Seasons of the Red King: Mutualism under ecological fluctuations

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Coevolution of two species is typically thought to favor the evolution of faster evolutionary rates helping a species keep ahead in the Red Queen race, where 'it takes all the running you can do to stay where you are'. In contrast, if species are in a mutualistic relationship, it was proposed that the Red King effect may act, where it can be beneficial to evolve slower than the mutualistic species. The Red King hypothesis proposes that the species which evolves slower can gain a larger share of the benefits. Furthermore interactions between species can naturally be assumed to be nonlinear in fashion, thus amenable to modeling by multiplayer games. However this complexity actually helps us move seamlessly between the the Red King (mutualism) and the Red Queen (antagonistic) kind of interactions. Incorporating ecological dynamics

In his book 'The History of Animals', Aristotle observes *'When the crocodile yawns, the trochilus flies into his mouth and cleans his teeth. The trochilus gets his food thereby, and the crocodile gets ease and comfort; it makes no attempt to injure its little friend, but, when it wants it to go, it shakes its neck in warning, lest it should accidentally bite the bird'* (Aristotle, 350 B.C.E.). The phenomenon described by Aristotle was termed as mutualism in 1873 by the Belgian zoologist Pierre van Beneden (Bronstein, 2003). Mutualistic relationships, interspecific interactions that benefit both species, have been empirically studied for many years (Boucher, 1985; Hinton, 1951; Wilson, 1983; Bronstein, 1994; Pierce et al., 2002; Kiers et al., 2003; Bshary and Noë, 2003) and also a considerable body of theory has been put forth trying to explain the evolution and maintenance of such relationships (Poulin and Vickery, 1995; Doebeli and Knowlton, 1998; Noë, 2001; Johnstone and Bshary, 2002;

Bergstrom and Lachmann, 2003; Hoeksema and Kummel, 2003; Akçay and Roughgarden, 2007; Bshary et al., 2008). The example described by Aristotle and most other examples of mutualisms lend themselves to the idea of direct reciprocity (Trivers, 1971) and thus can be studied using evolutionary game theory. The interactions in these models are usually dyadic. A representative of each species is chosen and the outcome of the interactions between these representatives determines the evolutionary dynamics within each of the two species. However, in many cases interactions between species cannot be reduced to such dyadic encounters (Stadler and Dixon, 2008).

For example, in the interaction between ants and aphids or butterfly larvae (Pierce et al., 1987; Hölldobler and Wilson, 1990) many ants tend to these soft bodies creatures, providing them with shelter and protection from predation and parasites in exchange for honeydew, a rich source of food for the ants (Hill and Pierce, 1989; Stadler and Dixon, 2008). This is not a one to one interaction between a larva and an ant, but rather a one to many interaction from the perspective of the larva. In this manuscript we focus on this kind of – possibly – many to many interactions between two mutualistic species.

To analyze how benefits are shared between the two mutualistic species, we make use of evolutionary game theory. Since we consider the interaction of two species, we resort to bimatrix games (Weibull, 1995; Hofbauer, 1996; Hofbauer and Sigmund, 1998). We consider a situation where benefits can be split in different ways. Note that the two strategies to generate the benefits and even the benefits themselves could be completely different, as in the example discussed above. If the two species can choose between being *"Generous"* or *"Selfish"* then in what way will the benefits be allocated? A model addressing this was proposed by Bergstrom and Lachmann (2003) with the payoff matrix

$$\begin{array}{ccc} & & \text{Species 2} \\ & & \begin{array}{cc} \text{Generous} & \text{Selfish} \end{array} \\ \text{Species 1} & \begin{array}{c} \text{Generous} \\ \text{Selfish} \end{array} & \begin{pmatrix} 1.5, 1.5 & 1, 2 \\ 2, 1 & 0, 0 \end{pmatrix}. \end{array}$$

The twist to this formulation is that the two interacting species can have different evolutionary rates. In coevolutionary arms races, where species are locked in antagonistic relationships such as host-parasites or predatory-prey, we observe the Red Queen effect (van Valen, 1973). In these cases a higher rate of evolution will be beneficial. However, in mutualistic relationships a slower rate of evolution was predicted to be more favorable (Bergstrom and Lachmann, 2003). We extend this approach to multiple players. Note that we do not increase the number of interacting species (Mack and Rudgers, 2008; Damore and Gore, 2011), but rather the number of interacting individuals between two species (also see (Wang et al., 2011)).

