle indicating the optimal set of strategies (i.e. r_1 and r_2) to maximize establishment probability within the given range of strategies. The shaded area in Figure 2b 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 Figure 2b), except when the slope of the trade-off line is less steep (circle on the dotted-dashed line in Figure 2b). These tendencies can be applied to some degree on non-linear trade-off 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 Figure 2b), 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 rela-

tionship with the symbiont and give up a mutualistic interaction.

Discussion

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 in 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 consisting of two phases, as we do here.

Mycorrhizal associations occupy a spectrum along the mutualism to parasitism continuum (Johnson et al. 1997). Mutualism and parasitism are defined by the relative difference between the performances 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. Our results suggest that a
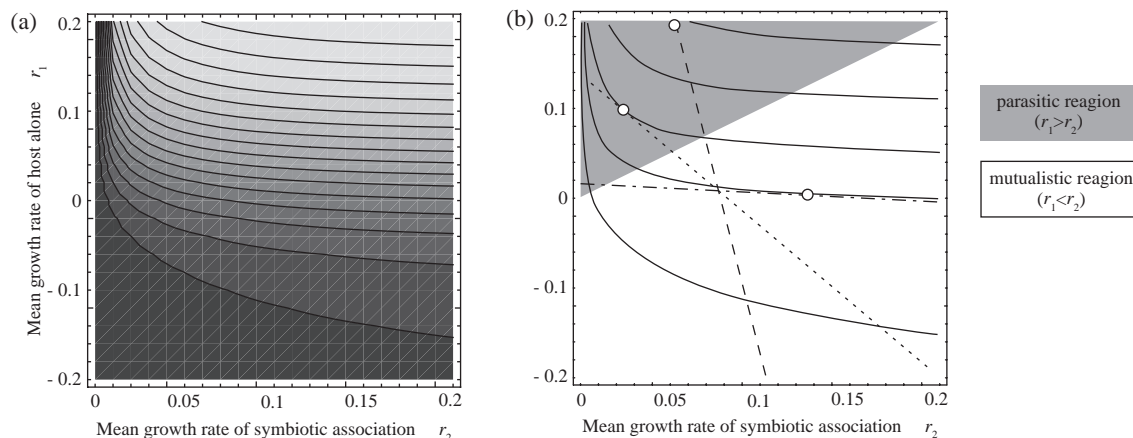

Figure 2. Contour plots of the establishment probability of a colony. (a) Plot in the r_2–r_1 space (same as Figure 1); lighter colors indicate higher probability. (b) The same plot with some virtual trade-off lines; white and shaded areas represent mutualistic ($r_1 < r_2$) and parasitic ($r_1 > r_2$) regions, respectively. Reprinted from Journal of Theoretical Biology, 261(1), A. Yamauchi *et al.*, pp. 74–82, Copyright © (2009) with permission from Elsevier.

host decision can orient the symbiotic relationship. As shown in Figure 2b, this relationship can emerge from the host strategy, rather than the symbiont strategy, which may conditionally 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 contribute to understand the variation in mycorrhizal associations from facultative to obligate symbiosis (Janos 1980).

In our analysis, we simplified some conditions of mycorrhizal associations for simplicity of analysis. It is assumed that once the symbiont reaches a host colony, all members of the colony immediately associate with the symbiont. We also ignored density dependence in the calculation of establishment probability. These restrictions should be relaxed in the future analysis.

Acknowledgements

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