# *The evolutionary game theory of interspecific mutualism in multi-species communities*

Shota Shibasaki

Department of General Systems Studies, Graduate School of Arts and Sciences, The University of Tokyo, Tokyo, 1538902, Japan

e-mail: shibasaki.sh@gmail.com

phone: +81 90 2548 5950

short running title: EGT of mutualism in multi-species communities

## 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 some conditions. This is called the Red King effect. After Bergstrom and Lachmann (2003) proposed Red King effect, it has been investigated in two species models. However, biological examples suggest that the mutualisms can include three or more species. Here, I modeled the evolutionary dynamics of mutualism in communities where there exist two or more species, and all species mutually interact with one another. Regardless of the number of species in the community, it is possible to derive conditions for the stable equilibria. In addition, I found that the conditions where faster or slower evolution is favored can change over the time. Interestingly, a correlation does not always exist between the evolutionary rates and the probability that the evolutionary dynamics converge to a favorable equilibrium for each species. This result suggests that predicting the effect of the evolutionary rates on the evolutionary fate of mutualisms will be difficult in nature.



Key words: evolutionary game theory (EGT), mutualism, Red Queen effect, Red King effect

# 1 Introduction

Mutualism, or cooperation between and among species, is widely spread in ecosystems. Two well known examples of mutualism are Müllerian mimicry and division of labor. In Müllerian mimicry, unpalatable species have evolved similar appearances, and they are each less likely to be predated upon because the predators effectively learn that these species are noxious (Müller, 1879). Although many empirical studies deal 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 & Smith-Vaniz, 1972). In division of labor, on the other hand, each species specializes certain tasks and exchanges different goods or services (Leigh, 2010). The 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 because the life cycles, the habitats, and the body plans of model species are innate while a mimic species has to change these aspects to mimic (Veller et al., 2017). 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 organism than another type of nutrient. Such mutualistic symbioses with varying degrees of conflict have been conceptualized by the by-matrix snowdrift game, defined by equation (1) (see Models for details).

Bergstrom & Lachmann (2003) modeled the evolutionary dynamics of the 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 species under some conditions. The slower evolutionary rate is caused, for example, by the longer generation time or the smaller mutation rate. The authors called this effect the Red King (RK) effect, which is converse to the Red Queen (RQ) effect (Van Valen, 1973), where the faster evolution is favored in antagonistic symbioses (and sometimes mutualistic symbioses as noted by Herre et al. (1999)). Although the model analyzed by Bergstrom and Lachmann was very simple (i.e., assuming a two-player game and infinite population sizes for both species), other researchers relaxed these assumptions and investigated the RK and/or RQ effects in mutualism with a degree of conflict. Gokhale & Traulsen (2012) found that in the multi-player snowdrift game of the two species model, RK effect can change to the RQ effect. Gao et al. (2015) uncovered that a reward mechanism in the multi-payer snowdrift game causes the shift between the RK and RQ effects. Veller et al. (2017) investigated the factors which changes the evolutionary rates of each species (generation time, mutation rates, selection strength, and population sizes) in finite population, and they found that the RK effect shift to the RQ effect and vice versa from the short time scale to the long time scale due to the 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 phenomenon is called as the

(Müllerian) mimicry ring, where three or more unpalatable species show the similar appearances to avoid predation (Sherratt, 2008). Examples of Müllerian mimicry rings include Appalachian millipedes (Marek & Bond, 2009), bumble bees (Plowright & Owen, 1980), cotton-stainer bugs (Zrzavý & Nedvěd, 1999), and *Heliconius* butterflies (Mallet & 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 with several phylogenetically broad fungal species (Hom & Murray, 2014).

Inspired by these biological examples, I investigated whether faster evolution or slower evolution is favored in communities that include more than two species. First, I built the model where $M$ species coexist and the population size of each species is infinitely large. This model is an extended version of Bergstrom & Lachmann (2003) with respect to the number of species in the communities. I shall show the conditions for a linear stable equilibrium of an arbitrary number of species in the communities, and a mixture of the RK and the RQ effects. Interestingly, in this model, all stable equilibria have the same number of generous species, wherein all individuals play the generous strategy and pay a larger cost. Then, the assumption of the infinite population size was relaxed, and I analyzed the communities where each species has a different population size. In this case, each stable equilibrium has various numbers of generous species, which never occurs if the population size of each species is infinitely large.

## 2 Models

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

| | | species $j$ | |
|---|---|---|---|
| | | Generous | Selfish |
| species $i$ | Generous | $(k, k)$ | $(1, 2)$ |
| | Selfish | $(2, 1)$ | $(0, 0)$ |

(1)

where $0 \leq k \leq 2$. As shown in equation (1), each species performs either a generous strategy or a selfish strategy, and the left payoff in each cell is for species $i$ and the right payoff is for species $j$. It is assumed that each individual performs the same strategy regardless of the partner species and that all species play the same game defined by equation (1).

In this model, the fitness of each species is determined only by the interspecific interactions (i.e., intraspecific interactions are ignored). Given the number of species in the community $M$, the evolutionary

Table 1: 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 |

dynamics of the fraction of generous individuals in species $i$ is given by the replicator dynamics as below:

$$\dot{x}_i = r_i x_i \left( f_i^{\mathrm{g}} - \bar{f}_i \right) \tag{2}$$

$$= r_i x_i (1 - x_i) \frac{1}{\sum_{j \neq i}^{M} N_j} \sum_{l \neq i}^{M} N_l \left\{ (k-3) x_l + 1 \right\}, \tag{3}$$

where $r_i$ is the evolutionary rate of species $i$, $f_i^{\mathrm{g}}$ 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 $i$. It should be noted that the intraspecific interaction is ignored and the interspecific interactions are weighted by the population sizes. The parameters in this model are summarized in Table 1.

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

**Definitions of the 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 linear relationship between the order of the evolutionary rates and the probability that each species become selfish.*

Although previous studies on the RK effect (Bergstrom & Lachmann, 2003; Gokhale & Traulsen, 2012) measured the sizes of basin of attraction wherein either of the two species becomes selfish, it is difficult to analyze in the same way in $M$ species communities due to the high dimensionality of the model and the existence of multiple stable equilibria (see Results). The assumption that the initial conditions should be uniformly distributed is important because other initial conditions can change the results; for example, if the initial conditions is that almost all individuals are generous in all species ($x_i(0) \approx 1$ for any $i$), the faster evolving species would become selfish (see Fig 2 for an example in the three species community).

# 3 Results

In this section, I shall show the conditions for linear stable equilibria and analyze the effect of the evolutionary rates on the evolutionary fate of each species. First, it is assumed that each species has an infinitely large population. Each stable equilibrium in this case has the same number of generous and selfish species given the value of $M$ and $k$. Then, the conditions where faster or slower evolution is favored is derived. Next, I relaxed the infinite population size assumption above, and assumed that the population sizes of each species various although they are enough large to use the ordinary differential equations. In this situation, each stable equilibria does not always have the same number of generous and selfish species.

