



# The evolutionary game of interspecific mutualism in the multi-species model

Shota Shibasaki<sup>a,b,\*</sup>

<sup>a</sup> Department of General Systems Studies, Graduate School of Arts and Sciences, The University of Tokyo, Tokyo, 1538902, Japan

<sup>b</sup> Department of Fundamental Microbiology, University of Lausanne, Quartier UNIL-Sorge, CH-1015 Lausanne, Switzerland



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## ABSTRACT

Mutualistic interspecific interactions, including Müllerian mimicry and division of labor, are common in nature. In contrast to antagonistic interactions, where faster evolution is favored, mutualism can favor slower evolution under certain conditions. This is called the Red King effect. Since Bergstrom and Lachmann (2003) proposed the Red King effect, it has been investigated only in two-species models. However, biological examples suggest that mutualism can include three or more species. Here, I modeled the evolutionary dynamics of mutualism in communities where involving two or more species, and in which all species mutually interact. Regardless of the number of species in the community, it is possible to derive conditions for stable equilibria. Although nonlinear relationships exist between the evolutionary rates and the evolutionary fate of each species in the multi-species communities, the model suggests that it is possible to predict whether faster evolution is favored or disfavored for the relatively rapidly evolving species; however, it is difficult to predict the evolutionary fate of species that evolve relatively slowly because their evolutionary dynamics are affected by the evolutionary fate of species evolving rapidly.

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## 1. Introduction

Mutualism, or cooperation between and among species, is widespread in ecosystems. Two well-known examples of mutualism are Müllerian mimicry and division of labor. In Müllerian mimicry, species unpalatable to a common predator have evolved similar appearances, and, as a consequence, they are each less likely to be predated upon because the predator learns rapidly that these species are noxious (Müller, 1879). Although many empirical studies have dealt with Müllerian mimicry in butterflies (Sherratt, 2008), other examples include moths (Sbordoni et al., 1979; Niehuis et al., 2007), poison frogs (Chiari et al., 2004), vipers (Sanders et al., 2006), and fish (Springer and Smith-Vaniz, 1972). In division of labor, on the other hand, each species specializes certain tasks and exchanges different goods or services (Leigh, 2010). Examples of division of labor are found in the relationships within the gut microbiota (Rakoff-Nahoum et al., 2016), between plants and mycorrhizae (Remy et al., 1994), and between ants and aphids (Way, 1963).

Conflict can arise in mutualism regarding the role of each species. In Müllerian mimicry, it could be more advantageous to

be a model species than a mimic while the life cycles, habitats, and body plans of model species are innate, mimic species should change these aspects (Veller et al., 2017), which would not directly have positive effects on the reproductive cycle of the mimic species. In division of labor, conflict can arise regarding species tasks (Wahl, 2002); when providing nutrients, one type of nutrient might have a greater cost for the provider than another type of nutrient. Such mutualistic symbioses with varying degrees of conflict have been conceptualized by the snowdrift game whose payoff matrix is given by Table 1, where  $0 \leq k < 2$ . This constraint in  $k$  implies a snowdrift game where one species does not have an advantage by changing the body plans or other phenotypes when the other species mimics the focal species; in the cases of division of labour, on the other hand, the snowdrift game is valid when both species do not have to do the same task that causes a larger cost than the other task. In this game, each species adopts either a generous strategy or a selfish strategy;  $(a, b)$  element represents the benefit of species  $i$  with strategy  $a$  when interacting species  $j$  with strategy  $b$ . Nash equilibria are reached, therefore, where one species plays the generous strategy and the other species plays the selfish strategy.

Bergstrom and Lachmann (2003) modeled the evolutionary dynamics of two-species mutualism with a degree of conflict and they found that the slower evolving species is more likely to reach a favorable equilibrium than the faster evolving species under

\* Corresponding author at: Department of Fundamental Microbiology, University of Lausanne, Quartier UNIL-Sorge, CH-1015 Lausanne, Switzerland.

E-mail address: [shibasaki.sh@gmail.com](mailto:shibasaki.sh@gmail.com)

**Table 1**  
Payoff matrix of the snowdrift game.

		species $j$	
		Generous	Selfish
species $i$	Generous	$k$	1
	Selfish	2	0

**Table 2**  
The parameters and variables in the model.

Notation	Interval	Description
$x_i$	$\in [0, 1]$	Fraction of generous individuals in species $i$
$r_i$	$> 0$	Evolutionary rate of species $i$
$N_i$	$> 0$	Relative population size of species $i$
$M$	$\geq 2$ (integer)	Number of species in the community

certain conditions. A slower evolutionary rate is caused, for example, by a longer generation time or a smaller mutation rate. The authors called this effect the Red King (RK) effect; this is the converse to the Red Queen (RQ) effect (Van Valen, 1973), where faster evolution is favored in antagonistic symbioses, and sometimes mutualistic symbioses as noted by Herre et al. (1999). Although the model developed by Bergstrom and Lachmann was very simple (i.e., assuming a two-player game and infinite population sizes for both species), other researchers have relaxed these assumptions and investigated the RK and/or RQ effects in mutualism that involves a degree of conflict. Gokhale and Traulsen (2012) found that in the multi-player snowdrift game in a two-species model, the RK effect can change to the RQ effect. Gao et al. (2015) revealed that a reward mechanism in the multi-payer snowdrift game causes the shift between the RK and RQ effects. Veller et al. (2017) investigated factors which change the evolutionary rate of each species (generation time, mutation rates, selection strength, and population sizes) in a finite population, and they found that the RK effect shifted to the RQ effect and vice versa from a short time scale to a long time scale due to stochasticity.

