Population dynamics of mutualisms

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Mutualistic relationships pose a conundrum for evolutionary theory. Species that exploit other species would do better than sustaining a long drawn out mutually costly relationship. However we do see mutualistic relationships amongst even the most unlikely partners .... Eco-evolutionary dynamics ...

mutualism │ evolutionary game theory │ multiple players

Introduction

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'* [**?**]. In 1873 the Belgian zoologist Pierre van Beneden termed this interaction as mutualism [1]. Mutualistic relationships, interspecific interactions that benefit both species, have been empirically studied for many years [2, 3, 4, 5, 6, 7, 8] and also a considerable body of theory has been put forth explaining the evolution and maintenance of such relationships [9, 10, 11, 12, 13, 14, 15, 16]. The example described by Aristotle and most other examples of mutualisms lend themselves to the idea of direct reciprocity [17] and have been thus extensively 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 [18].

For example, in the interaction between ants and aphids or butterfly larvae [19, 20] 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 [21, 18]. 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. Another well studied example is that of the plant-microbe mutualism where leguminous hosts prefer rhizobial symbionts that fix more nitrogen [7] or where plants provide more carbon resources to the fungal strains that are providing access to more nutrients [22]. However the interactions within the rhizobial symbionts community is usually ignored in the broader picture of the between species interactions however identifying and quantifying the intraspecific variation can be a daunting task [23]. Similarly for the interactions between the cleaner fish and their hosts [24, 25]. While the cohorts of cleaner fish together have been taken to determine the quality of a cleaning station, this can also drive variation of quality of cleaning within a cleaning station as per the interactions of individual cleaner fish amongst themselves. Furthermore, since by definition mutualistic relationships are between species, it is natural to imagine that the observed relationship may be seasonal and the interactions as not a continuous feature of the evolutionary dynamics of a single species. To assess the impact of this seasonality In this manuscript we focus on this kind of – possibly – many to many interactions between two mutualistic species.

In all, in this manuscript we look at the broader picture of mutualistic relationships and the ecology in which they are observed. We study the the cumulative effect os the within species and between species interactions and the importance of these relationships, seasonality and population dynamics taken together. 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 [26, 27, 28]. While initially attempting to avoid the question of how mutualisms evolve in the first place, we see that when studying the complex dynamics which are possible due to the rest of the evolutionary as well as ecological factors, we indirectly explain the evolution of interspecific mutualism as a byproduct of a complex eco-evolutionary process.

Model and Results

Usually when interspecies relationships such as mutualism (or antagonist relationships as in predator-prey) are considered, the within species interactions are ignored for the sake of convenience. Including intraspecies interactions can however result in qualitatively different and rich dynamics. In fact the coevolutionary dynamics between the two species is determined together by the inter as well as the intraspecific interactions.

Interspecies dynamics. Since we focus on mutualism the interspecies dynamics is given by the multiplayer version of the snowdrift game [13, 29, 30]. Each species consists of two types of individuals Generous G and Selfish S. The details of the game are included in the Appendix, but the gist is that if everyone is "Generous" and contributing in the generation of mutual benefits then one can get away with being a bit selfish. However both species cannot be completely "selfish" by definition of mutualism. Hence the pressure is on a specie in making the partner "Generous" while getting away itself by being "Selfish".

Intraspecies dynamics. We do not restrict ourselves to any particular interaction structure and thus can make use of the general multiplayer evolutionary games framework [31, 32]. The two types already described for the between species interactions are "Generous" and "Selfish". We assume the "Generous" individuals as "Cooperators" and the "Selfish" as "Defectors" for the within species interactions (see Appendix for otherwise). The cost benefit framework described in [33, 34]

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allows us to transition between four classic scenarios of evolutionary dynamics [35].
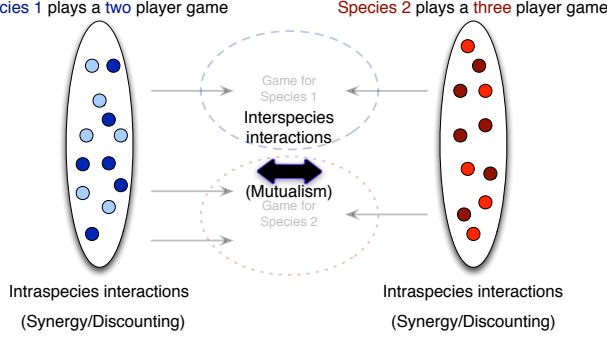
Combined dynamics.

Population dynamics.