## 3.1 Infinite population sizes

First, I assumed that the population size of each species is infinitely large ($N_i \to \infty$). The evolutionary dynamics in this case is represented as

$$\dot{x}_i = r_i x_i (1 - x_i) \left\{ 1 + (k - 3) \bar{x}_{j \neq i} \right\}, \tag{4}$$

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

$$\bar{x}_{j \neq i} = \frac{1}{M - 1} \sum_{j \neq i}^{M} x_j. \tag{5}$$

Notice that equation (4) is the same as the evolutionary dynamics proposed by Bergstrom & Lachmann (2003) when $M = 2$.

In the stable equilibria in equation (4), there exist $m$ generous species and $M - m$ selfish species. The number of generous species $m$ should satisfy the inequality below:

$$\frac{M - 1}{3 - k} < m < \frac{M - k + 2}{3 - k}. \tag{6}$$

The derivation is shown in Appendix A. It should be noted that there exists at most one integer $m$ that satisfies inequality (6) given the values of $k$ and $M$. In a community with three species ($M = 3$), for example, one species is generous ($m = 1$) and two species are selfish at a stable equilibrium 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 ($1 < k \leq 2$).

Although inequality (6) indicates that there exist $\binom{M}{m}$ equilibria in the dynamics defined by equation (4), it is unclear whether species $i$ is more likely to be generous or to be selfish. To clarify this point, I simulated the dynamics of the three and four species communities from various initial states. The evolu-

tionary rate of each species is given by $\boldsymbol{r} = (1/8, 1, 8)$ in the three species model, and $\boldsymbol{r} = (1/8, 1/2, 2, 8)$ in the four species model, respectively. The initial conditions are given by changing the fraction of generous individuals in each species (the step size 0.05). The total numbers of simulations in the three and four species models are $8,000$ and $16,000$, respectively. The probability that each species becomes selfish is shown in Fig. 1 and the relationship between the initial conditions and the stable equilibrium where the dynamics converge in the three species model is shown in Fig. 2.

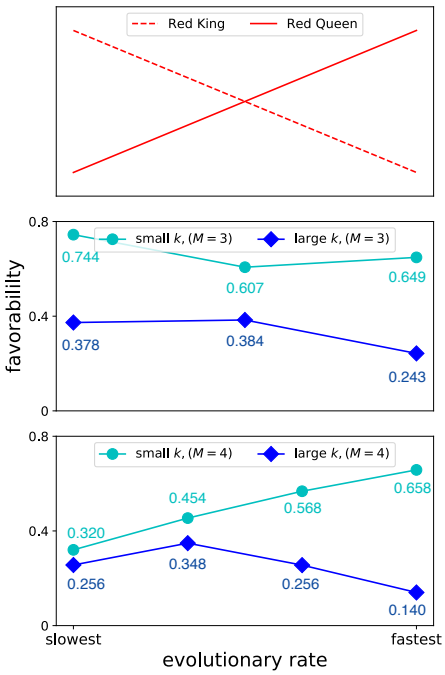


Figure 1: The evolutionary rates and the probability of becoming selfish species

The relationship between the order of the evolutionary rates and the probability that each species becomes selfish at stable equilibria (i.e., favorability) are shown. Top: the hypothetical results if RK effect or RQ effect operates; there should be a negative (positive) relationships between the order of evolutionary rates and the favorability. However, the results of computer simulations (Middle: three species, and Bottom: four species) do not show such relationships except for the case of small $k$ in the four species community. The parameters are: $\boldsymbol{r} = (1/8, 1, 8)$, and $k = 0.5$ (small) or $k = 1.5$ (large) in the three species model, and $\boldsymbol{r} = (1/8, 1/2, 2, 8)$ and $k = 0.5$ (small) or $k = 1.6$ (large) in the four species model.

Except for the case of the four species model with small $k$, there is no clear RQ effect nor RK effect in Fig. 1; there exists no linear relationship between the evolutionary rates and probabilities that each species becomes selfish (favorability). Rather, in the three species community, the slowly evolving species and the fast species are more favorable than the intermediate species if $k$ is small. When $k$ is large in the three species model, there exist no clear RQ nor RK effects either, although the difference of the probabilities of being selfish is small between the slow and the intermediate. In the four species model, there exist a convex relationship between the order of the evolutionary rates and the favorability when $k$ is large. On the other hand, there exists a positive relationship and, therefore, a RQ effect if $k$ is small. These results suggest there can be the mixture of the RQ effect and the RK effect in multi-species

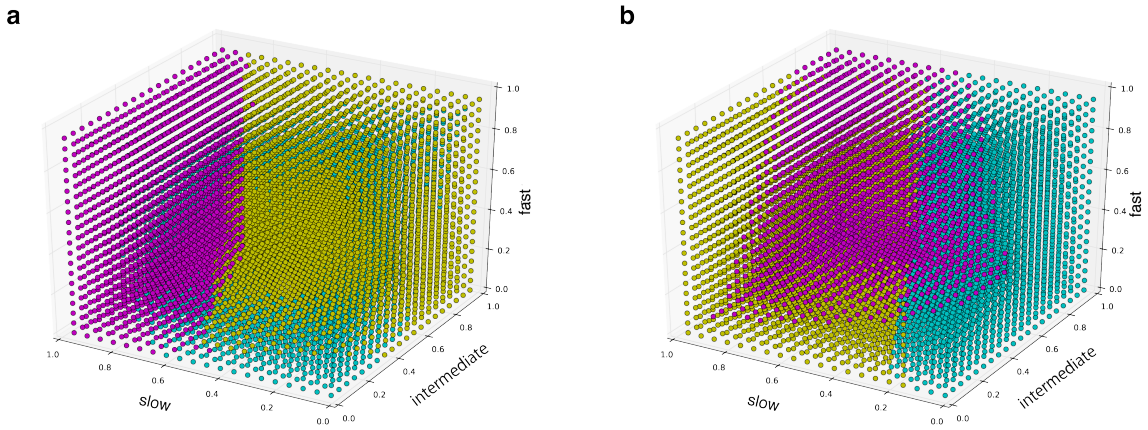


Figure 2: Initial conditions and the evolutionary fates.
The relationship between the initial conditions and the stable equilibria the dynamics converge to in the three species community is illustrated when (a) $k = 0.5$ (small $k$) and (b) $k = 1.5$ (large $k$). The colors of the dots show which stable equilibrium the dynamics converges to when the initial fractions of generous individuals in each species are given by the coordinates of the dots. (a) cyan: the slow and the intermediate are selfish while the fast is generous. yellow: the slow and the fast are selfish while the intermediate is generous. magenta: the intermediate and the fast are selfish while the slow is generous. (b) cyan: slow is selfish while the others are generous. yellow the intermediate is selfish while the others are generous. magenta: the fast is selfish while the others are generous.

communities.

To understand these results in detail, I investigated which species is the most liley to fix it's strategy first and whether this first fixed species is morel ikely to become generous or selfish in the three species and four species models, respectively. Tables 2 and 3 show that as evolutionary rate increases, the more the species is likely to be the first fixed species, regardless of the value of $k$. The direction of evolution of the first fixed species is, however, different according to the value of $k$. When $k$ is small, the first fixed species is more likely to evolve toward selfishness than generosity, indicating that faster evolution is favored in both three and four species models. On the other hand, slower evolution is favored when $k$ is large as the first fixed species is more likely to evolve toward generous species than selfish one.