We first recall the mutualistic relationship between two species in a two player game. Then we increase the number of players. We include asymmetry in evolutionary rates and discuss its effect both in two player and in multi-player games. We find that in situations where in two player setting it is beneficial to evolve at a slower rate, it can be detrimental in a multiplayer game.

Model and Results

Following (Bergstrom and Lachmann, 2003) we consider two species with two strategies, *"Generous"* and *"Selfish"*. Each species is better off being *"Selfish"* as long as the other one is *"Generous"*. If both are *"Selfish"*, then no mutualistic benefit is generated. Under these assumptions, the payoff matrix for the interactions is

$$\begin{array}{ccc} & & \text{Species 2} \\ & & \begin{array}{cc} G_2 & S_2 \end{array} \\ \text{Species 1} & \begin{array}{c} G_1 \\ S_1 \end{array} & \begin{pmatrix} a_{G_1,G_2}, a_{G_2,G_1} & a_{G_1,S_2}, a_{S_2,G_1} \\ a_{S_1,G_2}, a_{G_2,S_1} & a_{S_1,S_2}, a_{S_2,S_1} \end{pmatrix} \end{array}$$

where $a_{G_i,G_j} < a_{S_i,G_j}$ and $a_{S_i,S_j} < a_{G_i,S_j}$. The frequency of players playing strategy *"Generous"* (G_1) in species 1 is given by x and in species 2 (G_2) by y. The frequencies of players playing strategy *"Selfish"* (S_1 and S_2) are given by $1-x$ and $1-y$ in species 1 and 2, respectively.

Evolutionary game theory provides a natural way to include frequency dependence in the fitness of the different strategies ($f_{G_1}(y)$ and $f_{G_2}(x)$) (see Appendix). The replicator equations for the two species describing the time evolution of the frequencies of the *"Generous"* types in the two species are (Taylor and Jonker, 1978; Hofbauer and Sigmund, 1998, 2003)

$$\begin{aligned} \dot{x} &= r_x x \left(f_{G_1}(y) - \bar{f}_1(x,y) \right) \\ \dot{y} &= r_y y \left(f_{G_2}(x) - \bar{f}_2(x,y) \right). \end{aligned} \tag{1}$$

The parameters r_x and r_y are the evolutionary rates of the two species. We first recover the scenarios described in (Bergstrom and Lachmann, 2003) using the payoff entries given in the Introduction. If the evolutionary rates are equal ($r_x = r_y$), then the basins of attraction of (S_1, G_2) and (G_1, S_2) are of equal size (Fig. 1 Panel A). For unequal evolutionary rates, the species which is evolving slower (in our case species 1 with the rate $r_x = r_y/8$) has a larger domain of attraction (Fig. 1 Panel B). This asymmetry where most of the initial conditions lead to an outcome favouring the slower evolving species has been termed as the *Red King effect* (Bergstrom and Lachmann, 2003).

We now extend the above approach to multiplayer games. Note that the payoff matrix used above has the payoff structure of a standard snowdrift game (as $a_{G_i,G_j} < a_{S_i,G_j}$ and $a_{S_i,S_j} < a_{G_i,S_j}$).

For a multiplayer game we no longer have a 2×2 payoff matrix, but rather a payoff table. For this, we use the notation from (Souza et al., 2009) for a d-player snowdrift game. Only if there are at least M *"Generous"* players, a benefit is produced. Hence for $k < M$ generous players, being generous results in a loss of c/M. Due to this, the *"Selfish"* species also does not get anything, 0. If there are at least M generous players, then a benefit is produced. The *"Generous"* obtain $b - c/k$, but the *"Selfish"* obtain b at no cost. For species 2 we can write down a different payoff setup which could have different values for b, c, M, d etc. thus creating a "bi-table" game. For the time being, we assume that the payoff setups are symmetric for the two species and hence we just elucidate the details for species 1. The exact formulation of the payoffs and the calculations of fitness values are given in the Appendix.