Although these previous studies on the RK effect assume two-species communities, mutualisms can include more than two species. In the context of Müllerian mimicry, such a phenomenon is called a (Müllerian) mimicry ring, where three or more unpalatable species show similar appearances to avoid predation (Sherratt, 2008). Examples of Müllerian mimicry rings include Appalachian millipedes (Marek and Bond, 2009), bumble bees (Plowright and Owen, 1980), cotton-stainer bugs (Zrzavý and Nedvěd, 1999), and *Heliconius* butterflies (Mallet and Gilbert, 1995). In the context of division of labor, as well, mutualistic symbioses are not limited to one-to-one relationships. For example, green algae can display mutualism with several phylogenetically broad fungal species (Hom and Murray, 2014).

Inspired by these biological examples, I investigated whether it is possible to predict whether faster evolution or slower evolution is favored in communities that include more than two species. Although nonlinearity arises in multi-species communities and it is therefore difficult to say whether faster evolution or slower evolution is favored in the entire community, the model suggests that it is possible to predict whether faster or slower evolution is favored for only the species evolving relatively faster, especially if many species coexist in the community and their differences in the evolutionary rates are large.

## 2. Models

In this paper, I extend the original model of the Red King effect (Bergstrom and Lachmann, 2003) by generalizing the number of species in a community. Mutualistic symbioses with a degree of conflict are conceptualized by the bi-matrix snowdrift game, whose payoff matrix is given by Table 1.

In this model, the fitness of each species is determined only by interspecific interactions (i.e., intraspecific interactions are ignored). Given the number of species in the community  $M$ , the evolutionary dynamics of the fraction of generous individuals in species  $i$  is given by the replicator dynamics as below:

$$\dot{x}_i = r_i x_i (f_i^g - \bar{f}_i) \quad (1)$$

$$\begin{aligned} &= r_i x_i \frac{1}{\sum_{j \neq i} N_j} \sum_{l \neq i} N_l \{x_l k + (1 - x_l)\} \\ &\quad - \{x_l k + (1 - x_l)\} x_l - 2x_l (1 - x_l) \\ &= r_i x_i (1 - x_i) \frac{1}{\sum_{j \neq i} N_j} \sum_{l \neq i} N_l \{(k - 3)x_l + 1\}, \end{aligned} \quad (2)$$

where  $r_i$  is the evolutionary rate of species  $i$ ,  $f_i^g$  is the mean fitness of the generous individuals in species  $i$ ,  $\bar{f}_i$  is the mean fitness of species  $i$ , and  $N_i$  is the relative population size of species  $i$ . The parameters in this model are summarized in Table 2. It should be noted that the evolutionary rate  $r_i$  is determined by species  $i$ 's generation time, mutation rate and selection strength and this parameter represents the relative pace of adaptation. In this model, the intraspecific interaction is ignored and the interspecific interactions are weighted by the population sizes. Notice that assumptions on the initial conditions, or the initial fractions of generous individuals in each species are important because the evolutionary dynamics is affected by the initial conditions.

For clarity, I explicitly define Red King and Red Queen effects here. For convenience, let us call species  $i$  generous (selfish) when all individuals of species  $i$  become generous (selfish) at equilibrium states (i.e., the probabilities of  $x_i^* = 0$ , and  $x_i^* = 1$ , respectively).

**Definitions of Red King and Red Queen effects.** Given that the initial fractions of the generous individuals in each species  $x_i(0)$  are uniformly independent and identically distributed (i.i.d.), one can say the Red King (Red Queen) effect is operating when the slower (the faster) the species evolves, the more likely it is to become a selfish species. In other words, if the RK or RQ effect operates, there should be a monotonically negative or positive relationship between the order of the evolutionary rates and the probability that each species become selfish, respectively.

Although previous studies on the RK effect (Bergstrom and Lachmann, 2003; Gokhale and Traulsen, 2012) measured the sizes of the basins of attraction wherein either of the two species becomes selfish, it is difficult to analytically calculate the basins of attraction in the same way in  $M$ -species communities due to the high dimensionality of the model and the existence of multiple stable equilibria. One way to solve this problem is using a Monte Carlo method; i.e., calculating Eq. (2) with multiple initial conditions ( $x_1(0), \dots, x_M(0)$ ) randomly generated from a uniformly identical and independent distribution, and estimating the probability that focal species evolved selfishly. In this paper, I refer such probabilities to the *favorabilities*. In two-species communities, this measurement is approximately proportional to the sizes of basins of attraction, because there exist only two stable equilibria wherein either of species evolves selfishly and the other species becomes generous. In three- or more-species communities, on the other hand, the favorability of species  $i$  represents the sum of the basins of attraction where species  $i$  becomes selfish, as there exist more than two stable equilibria. In this study, 1,000 samples of initial conditions were generated in each Monte Carlo simulation to estimate the favorability of each species in three- and four-species communities. The Monte Carlo simulations were repeated in ten times in each conditions.

### 3. Results

In this section, I shall show the conditions for linear stable equilibria and analyze the effect of evolutionary rates on the evolutionary fate of each species. First, the conditions for the stable equilibrium state are derived, and then, the relationship between evolutionary rates and favorabilities is analyzed using the computer simulations. In the communities with a large value of  $M$ , however, the computational cost of the simulation is large. To avoid this problem, the analytic results are shown under conditions where the differences of the evolutionary rates are extremely large.