Table 2: Probability of the first fixed species and the evolutionary directions in the three species model

| | small $k$ | | | large $k$ | | |
|---|---|---|---|---|---|---|
| species | selfish | generous | total | selfish | generous | total |
| slow | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| intermediate | 0.035 | 0.000 | 0.035 | 0.000 | 0.024 | 0.024 |
| fast | 0.641 | 0.324 | 0.965 | 0.223 | 0.753 | 0.976 |

Equation (4) helps the understanding of the effect of $k$ on the direction of evolution. As $r_i > 0$ and $0 \leq x \leq 1$, the sign of $1 + (k-3)\bar{x}_{j \neq i}(t)$ determines the evolutionary direction of species $i$ (positive: generous, and negative: selfish) at given time $t$. As the initial fractions of generous individuals in each

Table 3: Probability of the first fixed species and the evolutionary directions in the four species model

| | small $k$ | | | large $k$ | | |
|---|---|---|---|---|---|---|
| species | selfish | generous | total | selfish | generous | total |
| slowest | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| 3rd fastest | 0.001 | 0.02 | 0.003 | 0.000 | 0.000 | 0.000 |
| 2nd fastest | 0.075 | 0.027 | 0.102 | 0.003 | 0.054 | 0.057 |
| fastest | 0.621 | 0.274 | 0.895 | 0.100 | 0.843 | 0.943 |

species is uniformly i.i.d., the mean of $\bar{x}_{j\neq i}(0)$ is

$$E\left(\bar{x}_{j\neq i}(0)\right) = 0.5. \tag{7}$$

Due to the assumption of the uniform distribution of $x_i(0)$, the distribution of $\bar{x}_{j\neq i}(0)$ is symmetric. Species $i$ is, therefore, more likely to initially evolve toward being generous (or being selfish) if and only if

$$\begin{aligned} 1 + (k-3)E\left(\bar{x}_{j\neq i}(0)\right) &\gtreqless 0 \\ \Leftrightarrow k &\gtreqless 1. \end{aligned} \tag{8}$$

The upper (lower) sign of inequality (8) is the condition where species $i$ is more likely to initially evolve toward being generous (selfish), which is consistent with the evolutionary directions of the first fixed species (Tables 2 and 3). Notice that inequality (8) holds with the arbitrary integer $M$. Fig. 3 illustrates the effect of $k$ on the initial evolutionary direction when $M = 3$.

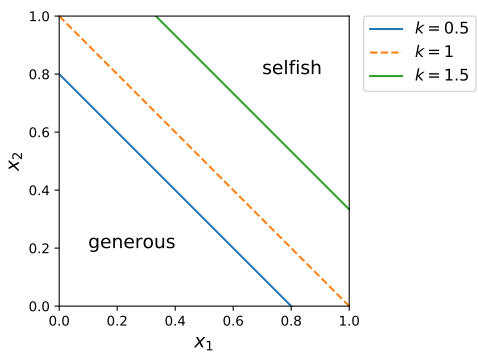


Figure 3: The effect of $k$ on the initial direction of evolution

Each three lines represents the line of $1 + (k-3)(x_1 + x_2)/2 = 0$ with various values of $k$ (blue: $k = 0.5$, orange: $k = 1$, green: $k = 1.5$). If the initial condition of the two species is uniformly i.i.d., the area under each line is where the third species initially evolves toward the generous species, while the area above the line is where the third species initially evolves toward being selfish. If $k = 0.5$ (or $k = 1.5$), the third species is more likely to initially evolve toward being selfish (generous) than being generous (selfish).

It should be noted that inequality (8) suggests the only initial evolutionary direction of each species;

the evolutionary direction can change over time as the fraction of generous individuals in each species changes. To obtain the evolutionary direction of species $i$ at arbitrary time $t$, it is necessary to find the sign of $1 + (k-3)\bar{x}_{j\neq i}(t)$, which is difficult to analytically calculate.

To analyze the effect of the evolutionary rates more deeply, let us assume the ideal situation where the differences in evolutionary rates between each species are large and only the fastest evolving species that has never fixed it's strategy can evolve toward generosity or selfishness while the remaining species do not change in their fractions of generous individuals. This assumption allows to predict whether each species is more likely to become selfish or generous. Under this assumption, the fastest evolving species is more likely to be a generous (selfish) species if $k > 1$ ($k < 1$), as shown in inequality (8). After the fastest species fixes it strategy, the other species fix their strategies in order of the evolutionary rates in this idealized situation. The probability that each species becomes selfish, however, depends on the number of species that have already fixed their strategies as generous species (i.e., the evolutionary fates of the faster species than focal one). Given that $f_0$ is the number of species which are fixed as selfish species and $f_1$ is the number of species which are fixed as generous species in $M$ species community, let us consider the evolutionary fate of the focal species species $f$, which is the $f_0 + f_1 + 1$ -th fastest species in the community. There remain $R = M - (f_0 + f_1)$ species (species $f$ and the slower species) that have not fixed their strategies yet. Using the fact that the fractions of generous individuals of these remaining species are uniformly i.i.d., the sign of $1 + (k-3)\bar{x}_{j\neq f}$ is calculated as below:

$$
\begin{aligned}
1 + (k-3)\bar{x}_{j\neq i} &= 1 + \frac{k-3}{M-1}\sum_{j\neq f} x_j \gtrless 0 \\
\Leftrightarrow 1 + \frac{k-3}{M-1}&\left(f_1 + \sum_{j\neq f,\text{remaining}} x_j\right) \gtrless 0 \\
\Leftrightarrow \frac{1}{R-1}&\sum_{j\neq f,\text{remaining}} x_j \lessgtr \frac{1}{R-1}\left(\frac{M-1}{3-k} - f_1\right),
\end{aligned}
\tag{9}
$$

where the upper (lower) sign is the case when species $f$ is more likely to be generous (selfish). Notice that the mean of the left hand side of inequality (9) is 0.5 and its distribution is symmetric, approximately following the normal distribution whose mean is 0.5 and the inverse of variance is $12(R-1)$ due to the law of large number, because the fractions of generous individuals in remaining species is uniformly i.i.d.. Therefore, the right hand side of inequality (9) is regarded as the threshold of the evolutionary direction of species $f$:

$$
T_f\left(f_0, f_1\right) \equiv \frac{1}{R-1}\left(\frac{M-1}{3-k} - f_1\right). \tag{10}
$$

If $T_f$ is larger (smaller) than 0.5, species $f$ is more likely to be generous (selfish), meaning that the slower (faster) evolution is favored. Notice that the value of $T_f$ changes as one species fixes its strategy. Equation (10), therefore, suggests the shift of the conditions where the faster or the slower evolution is