Fig. 1. Explain figure

Discussion

Appendix

Appendix

Average payoffs from interactions between species

The two species are assumed to be in a mutualistic relationship. Following [13, 29, 30], we make use of the multi-player version of the snowdrift game to represent a co-existence scenario. Each species has two types of individuals "Generous" (G) and "Selfish" (S). Say the frequency of G individuals in species 1 is given by x and that in species 2 by y Each individual from each species takes part in a d player interspecies game where it interacts with $d-1$ individuals from the other species. Of the $d-1$ the if k of them are G while $d-1-k$ are S then the payoff accrued by the individuals is given by,

$$f_{G_1}^{inter}(y) = \sum_{k=0}^{d_1-1} \binom{d_1-1}{k} y^k (1-y)^{d_1-1-k} \Pi_{G_1}(k+1) \quad [1]$$

$$f_{S_1}^{inter}(y) = \sum_{k=0}^{d_1-1} \binom{d_1-1}{k} y^k (1-y)^{d_1-1-k} \Pi_{S_1}(k). \quad [2]$$

for the two types in species 1. Analogously the fitness for the two types in species 2 can be written down as $f_{G_2}^{inter}(x)$ and $f_{S_2}^{inter}(x)$ which depend on the frequencies of G in species 1. The payoff for a G thus includes itself $(k+1)$ while for a S individual only the the number of G matter (k). The payoffs themselves are defined as in [29],

$$\Pi_{S_1}(k) = \begin{cases} b & \text{if } k \geq M \\ 0 & \text{if } k < M \end{cases} \quad [3]$$

$$\Pi_{G_1}(k) = \begin{cases} b - \frac{c}{k} & \text{if } k \geq M \\ -\frac{c}{M} & \text{if } k < M \end{cases} \quad [4]$$

The selfish players get the benefit b if the number of generous individuals in the interacting group, 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 ($\frac{c}{k}$), but is in vain for $k < M$.

Average payoffs from interactions within species

Within a species we do not assume a certain kind of interaction structure. Instead we model the interaction matrix by making use of a general framework of costs and non-linear benefits [33, 34] which can potentially encompass all different types of social interaction structures qualitatively. A crucial **assumption** which we make here is that the "Generous" individuals from the between species interactions are the "Cooperative" ones in the within species interaction and the "Selfish" ones are the "Defectors". Hence for species 1 the frequency of cooperators is just x and the defectors is $1-x$, the same as the "Generous" and "Selfish". Again for simplicity we **assume** a d player game being played within species, the same as in between species. Thus the fitnesses of cooperators and defectors are defined as [34],

$$f_{G_1}^{intra}(x) = \sum_{k=0}^{d_1-1} \binom{d_1-1}{k} x^k (1-x)^{d_1-1-k} \Gamma_{G_1}(k+1) \quad [5]$$

$$f_{S_1}^{intra}(x) = \sum_{k=0}^{d_1-1} \binom{d_1-1}{k} x^k (1-x)^{d_1-1-k} \Gamma_{S_1}(k). \quad [6]$$

where the payoffs are given by,

$$\Gamma_{S_1}(k) = \frac{\tilde{b}}{d_1} \sum_{i=0}^{k-1} \omega^i \quad [7]$$

$$\Gamma_{G_1}(k) = \Gamma_{S_1}(k) - \tilde{c}. \quad [8]$$

Thus the defectors get a fraction of the benefit which is scaled by the factor ω, which determines if the benefits are linearly accumulating ($\omega = 1$) for increasing number of cooperators, synergistically enhanced ($\omega > 1$) or saturating ($\omega < 1$). Note that the costs and benefits in the within species game need not be (and naturally so) the same as in between species ($b \neq \tilde{b}$ and $c \neq \tilde{c}$).

Average payoffs and dynamics

The average payoffs are then just assumed to be a linear combination of the interspecies and intraspecies interactions where the parameter p determines the strength of each of the interactions such that,

$$f_{G_1}(x,y) = p f_{G_1}^{inter}(y) + (1-p) f_{G_1}^{intra}(x) \quad [9]$$

$$f_{S_1}(x,y) = p f_{S_1}^{inter}(y) + (1-p) f_{S_1}^{intra}(x) \quad [10]$$

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

$$\bar{f}_1(x,y) = x f_{G_1}(y) + (1-x) f_{S_1}(y) \quad [11]$$

$$\bar{f}_2(x,y) = y f_{G_2}(x) + (1-y) f_{S_2}(x). \quad [12]$$

The time evolution of the "Generous" types in all the species will give us the complete dynamics of the system. However since the two interaction species are by definition different organisms, they can have different rates of evolution. Thus if species 1 evolves at the rate r_x while species 2 at rate r_y then we have,