#### 3.1. Stable equilibria

Assuming that each species has the same population size and that the population sizes are infinitely large ( $N_i = N \rightarrow \infty$  for  $i = 1, \dots, M$ ), the evolutionary dynamics are represented as

$$\dot{x}_i = r_i x_i (1 - x_i) \{1 + (k - 3) \bar{x}_{j \neq i}\}, \quad (3)$$

where  $\bar{x}_{j \neq i}$  is the average fraction of generous individuals other than species  $i$ :

$$\bar{x}_{j \neq i} = \frac{1}{M-1} \sum_{j \neq i} x_j. \quad (4)$$

Notice that Eq. (3) is the same as that for the evolutionary dynamics proposed by Bergstrom and Lachmann (2003) when  $M = 2$ . The situation where each species has relatively different but infinitely large population size is analyzed in Appendix B.

In the stable equilibria arising from Eq. (3), there exist  $m$  generous species and  $M - m$  selfish species. The number of generous species  $m$  should satisfy the inequality below:

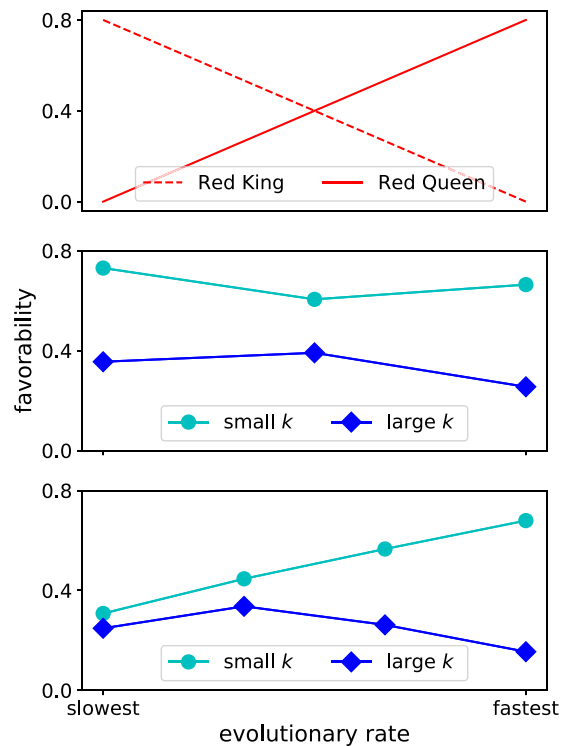
$$\frac{M-1}{3-k} < m < \frac{M-1}{3-k} + 1 \quad (5)$$

The derivation is shown in Appendix A. It should be noted that there exists at most one integer  $m$  that satisfies inequality (5) given the values of  $k$  and  $M$ . In a community with three species ( $M = 3$ ), for example, one species becomes generous ( $m = 1$ ) and other two species are selfish at stable equilibria if  $k$  is small ( $0 \leq k < 1$ ); on the other hand, there exist two generous species ( $m = 2$ ) and one selfish species at a stable equilibrium if  $k$  is large ( $1 < k < 2$ ).

Note that, however, there exists no integer  $m$  with a particular value of  $k$  given a value of  $M$  (e.g.,  $(k, M) = (1, 3), (1.5, 4)$ ). In such cases, at least one species has both generous and selfish individuals at an equilibrium state. Appendix A.2 shows that an equilibrium where at least one species includes both generous and selfish individuals cannot be linearly stable. Therefore, there is no linearly stable equilibria in that case; however, the maximum value of the real part of the eigenvalues of the Jacobian matrix at an equilibrium where both generous and selfish individuals coexist at least in one species population can be zero. In other words, this equilibrium may be stable at a higher order than the linear term. As it is difficult to analyze the higher order stability with an arbitrary value of  $M$ , I ignored such special cases following analysis.

#### 3.2. Computer simulation

Although inequality (5) indicates that there exist  $\binom{M}{m}$  stable equilibria in the dynamics defined by Eq. (3), it is unclear whether species  $i$  is more likely to evolve generously or selfishly because the initial conditions determine which stable equilibria the dynamics converge to (see Fig. C.1 for three-species communities). To clarify this point, the evolutionary dynamics in three- and four-species communities were simulated using the Monte Carlo simulations. The evolutionary rate of each species is given by  $\mathbf{r} = (1/8, 1, 8)$  in

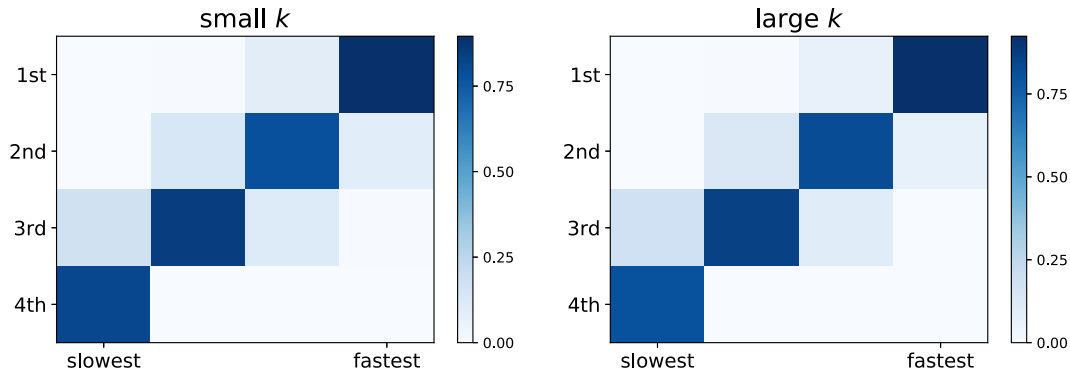


**Fig. 1.** The evolutionary rates and the probability of becoming selfish species. The relationship between the evolutionary rates and the mean probability that each species becomes selfish at stable equilibria (i.e., favorability) in the 10 replicates of the Monte Carlo simulations are shown. Note that the error bars (standard errors) are too small to see in point. Top: the hypothetical results if the RK effect or the RQ effect operates; there should be a negative (positive) relationship between the order of the evolutionary rate and the favorability. However, the results of computer simulations (Middle: three species, and Bottom: four species) did not show such relationships except for the case of small  $k$  in the four species community. The parameters are:  $\mathbf{r} = (1/8, 1, 8)$ , and  $k = 0.5$  (small) or  $k = 1.5$  (large) in the three-species model, and  $\mathbf{r} = (1/8, 1/2, 2, 8)$  and  $k = 0.5$  (small) or  $k = 1.6$  (large) in the four-species model. Note that if  $k = 1.5$  in the four-species model, inequality (5) does not represent the integer  $m: 2 < m < 3$ .