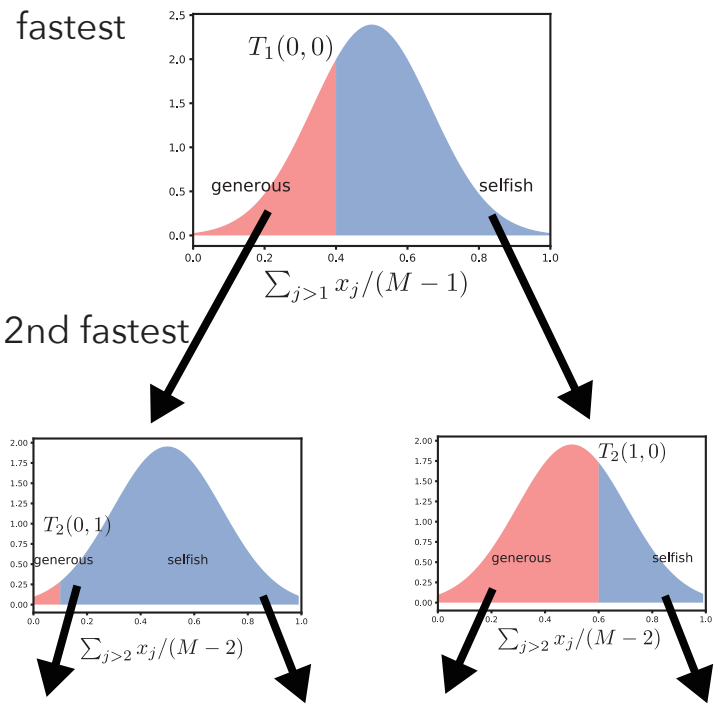


Figure 4: The schematic illustration of the shift of evolutionary direction over time

The threshold of the evolutionary direction can change as one one species fixes the strategy. Under the ideal conditions, the evolutionary fate of the fastest species ($i = 1$) is determined only by the value of $k$. The threshold for the second fastest species ($i = 2$) is determined not only by $k$ but also the strategy of the fastest species. Notice that the threshold for the second fastest species $T_2$ is different from that of the fastest species $T_1$ regardless of the evolutionary fate of the fastest species (generous: red and, selfish: blue, in top column).

favored over time (Fig 4).

In addition, it is possible to compute whether focal species $f$ is more likely to become generous or selfish under the ideal conditions. As it is mentioned above, the left hand side of Inequality (9) approximately follows the normal distribution where the mean is 0.5 and the inverse of the variance is $12(R-1)$. Given that the combination of $(f_0, f_1)$, the probability that focal species become generous or selfish is computable using the cumulative probability distribution of the normal distribution mentioned above. The probability of the combinations of $(f_0, f_1)$ can be sequentially obtained according to the evolutionary rates (Fig. 4). Therefore, one can compute the favorability of the focal species in the arbitrary values of $M$ and $k$. Examples of the favorabilities in the three of four species communities under the ideal conditions are shown in Fig. 5, which is similar to the results of the computer simulations in Fig. 1; there exists the nonlinear relationship between the evolutionary rates and the favorabilities.

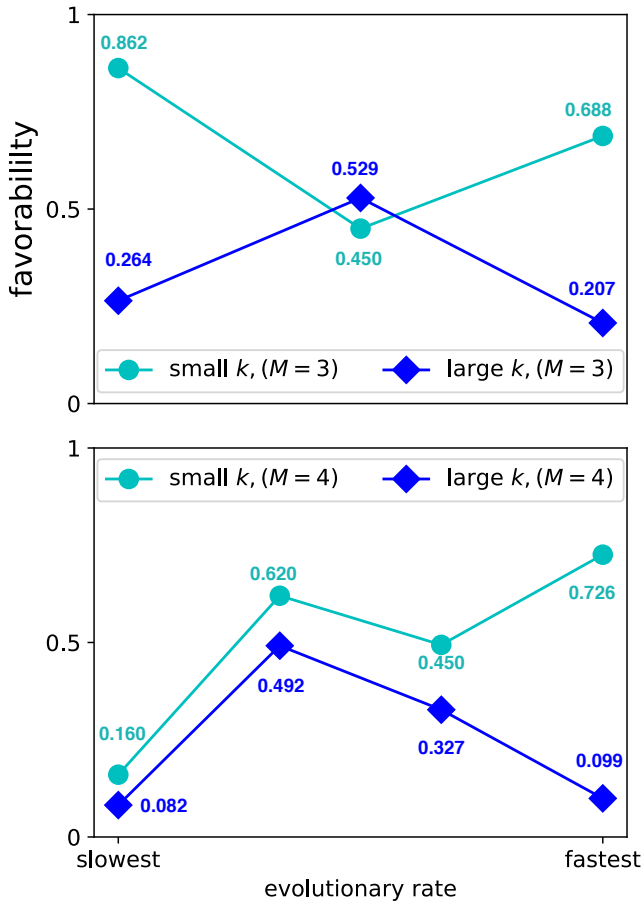


Figure 5: Favorabilities under the ideal conditions

The favorabilities of each species in the three species communities ($M = 3$) and the four species communities ($M = 4$) are computed under the ideal conditions. using different value 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 (9) is distributed according to the normal distribution if $R > 2$; otherwise the uniform distribution is used for the distribution of the left hand side in inequality (9).

The detail is explained in Appendix C.

The shift of the conditions whether the faster evolution or the slower evolution is favored under this ideal condition helps understanding the results of the computer simulation shown in Fig. 1, where all species can change the fractions of the generous individuals at the same time. Although the distribution of the fractions of generous individuals in each species changes over time in the computer simulation, the threshold of the evolutionary direction $T_f$ also changes as one species fixes its strategy, which is the reason of the mixture of RK and RQ effects. If the distribution of the fractions of generous individuals in the species that remain unfixed is obtained, it is possible to predict whether each species $i$ is more likely to evolve toward being selfish or generous at arbitrary time $t$. In this case, however, it is insufficient to calculate the mean of $\sum_{j \neq i,\text{remaining}} x_j(t)$ a in the right hand side of Inequality (9); it is necessary to calculate the probability density distribution of $\sum_{j \neq i,\text{remaining}} x_j(t)$ and comparing with $T_i$.

## 3.2 Various population sizes

Next, I relaxed the assumption that the population size of each species is infinitely large. Here, I assume that the population sizes are large enough that ordinary differential equations can be used, but each species has an arbitrary population size. Although Veller et al. (2017) show that population size has an effect on the evolutionary rates, it is assumed here that other factors such as the mutation rate or the generation time determine the evolutionary rates of each species.

In the case of the various population size model, the evolutionary dynamics defined in equation (3) are written as

$$\begin{aligned}\dot{x}_i &= r_i x_i \left(1 - x_i\right) \frac{1}{\sum_{j \neq i}^{M} N_j} N_l \left\{ \sum_{l \neq i}^{M} (k-3) x_l + 1 \right\} \\ &= r_i x_i \left(1 - x_i\right) \left\{ 1 + \sum_{j \neq i} w_{ij} \left(k - 3\right) x_j \right\}, \end{aligned} \tag{11}$$

where $w_{ij} = N_j / \sum_{l \neq i}^{M} N_l$. By giving $w_{ii} = 0$ for $i = 1, 2, \ldots, M$, one can find $\sum_{j=1}^{M} w_{ij} = 1$ for any $i$. This means that $w_{ij}$ is the weight of the effect of species $j$ on species $i$. In this model, the results shown in the previous section are rewritten by evaluating the weighted average of generous individuals $\sum_{j=1}^{M} w_{ij} x_j$.