Note that for $d = 2$, $M = 1$, $b = 2$, $c = 1$ we recover the matrix used in (Bergstrom and Lachmann, 2003). Even for these new fitness functions for multiplayer games, the dynamics are still given by the replicator equations (Hauert et al., 2006b; Pacheco et al., 2009; Gokhale and Traulsen, 2010). Also note that for two player games with $M = 1$, there are four fixed points on the vertices of the state space and the one internal one given by $x = y = 2(b - c)/(2b - c) = \frac{2}{3}$. The position of the interior fixed point is independent of the evolutionary rates. For a 20 player game, the basins of attractions are still of the same size, but the dynamics leading to the stable points on the vertices are completely different (Fig. 1 Panel C, $r_x = r_y$). The internal equilibrium has now shifted to $x = y = 0.063$. As before, we introduce an asymmetry in the evolutionary rates as $r_x = r_y/8$. Interestingly, we find that for a 20 player game (Fig. 1 Panel D, $r_x = r_y/8$) for the same asymmetric values of growth rates as in the two player case, most of the initial conditions in the simplex lead to a stable point where species 2 is selfish and species 1 is generous (G_1, S_2). This reverses the outlook which we got from $d = 2$. Everything else being the same, in the presence of multiple players, the Red King effect is not observed.

Next, we explore the exact process due to which the Red King effect vanishes. The replicator solutions of the two species creates quadrants in the simplex. Of these quadrants, the top right and the bottom left are of special interest as they contain the separatrix between the two basins of attraction. Consider the top right quadrant. Species 2 is represented by the $y - axis$, hence a faster evolution by species 2 results in most of the initial conditions leading to the outcome favorable for species 2, i.e. (G_1, S_2). An exactly opposite scenario is taking place in the bottom left quadrant. Hence in this quadrant as species 1 is evolving at a slower pace than species 2, most of the initial condition here lead to an outcome favoring