the three-species model, and  $\mathbf{r} = (1/8, 1/2, 2, 8)$  in the four-species model. The means of favorabilities, or the probabilities that each species evolves selfishly at the stable equilibrium in the ten replicates are shown in Fig. 1.

Except for the case of the four-species model with small  $k$ , there are no clear the RQ or RK effects (Fig. 1); the relationships between evolutionary rate and probability that each species becomes selfish (favorability) are not monotonic. In the three-species community when  $k$  is small, the slowest and the fastest evolving species show higher favorabilities than species evolving at an intermediate rate. When  $k$  is large in the three-species model, there are still no clear RQ or RK effects, although the difference in probability of being selfish between the slowly evolving species and the intermediate one is small. In the four-species model, there is a convex relationship between the order of the evolutionary rate and the favorability when  $k$  is large; on the other hand, there exists a positive relationship (the RQ effect) if  $k$  is small. These results suggest there can be a mixture of the RQ and RK effects in multi-species communities.

When the number of species in the community  $M$  is large, the analysis with the computer simulation is ineffective; although the numerical integration of the evolutionary dynamics given by Eq. (3) does not take a long time, the space of the initial conditions enlarges as  $M$  increases. In other words, the total computational cost for accurate Monte Carlo simulations increases as  $M$  increases. One way to avoid this problem is to assume the conditions where the fraction of generous individuals in only one species changes



**Fig. 2.** Order of the evolutionary rate and order of strategy fixation.

The relationship between the evolutionary rate (horizontal axis) of each species and the order of strategy fixation (vertical axis) in the four species model with small  $k$  ( $k = 0.5$ , left) and large ( $k = 1.6$ , right). The color of each cell represents the probability that focal species fixes its strategy at the given order. This figure used the all samples of the Monte Carlo simulations ( $10 \times 1,000 = 10,000$  samples in each case). Regardless of the value of  $k$ , there exist consistency between the order of the evolutionary rate and the order of strategy fixation; the species that is the most likely to fix its strategy first is the species evolving fastest, and the species that fixes its strategy last is the species with the slowest evolutionary rate. The evolutionary rates of species are the same as Fig. 1.

until this species fixes its strategy, while the other species do not evolve. Under these conditions, the value of  $\bar{x}_{j \neq i}$  does not change until species  $i$  fixes its strategy, and therefore, the evolutionary fate of species  $i$  is determined by the sign of  $1 + (k - 3)\bar{x}_{j \neq i}$  (positive: generous, and negative: selfish).

The computer simulations suggested that the order of fixation is consistent with the order of the evolutionary rate (Fig. 2); for example, the species evolving fastest is the species most likely to fix its strategy first. In other words, the effect of the initial conditions on the order of fixation is negligibly small, and the order of fixation is predictable from the order of the evolutionary rates.

### 3.3. Analysis with the large differences in the evolutionary rates

As the order of fixation can be estimated by the order of the evolutionary rate, let us assume a special conditions in which the differences in evolutionary rate between each species are quite large. Under these conditions, only the species evolving fastest and which has never fixed its strategy can evolve toward generosity or selfishness, while the fractions of generous individuals in remaining species do not change. In other words, each species fixes its strategy according to the order of the evolutionary rate, and the evolutionary direction of each species is determined by the initial conditions and the evolutionary fate of the species which have already fixed their strategies because the sign of  $1 + (k - 3)\bar{x}_{j \neq i}$  determines the evolutionary direction. Notice that it is necessary to calculate the probability distribution of the initial conditions because the evolutionary dynamics are affected by the initial conditions, although the dynamics are deterministic.

When species  $i$  is the  $i$ th fastest species in the  $M$  species community ( $i = 1, \dots, M - 1$ ), the focal species  $i$  is more likely to evolve generously or selfishly if and only if

$$1 + (k - 3)\bar{x}_{j \neq i} = 1 + \frac{k - 3}{M - 1} \sum_{j \neq i} x_j \geq 0$$

$$\Leftrightarrow 1 + \frac{k - 3}{M - 1} \left( f_1 + \sum_{j > i} x_j(0) \right) \geq 0$$

$$\Leftrightarrow \frac{1}{M - i} \sum_{j > i} x_j(0) \leq \frac{1}{M - i} \left( \frac{M - 1}{3 - k} - f_1 \right), \quad (6)$$

where  $f_1$  is the number of species which have already been fixed as generous species ( $f_1 = 0, 1, \dots, i - 1$ ). Notice that it is not necessary to consider the slowest species  $i = M$  because the evolutionary

fate of the slowest species is determined only by the evolutionary fate of the other species (if there already exist  $m$  generous species, the slowest species becomes selfish; otherwise, it becomes generous). The upper (lower) sign of Eq. (6) is the case when species  $i$  is more likely to be a generous (selfish) species. As the initial fraction of generous individuals in each species is uniformly i.i.d., the left-hand side of Eq. (6) represents the mean of  $M - i$  independent samples from the uniform distribution. Using the central limit theorem (CLT), the left-hand side of Eq. (6) approximately follows the normal distribution  $\mathcal{N}(\mu, \sigma_i^2)$  whose mean is  $\mu = 0.5$  and the inverse of the variance is  $1/\sigma_i^2 = 12(M - i)$ . CLT offers a good approximation even when  $M - i$  is small (Fig. C.2).