The stable exterior equilibrium ($x_i^* \in \{0, 1\} \quad \forall i$) should satisfy the conditions below:

$$\frac{1}{3-k} \begin{array}{ll} < & \sum_{j=1}^{M} w_{ij} x_j^* \quad \text{if } x_i^* = 0 \\ > & \sum_{j=1}^{M} w_{ij} x_j^* \quad \text{if } x_i^* = 1 \end{array} . \tag{12}$$

The derivation is shown in Appendix B. It should be noted that the population sizes do not affect the stability of each equilibrium in the case of $M = 2$. Inequalities (12) suggest that we need to evaluate matrix $W = \{w_{ij}\}$ and the value of $k$ for all possible $2^M$ combinations of the evolutionary fate of the species in the community (Fig. 6). Although the evolutionary rates its self do not change the stability of each equilibrium, they affect the size of the basin of attraction (Fig. 6b). On the other had, the value of $k$ and matrix $W$ (or the relative population size vector $\boldsymbol{N}$) change the stability of the interior equilibria (Fig. 6c). Interestingly, each stable equilibrium does not always hold the same number of generous (and of course, selfish) species given the values of $k$ and $\boldsymbol{N}$ (Fig. 6d), which never occurs in the infinite population size model. The intuition is as follows: the evolutionary dynamics of species $i$ is determined by how often each individual of species $i$ interacts with generous or selfish individuals of the other species. In other words, the number of generous or selfish individuals (not the number of species) is important. If one species with a large population size become generous, other species frequently interact with generous individuals, which leads the evolution toward selfish species, and vice versa.

In the model with various population sizes, the evolutionary direction of each species is determined by

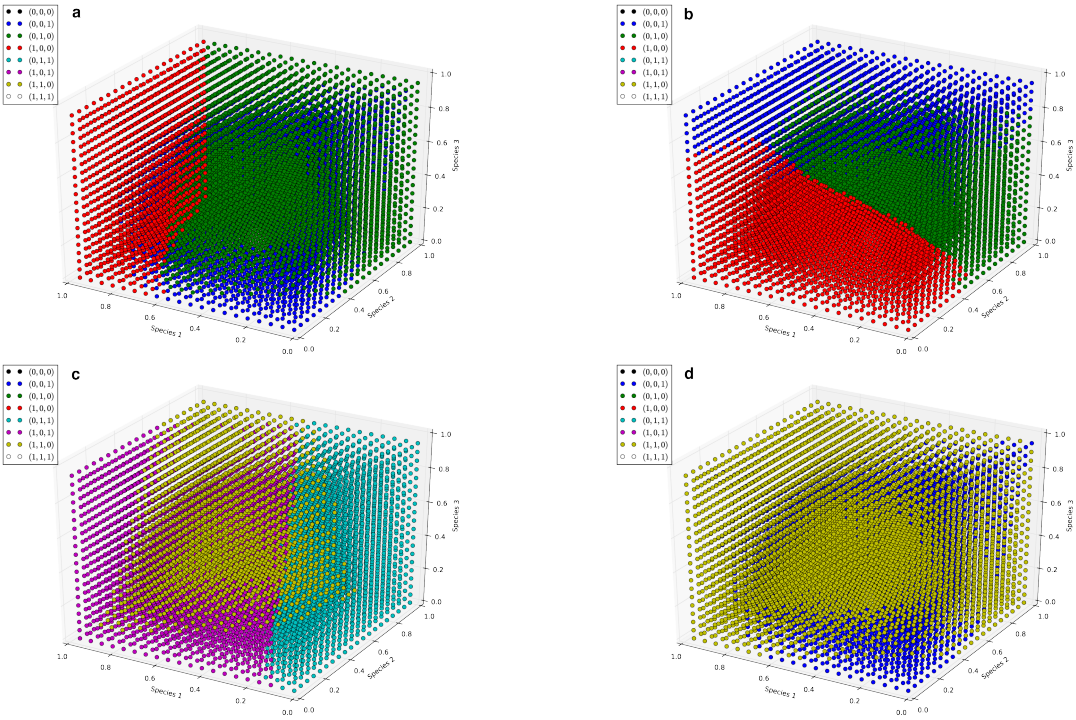


Figure 6: Examples of various population size model

If $M = 3$, there exist 8 candidates of the stable equilibrium. Each dot indicates the initial fractions of generous individuals, and the color of the dots represents which equilibrium the dynamics converge to. The parameters are (a): $\boldsymbol{r} = (1/8, 1, 8)$, $k = 0.5$, and $\boldsymbol{N} = (3, 3, 4)$, (b): $\boldsymbol{r} = (8, 1, 1/8)$, $k = 0.5$, and $\boldsymbol{N} = (3, 3, 4)$, (c):$\boldsymbol{r} = (1/8, 1, 8)$, $k = 1.5$, and $\boldsymbol{N} = (3, 3, 4)$, and (d): $\boldsymbol{r} = (1/8, 1, 8)$, $k = 0.5$, and $\boldsymbol{N} = (1, 1, 5)$.

$1+(k-3)\sum_{j\neq i} w_{ij}x_j(t)$ at arbitrary time $t$, which is difficult to analytically solve. However, it is possible to find the shift of the condition where faster or slower evolution is favored by rewriting inequality (12) as below:

$$\sum_{j,\text{remaining}} w_{ij}x_j \lesseqgtr \frac{1}{3-k} - \sum_{j,\text{generous}} w_{ij}. \tag{13}$$

The left hand side of inequality (13) are the weighted fractions of generous individuals in the species that have not fixed the strategies yet. The right hand side, on the other hand, is a function of the number of species that become generous, although it is weighted by $w_{ij}$.Notice that the value of the right hand side of inequality (13) changes as one species become generous, which suggests the shift of the condition whether faster evolution or slower evolution is favored.

# 4 Discussion

In this paper, I investigated the effect of evolutionary rates on mutualism by generalizing the model proposed by (Bergstrom & Lachmann, 2003). In particular, I modified their model with respect to of the number of species in the communities and the population sizes of each species. In both the infinite population size model and the various population size model, the conditions for the stable equilibria were derived (inequalities (6) and (12), respectively). If there exist only two species in the community, the evolutionary dynamics have two stable equilibria where one species becomes selfish and the other becomes generous (Bergstrom & Lachmann, 2003; Veller et al., 2017). On the other hand, the model in this paper shows that, if the species have infinite population sizes, there exist $\binom{M}{m}$ stable equilibria and that each of these stable equilibria should have $m$ generous species and $M - m$ selfish species. Although each stable equilibrium have the same number of generous species in the infinite population size model given the values of $M$ and $k$, the stable equilibria can have different number of generous species and selfish species one another in the various population model.