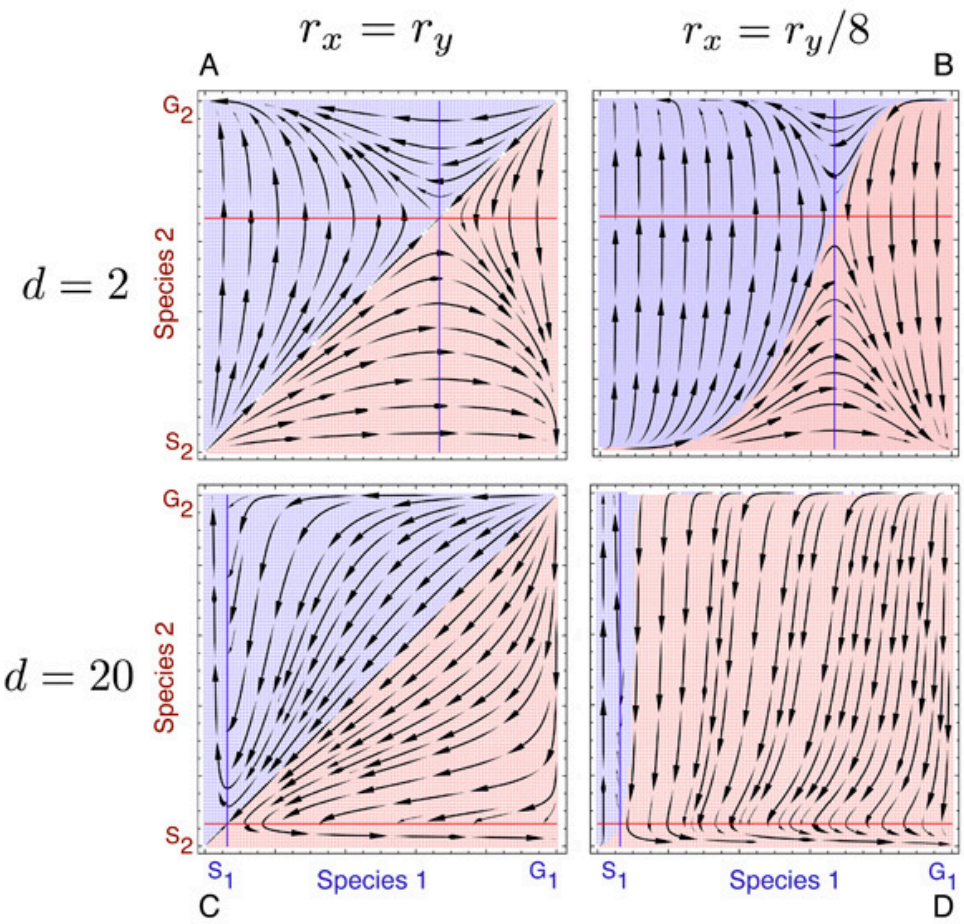

Figure 1: The composition of both species can range from all selfish (S) to all generous (G). If the other species is sufficiently generous, selfish behavior is favored in both species. However, if the other species is selfish, generous behavior is advantageous. This is captured by the snowdrift game discussed in the text. For equal evolutionary rates, $r_x = r_y$, the domains of attraction for the two outcomes (S_1, G_2) and (G_1, S_2) are of equal size (Panels A and C). The colors illustrate the regions leading to the outcomes favorable to species 1 (blue shaded area leading to (S_1, G_2)) and species 2 (red shaded area leading to (G_1, S_2)). For a two player game, $d = 2$, and $r_x = r_y/8$, the basin of attraction favorable to the slower evolving species 1 grows substantially (Panel B) (Bergstrom and Lachmann, 2003). For a twenty player game, $d = 20$, the basins of attractions have identical size for equal evolutionary rates, but the position of the internal equilibrium is shifted (Panel C). When species 1 evolves slower than species 2 in this situation, most of the initial conditions in the simplex lead to a solution which is unfavorable to species 1. Thus for 20 players instead of two, the Red King effect is reversed ($b = 2$ and $c = 1$).

species 1, i.e. (S_1, G_2). As long as the internal equilibrium is on the diagonal the Red King effect depends on the sizes of these quadrants. Changing the number of players alters the sizes of these two influential quadrants. For example consider the case of the twenty player game. The size of the bottom left quadrant is reduced to such an extent that almost the whole of the simplex leads to the outcome favorable for the faster evolving species.

Obviously, the bottom left and the top right quadrants have equal size when the internal equilibrium is at $x = y = 0.5$. For a fixed b and c we cannot select any arbitrary number of players d to obtain this equilibrium, as d is not a continuous variable. If the equilibrium is above $x = 0.5$, then a decrease in the evolutionary rate can be beneficial as demonstrated by the Red King effect. Conversely, if the equilibrium is below $x = 0.5$, then an increase in the evolutionary rate might be favorable. Hence the Red Queen dynamics would favour a species even in the mutualistic setting if the number of players is effective in positioning the equilibrium at $x < 0.5$.

Interspecific relationships are exceedingly complex (Blaser and Kirschner, 2007). It might be challenging to find the exact number of species interacting together to maintain the system (Doebeli and Knowlton, 1998; Bronstein and Barbosa, 2002; Bascompte et al., 2006) and furthermore to find if the interactions are balanced. Asymmetries have been considered in mutualistic species at the level of species or other properties of the system such as interactions (Noë et al., 1991), interaction lengths (Johnstone and Bshary, 2002) or growth rates (Bergstrom and Lachmann, 2003). Asymmetry in the number of interacting partners has only been recently tackled (Wang et al., 2011). Going back to the example of ants and larvae, a single larva is tended by multiple ants. Thus while from each ants point of view this is a two player game, for the larva this would be a multi-player game.