The right-hand side of Eq. (6), on the other hand, can be regarded as the threshold  $T_i$  for species  $i$ ; if the left-hand side of Eq. (6) is smaller (larger) than  $T_i$ , species  $i$  evolves as generous (selfish). This threshold is, however, affected by the evolutionary fates of the faster evolving species, which have already fixed their strategies:

$$T_i(f_1) \equiv \frac{1}{M - i} \left( \frac{M - 1}{3 - k} - f_1 \right). \quad (7)$$

From Eqs. (6) and (7), the favorability of species  $i$  is computable with arbitrary values of  $k$  and  $M$  (Fig. 3). Given a value for  $f_1$ , let us denote the conditional probability that species  $i$  becomes selfish as  $q_i(x_i^* = 0 | f_1)$ . Then, the favorability, or the unconditional probability that species  $i$  evolves selfishly ( $q_i(x_i^* = 0)$ ) is written as

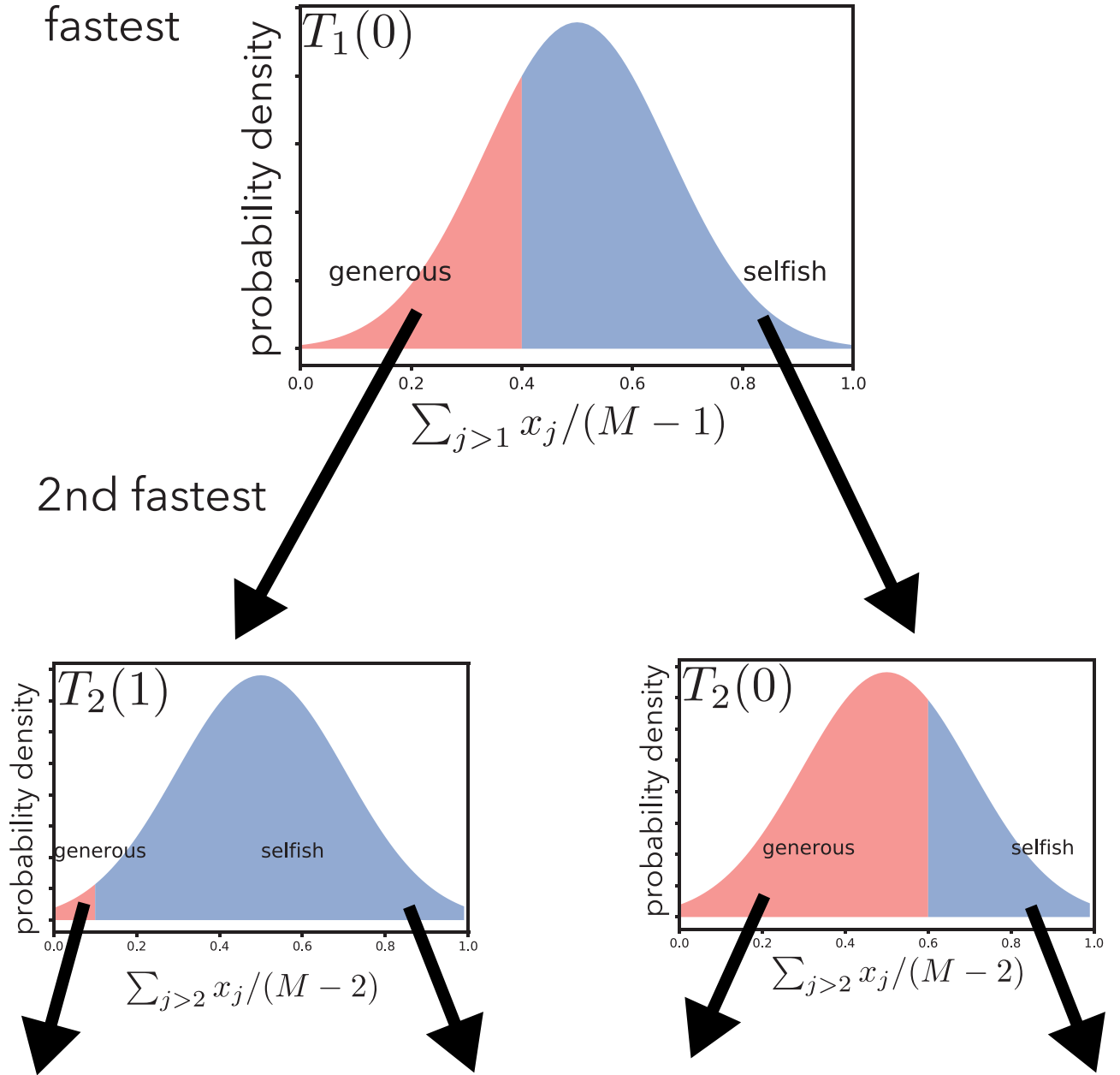
$$q_i(x_i^* = 0) = \sum_{f_1=0}^{i-1} p_i(f_1) q_i(x_i^* = 0 | f_1) \quad (8)$$

where  $p_i(f_1)$  is the probability density of  $f_1$  for species  $i$ . From Eq. (6), the conditional probability  $q_i(x_i^* = 0 | f_1)$  is derived as

$$q_i(x_i^* = 0 | f_1) = 1 - q_i(x_i^* = 1 | f_1)$$

$$= 1 - \int_0^{T_i(f_1)} \mathcal{N}(x | 0.5, \sigma_i^2) dx \quad (9)$$

where  $q_i(x_i^* = 1 | f_1)$  indicates the conditional probability that species  $i$  becomes generous given a value of  $f_1$ . Notice that these two conditional probabilities are affected by the value of  $f_1$ , but given the value  $f_1$ , the two conditional probabilities can easily be computed by calculating the cumulative probability function of the normal distribution  $\mathcal{N}(0.5, \sigma_i^2)$ .