More importantly, Figs. 1 and 5 show in the community with more than two species, RK effect and RQ effect do not always operate; rather, they can be mixed and the relationship between the order of evolutionary rates and the probability that each species becomes selfish can be complex. This is because the favorability of the evolutionary rates can change over time, and this can be understood by considering the ideal condition where only the fastest species that has not fixed its strategy yet can evolve while the remaining species do not evolve. Under such conditions, the fractions of generous individuals in the species that have not fixed their strategy yet are uniformly i.i.d., and the probability density distribution of the left hand side of inequality (9) approximately follows the normal distribution whose mean is 0.5 and the inverse of the variance is $12(R-1)$. As one species fixes it strategy, however, the right hand side of inequality (9) or $T_f$ changes. Intuitively, this is because the fixed species continues having an effect on the evolution of remaining species. Although it is difficult to obtain the probability density distribution of the left hand side of inequality (9) without the assumption of the ideal situation, the change of $T_f$ still occurs, and this is the reason why Fig. 1 can show the nonlinear relationships between the order of evolutionary rates and the favorability.

While (Veller et al., 2017) previously showed the shift between RK effect and RQ effect on short time scales and the long time scales, the models in this paper show the shift of the conditions where faster evolution or slower evolution is favored as one species fixes its strategy. This result predicts difficulty in comparing experimental results with the hypothesis of RK effect. In recent years, it has become possible to estimate the evolutionary rates of some species (for example, Rubin & Moreau (2016)). Even when the evolutionary rates of the two mutualistic species are estimated, however, it would be difficult to test the prediction from the theories whether the faster evolution or the slower evolution is favorable, because this study shows that if another species mutually interacts with the two species, this third species has an

effect of the favorability of the evolutionary rates of the two species. In other words, it is necessary to consider the all mutualistic interactions the focal species have for the comparison with theoretical studies.

Of course, this research has some limitations. First, it would be unnatural that all species play the same game defined by equation (1). The parameter $k$ could be replaced with $k_{ij}$, which a generous individual of species $i$ receives when interacting with a generous individual of species $j$. In addition, it is more natural if the community includes not only mutualistic interactions but also antagonistic interactions. Second, this paper assumes the 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 payers. Third, population sizes can change over time although the population sizes are fixed in this paper. The population dynamics can 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 Inequalities (12). Indeed, recent studies combine the public good game with population dynamics and show the maintenance of cooperation (Hauert et al., 2006) and complex dynamics (Gokhale & Hauert, 2016). Such eco-evolutionary dynamics can also be analyzed in the mutualism with a degree of conflict.

In summary, this study analyzed the evolution of mutualism in the multi-species communities by generalizing the model proposed by Bergstrom & Lachmann (2003). Whether each species has the same population size or not, the conditions for the stable equilibria can be derived. In addition, the models in this paper suggest that RK or RQ effect do not always operate in the communities with more than two species. This is because the conditions whether the faster evolution or the slower evolution is favored can change as one species fixes it strategy.

## Acknowledgement

The author thanks to Dr. P. Zee for his comments and English corrections in the manuscript. The author also thanks Y. Otake for her beneficial comments to the earlier manuscript. The author is a Research Fellow of the Japan Society for the Promotion of Science (JSPS), and this work was supported by Grant-in-Aid for JSPS Fellows (JP18J22388).

## Appendix A Stability analysis of infinite population sizes

Here, the linear stability of the equilibria in the model with infinite population sizes given by equation (4) is performed and I prove that stable equilibria are only those which has $m$ generous species and $M - m$ selfish species, where integer $m$ satisfies inequality (6).

The element of the Jacobian matrix of equation (4) at the equilibrium $\boldsymbol{x}^*$ is represented by

$$J(\boldsymbol{x}^*) = \begin{cases} r_i(1-2x_i^*)\{1+\frac{k-3}{M-1}\sum_{j\neq i}^{M} x_j^*\} & (j=i) \\ r_i x_i^*(1-x_i^*)\frac{k-3}{M-1} & (j\neq i) \end{cases}. \tag{14}$$

To analyze the stability of each equilibrium, I classified the equilibria into the two class: (i) an exterior equilibrium where all elements are either 0 or 1 ($\forall i, x_i^* \in \{0,1\}$), and (ii) an interior equilibrium which holds at least one element between 0 and 1 ($\exists i, 0 < x_i^* < 1$).

## Appendix A.1 Stability of exterior equilibria

In the case of an exterior equilibrium, the Jacobian matrix $J$ of such equilibrium is given by

$$J_{ij} = \begin{cases} 0 & (i\neq j) \\ -\frac{r_i}{M-1}\{-m(3-k)+(M-k+2)\} & (i=j, x_i^*=1) \\ \frac{r_i}{M-1}\{-m(3-k)+(M-1)\} & (i=j, x_i^*=0) \end{cases}. \tag{15}$$

where $m$ is the number of generous species at this equilibrium. As this Jacobian matrix is a diagonal matrix with am exterior equilibrium, the eigenvalues of the Jacobian matrix are the same as the diagonal elements of the Jacobian matrix. The exterior equilibrium is, therefore, linearly stable if and only if

$$\begin{cases} -m(3-k)+(M-k+2) > 0 \\ -m(3-k)+(M-1) < 0 \end{cases}. \tag{16}$$

Here, inequalities (6) are obtained.

## Appendix A.2 Stability of interior equilibria

Next, let consider the stability of the interior equilibria. The interior equilibria can divide into two sub-categories: a full interior equilibrium where all elements are between 0 and 1, and a partially interior equilibrium where some elements are between 0 and 1 while the other elements are either 0 or 1. In this section, the full interior equilibrium is first analyzed because the stability analysis for the full interior equilibrium is simple. Then, the analysis for the partially interior equilibrium is shown.

There exist a unique full interior equilibrium in the evolutionary dynamics given by equation (4):

$\boldsymbol{x}^* = \left((3-k)^{-1}, (3-k)^{-1}, \ldots, (3-k)^{-1}\right)$. The Jacobian matrix at this equilibrium is written as

$$J = \begin{pmatrix} 0 & K_1 & K_1 & \ldots & K_1 \\ K_2 & 0 & K_2 & \ldots & K_2 \\ K_3 & K_3 & 0 & & K_3 \\ \vdots & \vdots & & \ddots & \vdots \\ K_M & \ldots & & K_M & 0 \end{pmatrix}, \tag{17}$$

where $K_i = -r_i(2-k)/\{(3-k)(M-1)\} \leq 0$. As the Jacobian matrix is not a diagonal matrix in this case, it is difficult to directly calculate the eigenvalues.

Instead of this approach, I shall show that Routh-Hurwitz criteria do not hold in the case of the full interior equilibrium and, therefore, the full interior equilibrium is not stable. Here, Mathematical Induction shows that the coefficient of $M-1$th order in the characteristic equation is 0, which means that Routh-Hurwitz criteria do not hold (Murray, 2002, Appendix B.1).