An interesting situation arises when we couple asymmetric number of players and asymmetric evolutionary rates. Instead of the single parameter d, now we have d_1 and d_2 as the number of players for the two species 1 and 2. For symmetric evolutionary rates, if one species plays a more player game than the other species then there are more points in the simplex from where the selfish outcome is accessible. For equal number of players, it depends on the sizes of the quadrants if a species should have a faster or slower rate of evolution to get the upper hand in the mutualistic relationship. Hence, if a species is currently at a disadvantage, a modification of the number of players or the evolutionary rate can sometimes put it on equal footing with the other species. Due to asymmetric number of players the sizes of the basins of attraction depends not just on the sizes of the quadrants but the shape of the separatrix as well. Thus, it is possible to counter the Red King effect by changing the number of interacting agents (Fig. 2).

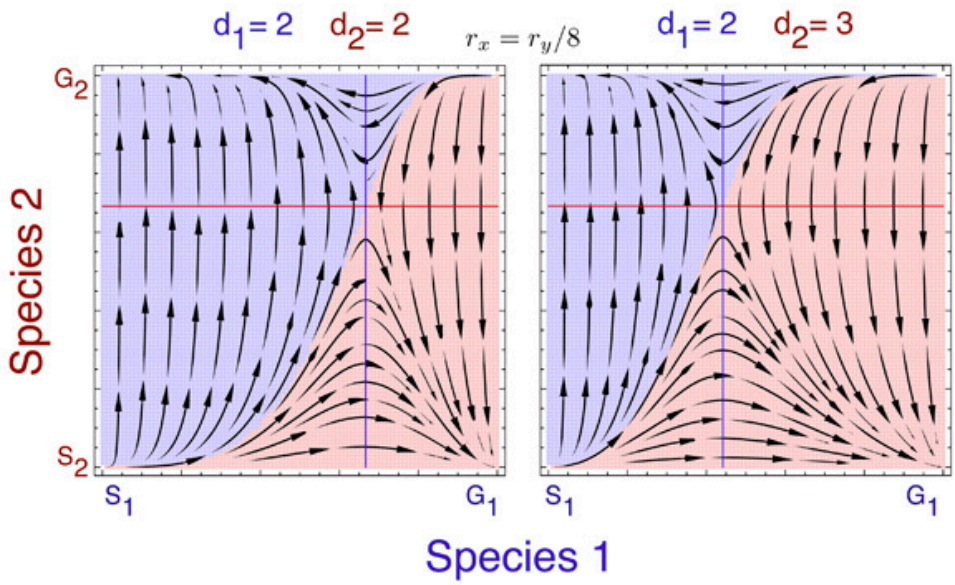

Figure 2: The Red King effect can be neutralized and/or even reversed if the number of players increases. Here we show the scenario explored in (Bergstrom and Lachmann, 2003) on the left panel; a two player game ($d_1 = d_2 = 2$) with $r_x = r_y/8$. Most of the points in the simplex lead towards the state favourable for species 1, (S_1, G_2). This changes when the number of players in species 2 increases from $d_2 = 2$ to $d_2 = 3$, i.e. now one individuals of species 2 interact with two individuals of species 1. The vertical and horizontal lines denote the positions where the the change in the strategy frequency is zero for species 1 and 2 respectively. The solution for species 1 (vertical, blue line) moves towards smaller x, increasing the size of the top right quadrant. For $d_1 = 2$ and $d_2 = 3$, it is given by $x = \frac{3(2b-c)-\sqrt{3(4bc-c^2)}}{2(3b-c)}$, whereas the the solution for species 2 is still $y = \frac{2(b-c)}{2b-c}$ (see Appendix). Thus, the quadrant favoring the species with a faster evolutionary rate grows. Since the number of players affects the size of these quadrants, it can eliminate or magnify the Red King effect.

Considering multi-player games provides a hitherto unexplored phenomenon in these kind of mutualism models. When a species interacts with a number of individuals of another species in a mutualistic relationship, it is possible that a certain quorum needs to be fulfilled. Client fish have been shown to choose cleaning stations with two cleaners over solitary cleaners (Bshary and Schäffer, 2002). A certain number of ants are required to save a myrmecophilous caterpillar from it's predator. It has been shown that the amount of larval secretions is correlated to the number of attending ants (Axén and Pierce, 1998).

