

# Eco-evolutionary dynamics of mutualisms

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## Abstract

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 ...

Keywords: mutualism, evolutionary game theory, multiple players

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24 

# 1 Introduction

25 As with many concepts, we can trace back the study of mutualism to Aristotle (Gotthelf),  
26 1991). Formally the Belgian zoologist Pierre van Beneden coined the term mutualism in  
27 1873 (Bronstein, 2003). Mutualistic relationships, interspecific interactions that benefit both  
28 species, have been empirically studied for many years (Boucher, 1985; Hinton, 1951; Wilson,  
29 1983; Bronstein, 1994; Pierce et al., 2002; Kiers et al., 2003; Bshary and Bronstein, 2004) and  
30 a considerable body of theory has been put forth explaining the evolution and maintenance  
31 of such relationships (Poulin and Vickery, 1995; Doebeli and Knowlton, 1998; Noë, 2001;  
32 Johnstone and Bshary, 2002; Bergstrom and Lachmann, 2003; Hoeksema and Kummel, 2003;  
33 Akçay and Roughgarden, 2007; Bshary et al., 2008). Most examples of mutualisms lend  
34 themselves to the idea of direct reciprocity (Trivers, 1971) and have thus been extensively  
35 studied using evolutionary game theory. The interactions in these models are usually dyadic:  
36 the fundamental interaction is between two individuals, one from each species, and the sum  
37 of many such interactions determines the evolutionary dynamics. However, in many cases  
38 interactions between species cannot be reduced to such dyadic encounters (Stadler and Dixon,  
39 2008).

40 For example, in the interaction between ants and aphids or butterfly larvae (Pierce et al.,  
41 1987; Hölldobler and Wilson, 1990) many ants tend to each of the soft bodied creatures, pro-  
42 viding them with shelter and protection from predation and parasites, in exchange for honey-  
43 dew, a rich source of food for the ants (Hill and Pierce, 1989; Stadler and Dixon, 2008). This  
44 is a one-to-many interaction from the perspective of the larva. Another well studied exam-  
45 ple of a one-to-many interaction is that of the plant-microbe mutualism wherein leguminous  
46 hosts prefer rhizobial symbionts that fix more nitrogen (Kiers et al., 2003), or where plants  
47 provide more carbon resources to fungal strains that are providing better access to nutrients  
48 (Kiers et al., 2011). Moving from a plant host to an animal host, a well studied example is  
49 that of the mutualistic relationship between the bioluminescent bacteria *Vibrio fischeri* and  
50 *Euprymna scolopes*, the bobtail squid (McFall-Ngai, 2014). Numerous bacteria are hosted in  
51 the crypts of the squid's light organ, where they produce light despite it being costly. The  
52 bacteria mature and develop within the squid, however those that fail to produce biolumines-  
53 cence are evicted. While the variation in the phenotypes of the interacting partners has been  
54 acknowledged, the usual analysis focuses on the interaction between the two species without  
55 addressing this additional complexity.

56 Identifying and quantifying the intraspecific variation can be a daunting task (Behm and

57 Kiers, 2014). Intraspecific interactions are usually studied in isolation and separate from the  
58 interspecies relationships. (need to mention this example first) While the cohorts of cleaner  
59 fish together have been taken to determine the quality of a cleaning station (Bshary and  
60 Schäffer, 2002; Bshary and Noë, 2003), this can also drive variation of quality of cleaning  
61 within a cleaning station via interactions of individual cleaner fish amongst themselves. In  
62 this manuscript we look at the broader picture of how the evolutionary dynamics are shaped  
63 when both the inter as well as intra species dynamics are taken together. We find that including  
64 the full range of interactions provides us with a set of rich and intricate dynamics which are  
65 not possible when one of these dimensions is ignored.

66 Mutualistic relationships are between species by definition, and timing may be crucial for  
67 their maintenance. (this next sentence is awkward but I haven't fixed it) Hence it is natural to  
68 imagine that the observed relationship may be seasonal and the interactions as not a continuous  
69 feature of the evolutionary dynamics of a single species. In a changing ecology changes in  
70 global climate might affect the timing of the point in a season when flowers mature and when  
71 their dispersers do, quite easily disrupting delicately balanced mutualistic interactions. Unless  
72 both of the interacting species can respond in a similar fashion such a mutualism will break  
73 down (Warren and Bradford, 2014).