*Proof.* First, let consider the case when $M = 2$. Then, the characteristic equation is written as

$$\begin{aligned} &|\lambda I - J| = 0 \\ \Leftrightarrow\ &\lambda^2 - K_1 K_2 = 0, \end{aligned} \tag{18}$$

where $\lambda$ is the eigenvalue of the Jacobian matrix given by equation (17), $I$ is the identity matrix, and $|\lambda I - J|$ is the determinant of matrix $\lambda I - J$. Obviously, the coefficient of $\lambda$ is zero.

Next, let assume that the coefficient of $M-1$th order in the characteristic equation is zero when

$M = 2, 3, \ldots, n$. If $M = n+1$, the characteristic equation is

$$
\begin{aligned}
|\lambda I - J| &= \begin{vmatrix} \lambda & -K_1 & \ldots & -K_1 \\ -K_2 & \lambda & & -K_2 \\ \vdots & & \ddots & \vdots \\ -K_{n+1} & -K_{n+1} & \ldots & \lambda \end{vmatrix} \\
&= \lambda \begin{vmatrix} \lambda & -K_2 & \ldots & -K_2 \\ -K_3 & \lambda & & -K_3 \\ \vdots & & \ddots & \vdots \\ -K_{n+1} & -K_{n+1} & \ldots & \lambda \end{vmatrix} \\
&\quad + \sum_{l=2}^{n+1} (-1)^l K_l \begin{vmatrix} -K_1 & -K_1 & \ldots & -K_1 \\ \vdots & \lambda & & \vdots \\ -K_i & \ldots & \ddots & -K_i \\ \vdots & \ldots & & \vdots \end{vmatrix}.
\end{aligned} \tag{19}
$$

The first term in equation (19) is

$$
\begin{aligned}
\lambda \begin{vmatrix} \lambda & -K_2 & \ldots & -K_2 \\ -K_3 & \lambda & & -K_3 \\ \vdots & & \ddots & \vdots \\ -K_{n+1} & -K_{n+1} & \ldots & \lambda \end{vmatrix} &= \lambda \left| \lambda I - J_{n \times n} \right| \\
&= \lambda^{n+1} + a_2 \lambda^{n-1} + \ldots,
\end{aligned} \tag{20}
$$

where $J_{n \times n}$ is $n \times n$ matrix while $J$ in equation (19) is $(n+1) \times (n+1)$ matrix. The second term in equation (19) is, on the other hand, the $n-1$th degree equation of $\lambda$. The coefficient of $n$th order in equation (19) is, therefor, zero.

From these result, Routh-Hurwitz criteria do not hold in the characteristic equation of the Jacobian matrix in equation (17) with the arbitrary integer of $M$. As all eigenvalues are negative if and only if the Routh-Hurwitz criteria hold, the full interior equilibrium is not stable. □

Next, let consider the stability of the partially interior equilibria. At a partially interior equilibrium, I denoted the number of selfish and generous species as $f_0$ and $f_1$, respectively. The number of remaining species is $R = M - (f_0 + f_1)$ and both generous individuals and selfish ones coexist within each species.

The elements of partially interior equilibrium is represented as below:

$$x_i^* = \begin{cases} 0 & \text{if species } i \text{ is selfish} \\ 1 & \text{if species } i \text{ is generous} \\ \frac{M-1+f_1(k-3)}{(R-1)(3-k)} & \text{otherwise} \end{cases} . \tag{21}$$

The Jacobian matrix of such equilibrium is written as equation (17), although $K_i = 0$ if $x_i^* = 0$ or 1. As the Mathematical Induction above again holds in this case, all partially interior equilibrium is not stable.

# Appendix B Stability analysis in various population size model

Here, I prove that in the various population size model, the stable exterior equilibria should satisfy inequalities (12) while the interior equilibria cannot be stable. The elements of Jacobian matrix for equation (11) are represented as

$$J_{ij} = \begin{cases} r_i(1-2x_i^*)\{1+(k-3)\sum_{j=1}^{M} w_{ij}x_j^*\} & (j=i) \\ r_i x_i^*(1-x_i^*)(k-3)w_{ij}x_j^* & (j \neq i) \end{cases} . \tag{22}$$

In the case of the exterior equilibria, Jacobian matrix is a diagonal matrix. An exterior equilibrium is stable if and only if all diagonal elements of Jacobian matrix are negative, which is the same as inequalities (12).

In the case of interior equilibria (both the full interior equilibrium and the partially ones), on the other hand, all diagonal elements of Jacobian matrix are zeros. As shown in Appendix A.2, Routh-Hurwitz criteria do not hold in the characteristic equation with such Jacobian matrix, although the row elements except for the diagonal elements in each row do not have the same values in this case.

# Appendix C The favorability analysis

Under the ideal conditions where only the fastest species that has never fixed its strategy can evolve, the favorabilities are computable according to inequality (9). As the initial fractions of generous individuals in each species are uniformly i.i.d., the distribution of the left hand side in inequality (9) is approximately the normal distribution where the mean is 0.5 and the inverse of the variance is $12*(R-1)$ if $R$ is large. If the values of $f_0$ and $f_1$ are given, on the other hand, we can calculate $T_f$ and the conditional probability that focal species $f$ become generous (and selfish) by using the cumulative probability distribution of the left hand side in inequality (9).

The probabilities of the combinations of $(f_0, f_1)$ for species $f$ are sequentially computable according to the order of the evolutionary rates as follows. For the fastest species, one can obtain the proba-

bility that the fastest species becomes generous and selfish, respectively. Notice that the probabilities $\mathrm{Prob}\,(f_0 = 0, f_1 = 1)$ and $\mathrm{Prob}\,(f_0 = 1, f_1 = 0)$ for the second fastest species is the same as the probability that the fastest species becomes generous or selfish, respectively. As one can obtain the conditional probability that the second fastest species become generous given the combinations of $(f_0, f_1)$ using the same method which is used for calculating the probability that the fastest species become generous or selfish, it is possible to compute the probability that the second species becomes generous or selfish, respectively.

Using $\mathrm{Prob}\,(f_0, f_1)$ for the second fastest species and the conditional probabilities that the second fastest species become generous or selfish, $\mathrm{Prob}\,(f_0, f_1)$ for the third fastest species is computable, meaning that the probabilities that the third fastest species become generous or selfish are also computable. Repeating this calculation, the favorability of the focal species is computable in the arbitrary number of species in the community $M$ and the value of $k$. The favorabilities of each species in three species communities and four species communities are shown in Fig. 5, suggesting the non-linear relationship between the evolutionary rates and favorabilities, as Fig. 1 does.

# Appendix D Code availability

The codes used in this research are available at https://github.com/ShotaSHIBASAKI/EGT-of-interspecific-mutualism.

## References


Bergstrom, C.T. & Lachmann, M. 2003. The Red King effect: When the slowest runner wins the coevolutionary race. *Proceedings of the National Academy of Sciences* **100**: 593–598. doi:10.1073/pnas.0134966100. URL http://www.pnas.org/cgi/doi/10.1073/pnas.0134966100.