Until now, we have considered this threshold to be one ($M = 1$). To begin with the simplest multiplayer case, we consider a symmetric three player game with different thresholds in either species to start off the benefits of mutualistic relations (say for species 1 the threshold is M_1 and similarly for species 2 is M_2 where in general M_i can range from 1 to d_i).

The payoff matrices become asymmetric due to the different thresholds for the two species. Here, it matters which dynamics we are studying, the usual replicator dynamics or the modified replicator equations (Figs. 3 and 4) (see Appendix) as they can result in different sizes of the basins of attraction. We can also change the nature of the game from coexistence to coordination by manipulating these thresholds (Souza et al., 2009) and hence intuitively translate between different social dilemmas when studying multi-player games.

Discussion

Development of a game theoretical approach for mutualism requires a different outlook from the social dilemmas field (Bshary and Bronstein, 2004). In a mutualistic framework, it is best for the two species to cooperate with each other. We do not ask the question how these mutualisms arise. Rather when they do, what is the best strategy to contribute towards the common benefit (Bshary and Noë, 2003; Bowles and Gintis, 2003)? It would be possible to include the interactions between the individuals of the same species, as has been explored experimentally recently (Wang et al., 2011). But then, we would be shifting our focus from the problem of interspecific mutualism to intraspecific cooperation (Bshary et al., 2008). Here, we have focused on the interspecific interactions, where the interacting partners are always picked from the other species (Schuster et al., 1981). Bergstrom and Lachmann have shown that in such a mutualistic scenario, the species which evolves slower can get away with being selfish and force the other species to make a generous contribution. They termed this as the Red King effect. If we include multiple players then the Red King effect is much more complex.

For simplicity, usually pairwise interactions are assumed in game theoretical arguments. For modeling collective phenomenon, multiplayer games may be necessary. The exact number

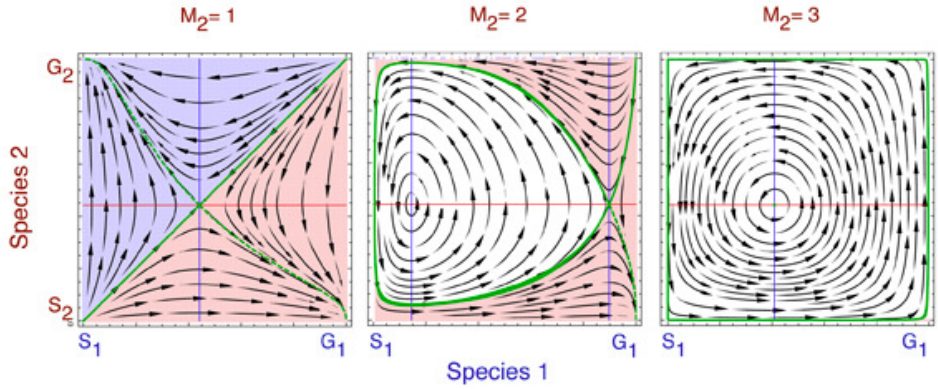

Figure 3: A three player game with asymmetric thresholds, but $r_x = r_y$. Species 1 and species 2 are both playing a three player game. For species 1, it is enough if one individual is *"Generous"* to produce the benefit ($M_1 = 1$). For species 2, however, the minimum number of *"Generous"* players required to produce any benefit strongly affects the replicator dynamics. For $M_2 = M_1 = 1$, we observe the basins of attraction discussed above. The manifolds for the saddle point plotted forward in time (dashed green lines) and backward in time (solid green lines) can be used to define the basins of attraction. For $M_2 = 2$, we observe a region with closed orbits in the interior (white background), almost all initial conditions outside this region lead to (G_1, S_2). For $M_2 = 3$, we observe closed orbits in almost the whole simplex. To avoid negative payoffs and to facilitate the comparison with other dynamics, we have added a background fitness of 1.0 to all payoffs, but this does not alter the dynamics here.