74 We tackle this seasonality by varying the duration of the impact of intraspecies and inter-  
75 species dynamics. (do we? not obvious where the duration enters - we have  $p$  but that's not a  
76 duration.) (Yes I am working on it right now! :) Furthermore to complete the ecological pic-  
77 ture we study not just the evolutionary but the population dynamics of the mutualists. Allow-  
78 ing for population dynamics informs us as to the population densities we might expect to find  
79 among mutualistic interactions in nature. (??) (better?) We demonstrate the crucial nature of  
80 the feedback between population and evolutionary dynamics which can maintain mutualisms  
81 preventing either or both species from going extinct. We make use of evolutionary game the-  
82 ory to analyze how benefits are shared between the two mutualistic species (Weibull, 1995;  
83 Hofbauer, 1996; Hofbauer and Sigmund, 1998). Beginning with the previously studied inter-  
84 species dynamics as the foundational framework (Gokhale and Traulsen, 2012) we increase  
85 the complexity of the system by including intraspecies dynamics, population dynamics and  
86 seasonality. The rich dynamics observed provides us with novel insights about the immense  
87 asymmetries in mutualisms and the fragility of such delicately balanced interactions.

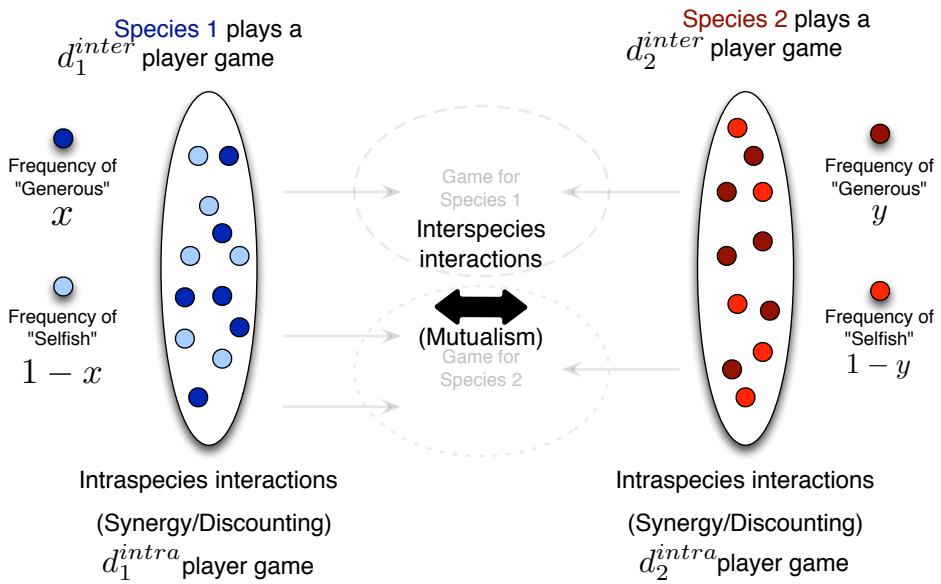


Figure 1: **Evolutionary dynamics with combined inter-intra species dynamics.** We assume the interactions between species to be mutualistic described by the snowdrift game (Bergstrom and Lachmann, 2003; Souza et al., 2009; Gokhale and Traulsen, 2012). Species 1 plays a  $d_1^{inter}$  player game with Species 2 while Species 2 plays a  $d_2^{inter}$  player game. Each species has two types of players “Generous” and “Selfish” who besides interacting with the members of other species, also take part in intra species dynamics. For the intra species interactions we assume a general framework of synergy and discounting which can recover the *classical* outcomes of evolutionary dynamics(Eshel and Motro, 1988; Hauert et al., 2006b; Nowak, 2006) (Would it be good to include something like “proportion of generous:  $x$ ” on the left/blue side of the figure at the bottom, and “proportion of generous:  $y$ ” on the right?) (Done)

88 **2 Model and Results**

89 **2.1 Interaction dynamics**

90 **2.1.1 Interspecies**

91 Since we focus on mutualism the interspecies dynamics is given by the multiplayer version  
92 of the snowdrift game (Bergstrom and Lachmann, 2003; Souza et al., 2009; Gokhale and  
93 Traulsen, 2012) (also known as hawk-dove, or chicken). In this, a common benefit is possible  
94 but there is a cost to contributing and species do not need to contribute equally. However the  
95 individuals in each species could get away with contributing a bit less than other individuals.  
96 (Awkward wording I think, but I haven't fixed yet.) Hence for example if producing brighter  
97 light comes at a premium for the *Vibrio* in the squid then the dimmer *Vibrio* would be better  
98 off (Note that not producing any light is not an option as it results in eviction). We assume that  
99 each species consists of two types of individuals "Generous"  $G$  and "Selfish"  $S$ . If enough  
100 individuals are "Generous" and contributing to the generation of mutual benefits then other  
101 individuals can get away with being selfish (not contributing). But all individuals in the game  
102 lose out if not enough are generous. Hence both species cannot be completely "selfish", as  
103 per the definition of mutualism. This interaction framework corresponds to that of a multi  
104 player version of a snowdrift game and is discussed in detail in the Supplementary Material  
105 (SI). Hence the pressure is on a species to make the partner "Generous" while getting away  
106 itself by being "Selfish". The fitness of each of the types within a species thus depends on the  
107 composition of the other species. Denoting the frequency of the "Generous" types in Species  
108 1 ( $G_1$ ) as  $x$ , and that in Species 2 ( $G_2$ ) as  $y$ , the fitness of  $G_1$  is given by  $f_{G_1}^{inter}(y)$  and that of  
109  $G_2$  as  $f_{G_2}^{inter}(x)$ .