Chiari, Y., Vences, M., Vieites, D.R., Rabemananjara, F., Bora, P., Ramilijaona Ravoahangimalala, O. & Meyer, A. 2004. New evidence for parallel evolution of colour patterns in Malagasy poison frogs (Mantella). *Molecular Ecology* **13**: 3763–3774. doi:10.1111/j.1365-294X.2004.02367.x.

Gao, L., Li, Y.T. & Wang, R.W. 2015. The shift between the Red Queen and the Red King effects in mutualisms. *Scientific reports* **5**: 8237. doi:10.1038/srep08237. URL http://www.ncbi.nlm.nih.gov/pubmed/25649177.

Gokhale, C.S. & Hauert, C. 2016. Eco-evolutionary dynamics of social dilemmas. *Theoretical Population Biology* **111**: 28–42. doi:10.1016/j.tpb.2016.05.005. URL http://dx.doi.org/10.1016/j.tpb.2016.05.005.

Gokhale, C.S. & Traulsen, A. 2012. Mutualism and evolutionary multiplayer games: revisiting the Red King. *Proceedings of the Royal Society B: Biological Sciences* **279**: 4611–4616. doi:10.1098/rspb.2012.1697. URL http://rspb.royalsocietypublishing.org/cgi/doi/10.1098/rspb.2012.1697.

Hauert, C., Holmes, M. & Doebeli, M. 2006. Evolutionary games and population dynamics: maintenance of cooperation in public goods games. *Proceedings of the Royal Society B: Biological Sciences* **273**: 3131–3132. doi:10.1098/rspb.2006.3717. URL http://rspb.royalsocietypublishing.org/cgi/doi/10.1098/rspb.2006.3717.

Herre, E.A., Knowlton, N., Mueller, U.G. & Rehner, S.A. 1999. The evolution of mutualisms: exploring the paths between conflict and cooperation. *Trends in Ecology and Evolution* **14**: 49–53.

Hom, E.F.Y. & Murray, A.W. 2014. Niche engineering demonstrates a latent capacity for fungal-algal mutualism. *Science* **345**: 94–98. doi:10.1126/science.1253320. URL http://www.sciencemag.org/cgi/doi/10.1126/science.1253320.

Leigh, E.G. 2010. The evolution of mutualism. *Journal of Evolutionary Biology* **23**: 2507–2528. doi:10.1111/j.1420-9101.2010.02114.x.

Mallet, J. & Gilbert, L.E. 1995. WHY ARE THERE SO MANY MIMICRY RINGS - CORRELATIONS BETWEEN HABITAT, BEHAVIOR AND MIMICRY IN Heliconius BUTTERFLIES. *Biological Journal of the Linnean Society* **55**: 159–180. doi:10.1111/j.1095-8312.1995.tb01057.x.

Marek, P.E. & Bond, J.E. 2009. A Müllerian mimicry ring in Appalachian millipedes. *Proceedings of the National Academy of Sciences of the United States of America* **106**: 9755–60. doi:10.1073/pnas.0810408106. URL /pmc/articles/PMC2700981/?report=abstract.

Müller, F. 1879. Ituna and Thyridia: a remarkable case of mimicry in butterflies. *Transactions of the Entomological Society of London* pp. xx–xxix. doi:10.1017/CBO9781107415324.004. URL http://scholar.google.com/scholar?hl=en&btnG=Search&q=intitle:Ituna+and+Thyridia;+a+remarkable+case+of+Mimicry+in+Butterflies#0.

Murray, J.D. 2002. *Mathematical Biology : I . An Introduction*, 3rd edn. Springer, New York.

Niehuis, O., Hofmann, A., Naumann, C.M. & Misof, B. 2007. Evolutionary history of the burnet moth genus Zygaena Fabricius, 1775 (Lepidoptera: Zygaenidae) inferred from nuclear and mitochondrial sequence data: Phylogeny, host-plant association, wing pattern evolution and historical biogeography. *Biological Journal of the Linnean Society* **92**: 501–520. doi:10.1111/j.1095-8312.2007.00858.x.

Plowright, R.C. & Owen, R.E. 1980. THE EVOLUTIONARY SIGNIFICANCE OF BUMBLE BEE COLOR. *Evolution* **34**: 622–637.

Rakoff-Nahoum, S., Foster, K.R. & Comstock, L.E. 2016. The evolution of cooperation within the gut microbiota. *Nature* **533**: 255–259. doi:10.1038/nature17626. URL http://www.nature.com/doifinder/10.1038/nature17626.

Remy, W., Taylor, T.N., Hass, H. & Kerp, H. 1994. Four hundred-million-year-old vesicular arbuscular mycorrhizae. *Proceedings of the National Academy of Sciences of the United States of America* **91**: 11841–11843. doi:10.1073/pnas.91.25.11841.

Rubin, B.E.R. & Moreau, C.S. 2016. Comparative genomics reveals convergent rates of evolution in antplant mutualisms. *Nature Communications* **7**: 12679. doi:10.1038/ncomms12679. URL http://www.nature.com/doifinder/10.1038/ncomms12679.

Sanders, K., Malhotra, A. & Thorpe, R. 2006. Evidence for a Mullerian mimetic radiation in Asian pitvipers. *Proceedings of the Royal Society B: Biological Sciences* **273**: 1135–1141. doi:10.1098/rspb.2005.3418. URL http://rspb.royalsocietypublishing.org/cgi/doi/10.1098/rspb.2005.3418.

Sbordoni, V., Bullini, L., Scarpelli, G., Forestiero, S. & Rampini, M. 1979. Mimicry in the burnet moth Zygaena ephialtes: population studies and evidence of a BatesianMüllerian situation. *Ecological Entomology* **4**: 83–93. doi:10.1111/j.1365-2311.1979.tb00563.x.

Sherratt, T.N. 2008. The evolution of Müllerian mimicry. *Naturwissenschaften* **95**: 681–695. doi:10.1007/s00114-008-0403-y.

Springer, V.G. & Smith-Vaniz, W.F. 1972. Mimetic relationships involving fishes of the family Blenniidae. *Smithsonian Contributions to Zoology* **112**: 1–36. doi:10.5479/si.00810282.112.

Van Valen, L. 1973. A new evolutionary law. *Evolutionary Theory* **1**: 1–30.

Veller, C., Hayward, L.K., Hilbe, C. & Nowak, M.A. 2017. The Red Queen and King in finite populations. *Proceedings of the National Academy of Sciences* **114**: E5396–E5405. doi:10.1073/pnas.1702020114. URL http://www.pnas.org/lookup/doi/10.1073/pnas.1702020114.

Wahl, L.M. 2002. Evolving the division of labour: Generalists, specialists and task allocation. *Journal of Theoretical Biology* **219**: 371–388. doi:10.1006/jtbi.2002.3133.

Way, M.J. 1963. Mutualism between ants and honeydew producing homopterans. *Annual review of entomology* **8**: 307–344. doi:10.1146/annurev.en.08.010163.001515.

Zrzavý, J. & Nedvěd, O. 1999. Evolution of mimicry in the New World Dysdercus (Hemiptera: Pyrrhocoridae). *Journal of Evolutionary Biology* **12**: 956–969. doi:10.1046/j.1420-9101.1999.00102.x.