of players is a matter of choice, though. Group size distributions give us an idea about the mean group size of a species. Instead of using pairwise interactions or an arbitrary number of individuals to form a group, we could use the mean group sizes as the number of interacting individuals. Group size is known to be of importance in mutualisms (Wilson, 1983). As we have seen here, it can be a influential factor in deciding how the benefits are shared. Countering the Red King or enhancing its effect is possible by altering the group size. Hence can the group size itself be an evolving strategy? The study of group size distributions has been tackled theoretically (Krause and Ruxton, 2002; Hauert et al., 2002; Niwa, 2003; Hauert et al., 2006a, 2008; van Veelen et al., 2010; Sumpter, 2010; Brännström et al., 2011; Peña, 2011) and empirically in various species ranging from house sparrows to humans (Zipf, 1949;

Krause and Ruxton, 2002; Sumpter, 2010; Griesser et al., 2011). In our example of ants and butterfly larvae, it has been observed that a larva was most successful in getting more ant attendants in a group of four larvae (Pierce et al., 1987). It would be interesting to see if the distributions in mutualistic species peak at the group size which is the best response to their symbiont partners choices. Future work would also involve including intraspecific interactions and how they might affect interspecific relationships (as in Bshary et al. (2008)). It has been shown in Axén and Pierce (1998) that the amount of larval secretions is also influenced by the quality of the other larvae in the group. Another method of introducing asymmetry is to have different payoff tables for the two species (i.e. different benefits and costs for the two species). Also we have just considered two strategies per species. Asymmetric number of strategies can induce further asymmetries in the interaction (Schuster et al., 1981). The intricacies of multiplayer games lend themselves to study such systems, but they also show that mutualisitc interactions may be far more complex than often envisioned. Applying multiplayer game theory to mutualism unravels this dynamics between species and can be used to understand the complexity of these non-linear systems.

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Appendix

Average payoffs in the bimatrix game

Two player setting

We can write down the payoff matrices for the two species separately denoted by A and B as,

$$A = \text{Species 1} \begin{array}{c} \\ G_1 \\ S_1 \end{array} \begin{array}{c} \text{Species 2} \\ \begin{array}{cc} G_2 & S_2 \end{array} \\ \begin{pmatrix} a_{G_1,G_2} & a_{G_1,S_2} \\ a_{S_1,G_2} & a_{S_1,S_2} \end{pmatrix} \end{array} \quad \text{B} = \text{Species 2} \begin{array}{c} \\ G_2 \\ S_2 \end{array} \begin{array}{c} \text{Species 1} \\ \begin{array}{cc} G_1 & S_1 \end{array} \\ \begin{pmatrix} a_{G_2,G_1} & a_{G_2,S_1} \\ a_{S_2,G_1} & a_{S_2,S_1} \end{pmatrix} \end{array}.$$

The frequency of the players playing strategy *"Generous"* in species 1 is given by x and that in species 2 by y. As the population size is kept constant the reciprocal frequencies of the players playing *"Selfish"* strategy are $1-x$ and $1-y$ in the two species respectively.

Multiplayer setting

For a multiplayer snowdrift game, the payoff entries are defined as (Souza et al., 2009),

$$\Pi_{S_1}(k) = \begin{cases} b & \text{if } k \geq M \\ 0 & \text{if } k < M \end{cases} \tag{2}$$

$$\Pi_{G_1}(k) = \begin{cases} b - \frac{c}{k} & \text{if } k \geq M \\ -\frac{c}{M} & \text{if } k < M \end{cases} \tag{3}$$

The selfish players get the benefit b if the number of generous individuals in both species combined, k, is greater than or equal to the threshold M. For the generous individuals, their effort is subtracted from the payoffs. The effort is shared if the quorum size is met ($\frac{c}{M}$), but happens in vain for $k < M$. The fitnesses of the two strategies in species 1 are given by,

$$f_{G_1}(y) = \sum_{k=0}^{d-1} \binom{d-1}{k} y^k (1-y)^{d-1-k} \Pi_{G_1}(k+1) \tag{4}$$

$$f_{S_1}(y) = \sum_{k=0}^{d-1} \binom{d-1}{k} y^k (1-y)^{d-1-k} \Pi_{S_1}(k). \tag{5}$$