$$\dot{x} = r_x x \left(f_{G_1}(y) - \bar{f}_1(x,y) \right)$$
$$\dot{y} = r_y y \left(f_{G_2}(x) - \bar{f}_2(x,y) \right). \quad [13]$$
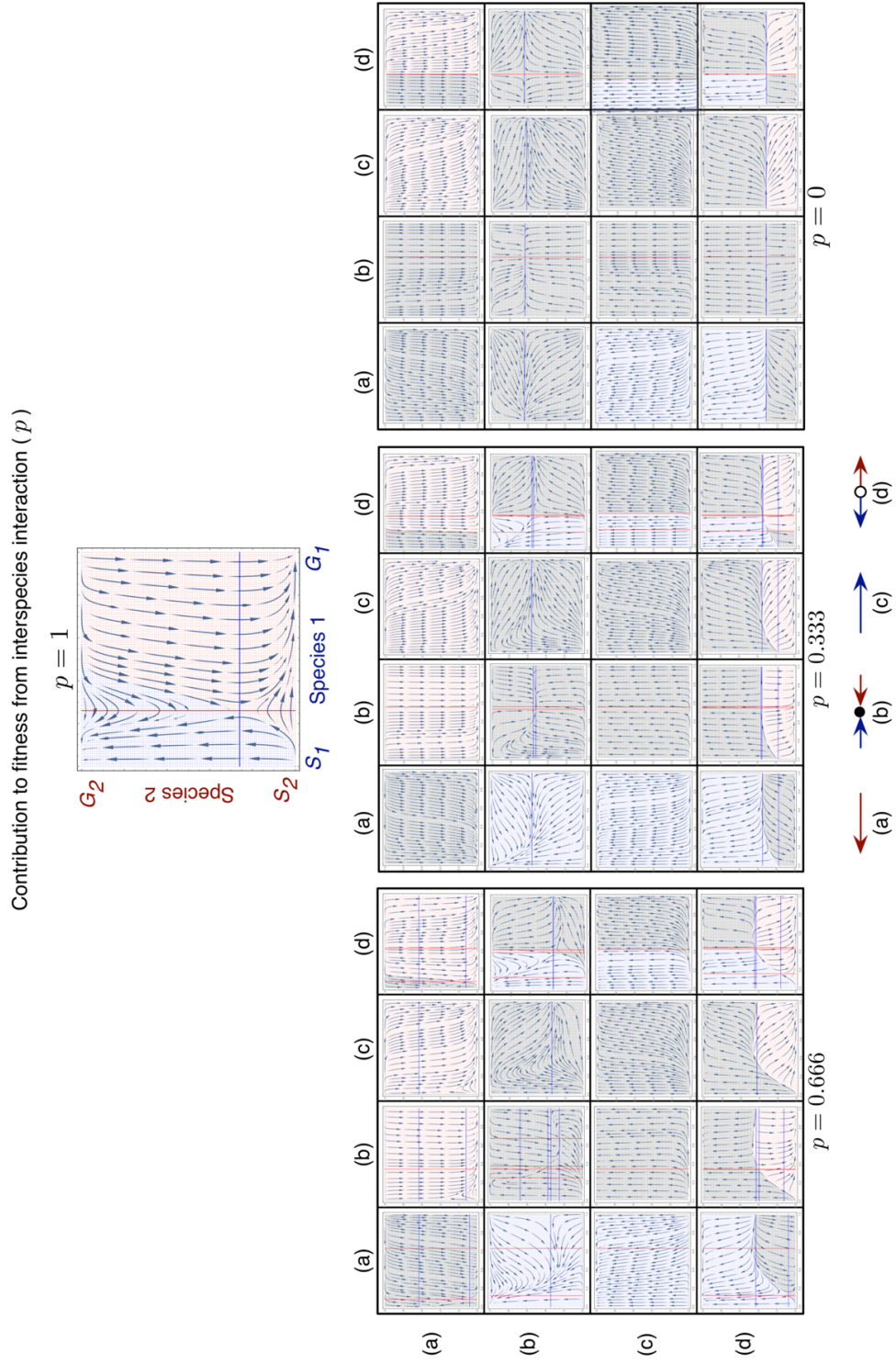
Fig. 2. $d_1 = d_2 = 5$, $b = 2$, $r_x = r_y/8$, $M_1 = M_2 = 1$ and $c = 1$ for the interspecies game. As for the intraspecies games (a), (b), (c) and (d) the exact same parameter values as in [34].