**Fig. 3.** Schematic illustration of the analysis under the condition of large evolutionary-rate differences.

The threshold of the evolutionary direction is determined by the evolutionary fate of the species which have already fixed their strategies. Under the condition of large evolutionary-rate differences, the evolutionary fate of the fastest species ( $i = 1$ ) is determined only by the value of  $k$ . In other words, the favorability for the species evolving fastest is computable with arbitrary values of  $M$  and  $k$ . The threshold for the second fastest species ( $i = 2$ ) is determined not only by  $k$  but also by the evolutionary fate of the fastest species (left: generous and right: selfish). Notice that the probability  $p_2(1)$  ( $p_2(0)$ ) is the same as the probability that the fastest species becomes generous (selfish). The favorability of the second fastest species is, therefore, also computable. In addition, from the computation above, the probability density of  $f_1$  for the third fastest species  $p_3(f_1)$  can be calculated.

The probability density  $p_i(f_1)$  is, on the other hand, is derived by

$$p_i(f_1) = p_{i-1}(f_1 - 1)q_{i-1}(x_{i-1}^* = 1|f_1 - 1) + p_{i-1}(f_1)q_{i-1}(x_{i-1}^* = 0|f_1). \quad (10)$$

In short, one can recursively calculate the favorability of species  $i$ ,  $q_i(x_i^* = 0)$ .

For the fastest evolving species ( $i = 1$ ), for example,  $p_1(0) = 1$  and the favorability of the fastest species is derived by

$$q_1(x_1^* = 0) = q_1(x_1^* = 0|0). \quad (11)$$

To calculate the favorability of the second fastest species, on the other hand, it is necessary to calculate the probability densities of

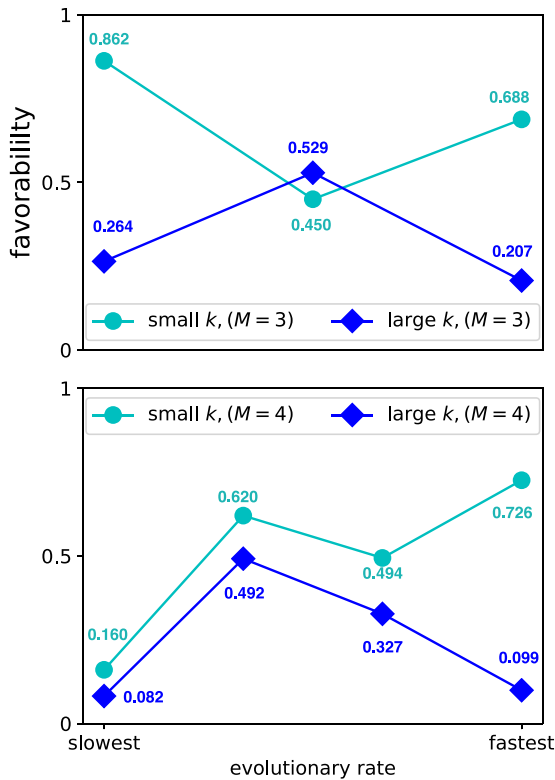
$f_1$  (i.e.,  $p_2(0)$  and  $p_2(1)$ ). However, these probabilities are the same as the probability that the fastest species becomes selfish or generous, respectively. The favorability of the second fastest species is, therefore, derived as follows:

$$\begin{aligned} q_2(x_2^* = 0) &= p_2(1)q_2(x_2^* = 0|1) + p_2(0)q_2(x_2^* = 0|0) \\ &= q_1(x_1^* = 1|0)q_2(x_2^* = 0|1) + q_1(x_1^* = 0|0)q_2(x_2^* = 0|0). \end{aligned} \quad (12)$$

For the third fastest species ( $i = 3$ ), the probability density of ( $f_1$ ) is derived as follows:

$$p_3(0) = q_2(x_2^* = 0|0)q_1(x_1^* = 0|0) \quad (13a)$$





**Fig. 4.** Favorabilities when the evolutionary-rate differences are large.

The favorabilities of each species in the three-species communities ( $M = 3$ ) and the four species communities ( $M = 4$ ) computed under the conditions of large differences in the evolutionary rates, using different values of  $k$  (in the three-species communities,  $k = 0.5$  for small  $k$  and  $k = 1.5$  for large  $k$  whereas  $k = 0.5$  for small  $k$  and  $k = 1.6$  for large  $k$  in the four-species community). It is assumed that the left-hand side of Inequality (6) is distributed according to the normal distribution if  $i = 1, 2, \dots, M-2$ ; when  $i = M-1$ , the uniform distribution is used for the distribution of the left hand side in inequality (6). Notice that it is unnecessary to consider the case of the slowest species ( $i = M$ ); the evolutionary fate of the slowest species is deterministic once the other species fix their strategies.