110 **2.1.2 Intraspecies**

111 For intraspecies dynamics we do not restrict ourselves to any particular interaction structure  
112 and thus can make use of the general multiplayer evolutionary games framework (Gokhale  
113 and Traulsen, 2010, 2014). Moving from the interspecies dynamics, the two types already  
114 described are "Generous" and "Selfish". Thus we already have each species containing two  
115 different types of individuals. It is possible that a different categorisation exists within a  
116 species however for the sake of simplicity we study the dynamics between "Generous" and  
117 "Selfish" types within a species. However the individuals which are "Generous" for the inter-  
118 species interaction may/may not be more giving or in a sense "Cooperators" for intraspecies  
119 dynamics. Thus we need a flexible cost-benefit framework to model the intraspecies dynamics  
120 which can be easily tuned to the particular situation. The cost benefit framework described

in (Eshel and Motro, 1988; Hauert et al., 2006b) allows us to transition between four classic scenarios of evolutionary dynamics (Nowak and Sigmund, 2004). For example in our case we can have a dominance of the “Generous” type or the “Selfish” type or both the types can invade from rare resulting in a co-existence or bistability if both pure strategies are mutually non-invasive. For the intra species interactions the fitness of a  $G_1$  is then given by  $f_{G_1}^{intra}(x)$  and that of  $G_2$  is given by  $f_{G_2}^{intra}(y)$  and similarly for the “Selfish” types.

## 2.2 Combined dynamics

Putting together intra and interspecific dynamics provides a complete picture of the possible interactions occurring. While we are interested in mutualism at the level of the interspecies interactions there are four possible interactions within each species (Nowak and Sigmund, 2004; Hauert et al., 2006b) (dominance of either type, coexistence or bistability)((briefly spell them out here, I think))(Done). Since the within species interactions for the two different species do not need to be the same, there are in all sixteen different possible combinations. Assuming additivity in the fitnesses of inter and intraspecies fitnesses, the combined fitness of each of the two types in the two species are given by,

$$\begin{aligned} f_{G_1}(x, y) &= pf_{G_1}^{inter}(y) + (1 - p)f_{G_1}^{intra}(x) \\ f_{S_1}(x, y) &= pf_{S_1}^{inter}(y) + (1 - p)f_{S_1}^{intra}(x) \\ f_{G_2}(x, y) &= pf_{G_2}^{inter}(x) + (1 - p)f_{G_2}^{intra}(y) \\ f_{S_2}(x, y) &= pf_{S_2}^{inter}(x) + (1 - p)f_{S_2}^{intra}(y) \end{aligned} \quad (1)$$

The parameter  $p$  tunes the impact of each of the interactions on the actual fitness that eventually drives the evolutionary dynamics. For  $p = 1$  we recover the well studied case of the Red King dynamics (Gokhale and Traulsen, 2012) of the snowdrift game, while for  $p = 0$  the dynamics of the two species are essentially decoupled and can be individually studied by the synergy/discounting framework of nonlinear social dilemmas (Hauert et al., 2006b). Our interest here is in the continuum and the intermediate values of  $p$ . However that means we need to track the qualitative dynamics of sixteen possible intraspecies dynamics as  $p$  changes gradually from close to 0 to close to 1 (SI). The time evolution of the “Generous” types in both species is then given by,

$$\begin{aligned} \dot{x} &= r_x x \left( f_{G_1}(x, y) - \bar{f}_1(x, y) \right) \\ \dot{y} &= r_y y \left( f_{G_2}(x, y) - \bar{f}_2(x, y) \right). \end{aligned} \quad (2)$$

145 This approach provides us with a powerful method to incorporate a multitude of realistic  
146 concepts in the analysis. For example the number of players involved in a game, which has  
147 been shown to be a crucial factor in determining the evolutionary dynamics could be different  
148 for each interactions, inter and intra species interactions for Species 1 ( $d_1^{inter}$ ,  $d_1^{intra}$ ) and simi-  
149 larly for Species 2 ( $d_2^{inter}$ ,  $d_2^{intra}$ ). The interspecies interactions are proxied by the multiplayer  
150 Snowdrift game which can incorporate threshold effects. For example a certain number of  
151 “Generous” cleaner fish may be required to clean the host or a certain number of “Generous”  
152 ants required to protect larva from predators. We can have  $M_1$  and  $M_2$  as the thresholds in  
153 the two species. Since the interaction matrices for the inter and intra species dynamics are  
154 completely different in principle we can have different costs and benefits for the four games  
155 (Two snowdrift games from the perspective of each species and the intragames within each  
156 species).