Following the same procedure for the two strategies in species 2 leads to the average fitness

$$\bar{f}_1(x,y) = x f_{G_1}(y) + (1-x) f_{S_1}(y) \tag{6}$$
$$\bar{f}_2(x,y) = y f_{G_2}(x) + (1-y) f_{S_2}(x). \tag{7}$$

Dynamics in asymmetric conditions

We have addressed two kinds of asymmetries in the game, the number of player and the thresholds in the two species. We denote the number of players for species 1 and species 2 as d_1 and d_2, respectively, as in Fig. 2. That is if species 2 is playing a d_2 player game it means that one player from species 2 interacts with $d_2 - 1$ players of species 1. For an asymmetry in the thresholds we use the two parameters $M_1 \geq 1$ and $M_2 \geq 1$ for the two species, respectively.

For asymmetric bimatrix games, there is a difference in the dynamics between the standard replicator dynamics and the alternative dynamics put forward by Maynard-Smith (Maynard Smith, 1982). For this dynamics, the average fitness of each species appears as a denominator,

$$\begin{aligned} \dot{x} &= r_x x \left(f_{G_1}(y) - \bar{f}_1(x,y) \right) / \bar{f}_1(x,y) \\ \dot{y} &= r_y y \left(f_{G_2}(x) - \bar{f}_2(x,y) \right) / \bar{f}_2(x,y). \end{aligned} \tag{8}$$

In our asymmetric bimatrix game, the fixed point stability is affected by the choice of the dynamics, in contrast to the case of symmetric games. In Fig. 4, we illustrate that the dynamics is different between the usual replicator dynamics and Eqs. 8

For $d_1 = d_2 \geq 5$, the exact coordinates of the fixed point must be computed numerically (Abel, 1824; Stewart, 2004).

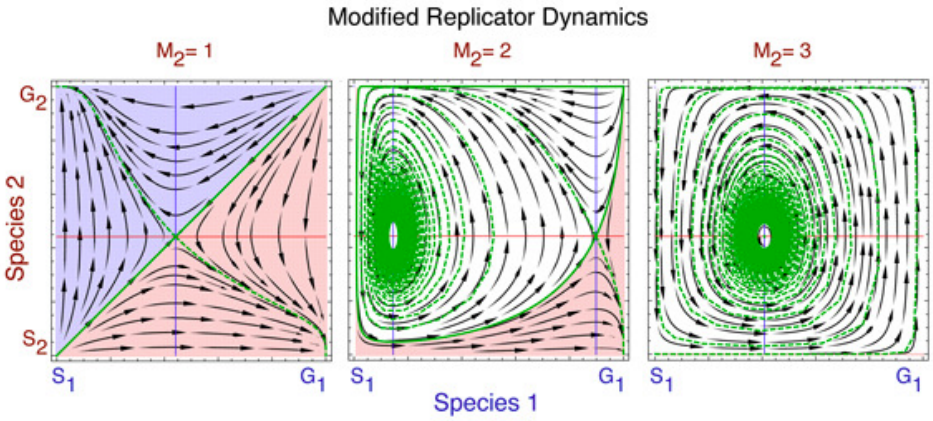

Figure 4: For the same parameters as in Fig. 3, the modified replicator dynamics given by Eqs. 8 leads to a different dynamics. For $M_1 = M_2 = 1$ (left), the dynamics is the same as for the standard replicator dynamics. For $M_2 = 2$ (middle) and $M_2 = 3$ (right), the formerly neutrally stable fixed point in the interior becomes a stable focus. Moreover, for $M_2 = 2$, the basin of attraction of (G_1, S_2) becomes much larger with the modified replicator dynamics. Again, we have added a background fitness of 1.0 to all the payoff entries so that all payoffs are positive.