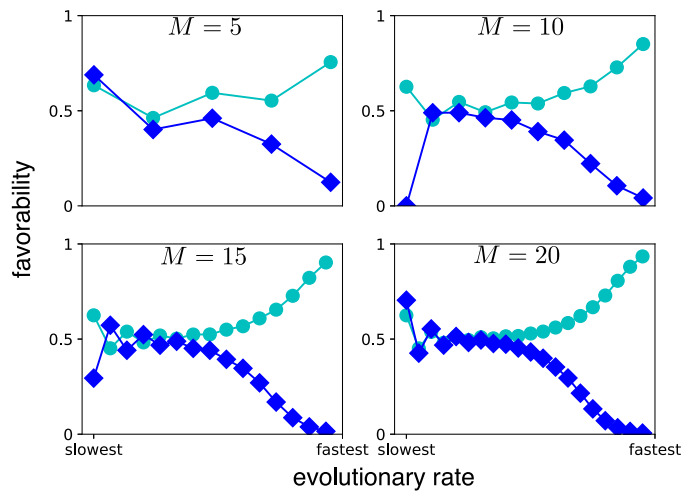
$$p_3(1) = q_2(x_2^* = 1|0)q_1(x_1^* = 0|0) + q_2(x_2^* = 0|1)q_1(x_1^* = 1|0) \quad (13b)$$

$$p_3(2) = q_2(x_2^* = 1|1)q_1(x_1^* = 1|0). \quad (13c)$$

By substituting Eq. (7) into Eq. (9), the conditional probability that the species evolving third fastest becomes selfish are achieved, and then, the favorability of the third fastest species is derived from Eq. (8). Therefore, for any value of  $i$ , the favorability of species  $i$  is computable from the conditional probabilities that the species evolving faster than  $i$  becomes selfish.

Fig. 4 shows the results of analysis of the relationship between evolutionary-rates and favorabilities under the condition of the quite large evolutionary rate differences. As per results of the computer simulations (Fig. 1), there exist nonlinear relationships between evolutionary rates and favorabilities. Although the favorabilities are quantitatively different between the computer simulation and the analysis, there exist some similarities; when  $M = 3$ , both show the concave (convex) curve with small (large)  $k$ . When  $M = 4$  the large value of  $k$  show the similar result, although the small value of  $k$  show the different result in the favorability of the second fastest species (Fig. 4).

The advantage of analysis under the condition of large evolutionary-rate differences is that communities with a large number of species can be analyzed, avoiding what would otherwise involve quite large computational costs in the computer simulation. Although there still exist nonlinear relationships between evolutionary rates and favorabilities when  $M$  is large (e.g.,  $M = 20$ ),



**Fig. 5.** Favorabilities under the condition of large evolutionary-rate differences in larger communities.

Favorabilities under the condition where the differences in the evolutionary rates are large, when  $M = 5, 10, 15$ , and  $20$  are shown. In each value of  $M$ , two values of  $k$  are used (cyan circle:  $k = 0.5$ , and blue square  $k = 1.5$ ). Although there exist nonlinear relationships between the evolutionary rates and the favorabilities, the models with large value of  $M$  show that the faster the evolutionary rate is, the more the focal species is likely to evolve as generous (selfish) if  $k = 0.5$  ( $k = 1.5$ ); however, for the species with the intermediate evolutionary rates, the difference of evolutionary rates have a small effect on the difference of favorabilities, and it is difficult to find any tendency in the relatively slowly evolving species. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

there is a pattern which is difficult to find when  $M$  is small (Fig. 5. See Fig. C.3 for larger  $M$ ); if the focal species has a relatively fast evolutionary rate, the faster the species evolves, the larger (the smaller) the favorability of that species is when  $k$  is small (large). The favorabilities species with relatively intermediate evolutionary rates show little change (around 0.5), meaning that the difference in evolutionary rates has little effect on favorabilities for these species. However, the species with relatively slow evolutionary rate, especially the slowest species, it is difficult to find a pattern. To sum up, under the condition of the large evolutionary-rate differences, communities with large number of species (large  $M$ ) can show the pattern for evolutionary rates and favorabilities of species with relatively fast or intermediate evolutionary rates.

#### 4. Discussion

In this paper, the effect of evolutionary rate on mutualism is investigated by generalizing the model proposed by Bergstrom and Lachmann (2003). In particular, I modified their model with respect to the number of species in the communities and the population sizes of each species. Although the evolutionary dynamics are deterministic, the stable equilibrium where the dynamics converge depends on the initial conditions, and therefore, the favorability or the probability that the focal species become selfish at a stable equilibrium should be evaluated.

In the original two-species model of the Red King effect (Bergstrom and Lachmann, 2003), the stable equilibria are where one species becomes generous and the other species becomes selfish. At such stable equilibria, the selfish species receives a larger benefit than the generous species, and one may say that the selfish species is a “winner” and that the generous species is a “loser”. In the multi-species model described in this paper, on the other hand, the selfish species are not always such “winners”. For example, in the three species model where all species have the same population size, there exist 1 generous and 2 selfish species at the stable equilibria when  $0 \leq k < 1$ , while the stable equilibria have 2

generous and 1 selfish species when  $1 < k < 2$ . In the latter case, the selfish species receive a payoff of 4 while the generous species receive a payoff of  $k + 1$  each, meaning that the selfish species “wins” over the both of the two generous species. However, if  $0 \leq k < 1$ , the payoffs of all species is 2; both the selfish species and the generous species receive the same benefit; and no species “wins”.