Asymmetries

This between and within species model is a powerful way of introducing a lot of variability into the dynamics,

$$d_1 \neq d_2 \qquad [\mathbf{14}]$$

$$d^{inter} \neq d^{intra} \qquad [\mathbf{15}]$$

$$M_1 \neq M_2 \qquad [\mathbf{16}]$$

$$b \neq \tilde{b} \qquad [\mathbf{17}]$$

$$c \neq \tilde{c} \qquad [\mathbf{18}]$$

$$r_x \neq r_y \qquad [\mathbf{19}]$$

$$\vdots \qquad [\mathbf{20}]$$

and various combinations of these. We should justify why we don't do this here and why we do vary the ones that we do.

Dynamics in asymmetric conditions

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 [**?**]. For this dynamics, the average fitness of each species appears as a denominator,

$$\dot{x} = r_x x \left(f_{G_1}(y) - \bar{f}_1(x,y) \right) / \bar{f}_1(x,y)$$

$$\dot{y} = r_y y \left(f_{G_2}(x) - \bar{f}_2(x,y) \right) / \bar{f}_2(x,y). \qquad [\mathbf{21}]$$

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.

For $d_1 = d_2 \geq 5$, the exact coordinates of the fixed point must be computed numerically [36, 37].

Population dynamics

For brevity we begin with the description of population dynamics in Species 1. The two types in Species 1, "Generous" and "Selfish" need not sum up to 1 i.e. the population may not always be at its carrying capacity. Hence if the empty space in the niche occupied by Species 1 is z_1, then we have $x_1 + x_2 + z_1 =$ where x_1 and x_2 are the densities of "Generous" and "Selfish" types. The population dynamics then is dictated by,

$$\dot{x_1} = r_x x_1 (z_1 f_{G_1} - e_1) \qquad [\mathbf{22}]$$

$$\dot{x_2} = r_x x_2 (z_1 f_{S_1} - e_1) \qquad [\mathbf{23}]$$

$$\dot{z_1} = -\dot{x_1} - \dot{x_2} \qquad [\mathbf{24}]$$

and for species 2

$$\dot{y_1} = r_y y_1 (z_2 f_{G_2} - e_2) \qquad [\mathbf{25}]$$

$$\dot{y_2} = r_y y_2 (z_2 f_{S_2} - e_2) \qquad [\mathbf{26}]$$

$$\dot{y_1} = -\dot{y_1} - \dot{y_2} \qquad [\mathbf{27}]$$

We have e_1 and e_2 as the death rates for the two species. Setting $e_1 = \frac{z_1(x_1 f_{x_1} + x_2 f_{x_2})}{x_1 + x_2}$ and $e_2 = \frac{z_2(y_1 f_{G_2} + y_2 f_{S_2})}{y_1 + y_2}$ we recover the two species replicator dynamics as in Eqs. 21. The fitnesses however need to be reevaluated in this setup. For example in Species 1 the fitness for type G_1 is,

$$f_{G_1}^{inter} = \sum_{S=2}^{d_1} \binom{d_1 - 1}{S - 1} z_2^{d_1 - S} (1 - z_2)^{S-1} P_G^{inter}(S, y_1, y_2, z_2) \qquad [\mathbf{28}]$$

$$f_{G_1}^{intra} = \sum_{S=2}^{d_1} \binom{d_1 - 1}{S - 1} z_1^{d_1 - S} (1 - z_1)^{S-1} P_G^{intra}(S, x_1, x_2, z_1) \qquad [\mathbf{29}]$$

$$f_{G_1} = f_{G_1}^{inter} + f_{G_1}^{intra} \qquad [\mathbf{30}]$$

and similarly for type S_1 where the payoff functions are defined as,

$$P_G^{inter}(S, p, q, r) = \sum_{k=0}^{S-1} V(S, p, q, r) \Pi_{G_1}(k+1) \qquad [\mathbf{31}]$$

$$P_G^{intra}(S, p, q, r) = \sum_{k=0}^{S-1} V(S, p, q, r) \Gamma_{G_1}(k+1) \qquad [\mathbf{32}]$$

$$P_S^{inter}(S, p, q, r) = \sum_{k=0}^{S-1} V(S, p, q, r) \Pi_{S_1}(k) \qquad [\mathbf{33}]$$

$$P_S^{intra}(S, p, q, r) = \sum_{k=0}^{S-1} V(S, p, q, r) \Gamma_{S_1}(k) \qquad [\mathbf{34}]$$

where $V(S, p, q, r) = \binom{S-1}{k} \left(\frac{p}{1-r} \right)^k \left(\frac{q}{1-r} \right)^{S-1-k}$ is the probability of having a k "Generous"(Cooperator) individuals and $S - 1 - k$ "Selfish"(Defector) individuals in the inter(intra) species game. and the actual payoffs are calculated as per Eqs. 4 and 8.

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