Better interpretations of what constitute generous and selfish studies would be as follows; a generous strategy produces a benefit to other species (e.g., producing a leaky resource that serves as an energy for the producer species and other species), while the selfish strategy is a role which pays a small cost but does not produce benefits unless other species play the generous strategy (e.g., producing enzyme which makes the resource available more effectively). While a selfish species always receives a larger benefit from the generous species than the selfish one, a generous species receives more (or less) benefits from the selfish species than the generous one when  $0 \leq k < 1$  (or  $1 < k < 2$ ). In the context of the division of labor of producing the leaky resource and the enzyme, the diffusion rate of the enzyme can be a measure of  $k$ . For example,  $0 \leq k < 1$  represents the case where the diffusion rate of the enzyme is large and both the generous species and the selfish species use the leaky resource effectively due to the enzyme the selfish species produces. The difference in the payoffs for the two species would represent the differences in the cost of producing the resource or the enzyme. In the situation where the diffusion rate of the enzyme is low ( $1 < k < 2$ ), only the selfish species make use of the resource effectively due to the benefit of the enzyme while the generous species cannot access the enzyme. In such a situation, it would be better for the generous species if the other species play the generous strategy and increase the amount of the leaky resource. Interpreted this way, a generous species can be regarded as one which provides the benefit of mutualism through the community, while a selfish species can be regarded as one that selfishly maximizes its potential payoff.

While the two-species model of the two player game shows the positive or negative correlations between evolutionary rates and favorabilities (Bergstrom and Lachmann, 2003; Veller et al., 2017), the computer simulation (Fig. 1) and the analysis under the condition of the large evolutionary-rate differences (Fig. 4) in this paper represent the non-monotonic relationship between evolutionary rates and favorabilities in the three- or four-species communities. Although the computer simulations of communities with the large value of  $M$  take a long time, the assumption of the large evolutionary-rate differences enables analysis of communities where many species coexist. Although the nonlinear relationship between evolutionary rates and favorabilities remains when  $M$  increases, one can find a clear pattern in the relationship (Fig. 5); the species evolving relatively fast have larger (smaller) favorabilities as the focal species evolves faster when  $k$  is small ( $k$  is large), while the favorabilities of species with relatively intermediate evolutionary rates are around 0.5. For the relatively slowly evolving species, however, it is difficult to find any tendency.

Such pattern suggests that faster evolution is favored (disfavored) for the relatively rapidly evolving species in a community with many species if  $k$  is smaller (larger) than 1. This result is consistent with the original two-species model (Bergstrom and Lachmann, 2003), where the Red Queen effect (the King effect) operates when  $k < 1$  ( $k > 1$ ). This consistency would arise from the fact that faster evolving species are more sensitive to the value of  $k$ . Eq. (7) suggests that the evolutionary direction is more sensitive to the values of  $k$ , when the focal species evolves faster (smaller  $i$ ), because  $f_1$  is equal or smaller than  $i - 1$ . In other words, the evolutionary fate of the species evolving faster is sensitive to the value of  $k$ , while the slowly evolving species is more sensitive to the evolutionary fate of the faster evolving species, which would lead to

the difficulty of finding a pattern for the relatively slow species. Notice that an exception is the case where  $M = 2$ ; if the evolutionary fate of the species evolving faster is determined, then that of the slower species is also determined as there exist only two stable equilibrium states. Therefore, in multi-species communities, only the evolutionary fate of the species relatively faster is predictable from the value of  $k$ , the payoff when a generous species interacts with other generous species.

It should be noted that in the multi-species communities, a pair of species sampled from the community does not always show the RQ or RK effects expected from the values of  $k$  and their evolutionary rates. When both of the two species evolves in the relatively intermediate rates, and  $M$ , the total number of species in the community, is enough large, for example, their favorabilities would be very similar. When  $M$  is small but not two (i.e.,  $M = 3, 4, 5$ ), on the other hand, a pair of species can suggest RQ effect although the value of  $k$  predicts RK effect, and vice versa (e.g., Figs. 4 and 5). Therefore, when the empirical results contradict with the prediction by the two-species models, it would be possible that there exist one or more species join in the mutualistic symbiosis.

Of course, this research has some limitations. First, it would be unnatural that all species play the same game defined by Table 1. The parameter  $k$  could be replaced with  $k_{ij}$ , which represent what a generous individual of species  $i$  receives when interacting with a generous individual of species  $j$ . In addition, it is more natural if a community includes not only mutualistic interactions but also antagonistic interactions. Second, this paper assumes only two distinct strategies, selfish or generous. However, it is possible to consider continuous trait values where the payoff is then given by the difference of the trait values of the players. Although the distinct strategies could be enough in the context of division of labor, continuous traits model would be more valid in the context of mimicry as each species would have a different appearance and their costs to mimic the model species would be different. Third, population sizes can change over time in nature although the population sizes are fixed in this paper. Population dynamics could change the results in this study because the population size affects the evolutionary rates (Veller et al., 2017) and the stability of the equilibria, as shown in Appendix B. Indeed, recent studies that combined the public goods game with population dynamics and showed the maintenance of cooperation (Hauert et al., 2006) and complex dynamics (Gokhale and Hauert, 2016). Such eco-evolutionary dynamics can also be analyzed in mutualism with a degree of conflict.

## 5. Conclusions

In summary, this study analyzed the evolution of mutualism in multi-species communities by generalizing the two-species model proposed by Bergstrom and Lachmann (2003). In the multi-species communities, the favorabilities is not always a monotonic increasing or decreasing function of the order of the evolutionary rate. This suggests that a pair of species in the multi-species community can show the different relationship predicted by the two-species model. In addition, the value of the payoff for generous species  $k$  when they interact with other generous individuals is useful only to predict the evolutionary fate of species evolving relatively fast.

## Code availability

The codes used in this research are available at [Github](#).

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### Supplementary material

Supplementary material associated with this article can be found, in the online version, at doi:[10.1016/j.jtbi.2019.03.026](https://doi.org/10.1016/j.jtbi.2019.03.026).

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