157 We can have a diverse and rich set of dynamics possible which brings into question the  
158 study of coevolution based on only interspecies interactions. For the full spectrum of possible  
159 dynamics see Figure A.1. Even if we make a large number of assumptions and even if the  
160 intraspecies dynamics accounts for only 33% ( $1 - p$ ) of the cumulative fitness, we can see  
161 drastically different qualitative dynamics which is capable of explaining the persistence of  
162 exploiters.

## 163 2.3 Population dynamics

164 Until now we have considered that each species consists of two types of individuals and they  
165 make up the population of that species. However populations sizes change over time. As-  
166 suming that ecological changes are fast enough that they can be averaged out, we can usually  
167 ignore their effect on the evolutionary dynamics. It is now possible to show that evolution  
168 can happen at fast timescales, comparable to those of the ecological dynamics (add citations  
169 with examples). Hence we need to tackle not just evolutionary but eco-evolutionary dynamics  
170 together.

To include population dynamics in the previously considered scenario, we reinterpret  $x_1$  now as the fraction of “Generous” types and  $x_2$  as the fraction of “Selfish” types in Species 1. Also now we have  $z_1 = 1 - x_1 - x_2$  as the empty spaces in the niche occupied by Species 1. Similarly we have  $y_1$ ,  $y_2$  and  $z_2$  (Fig. 3). This approach has previously been explored in terms of social dilemmas in (Hauert et al., 2006a). We adapt and modify it for the two species and hence now the dynamics of this complete system is determined by the following set of

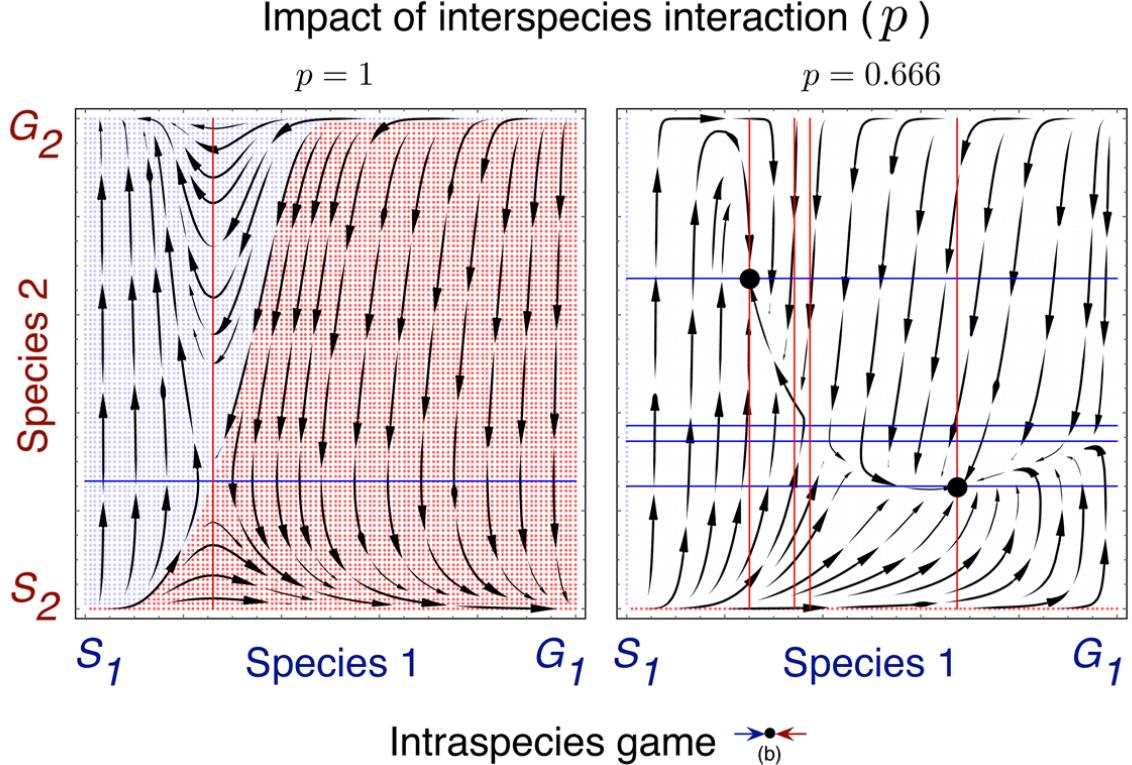
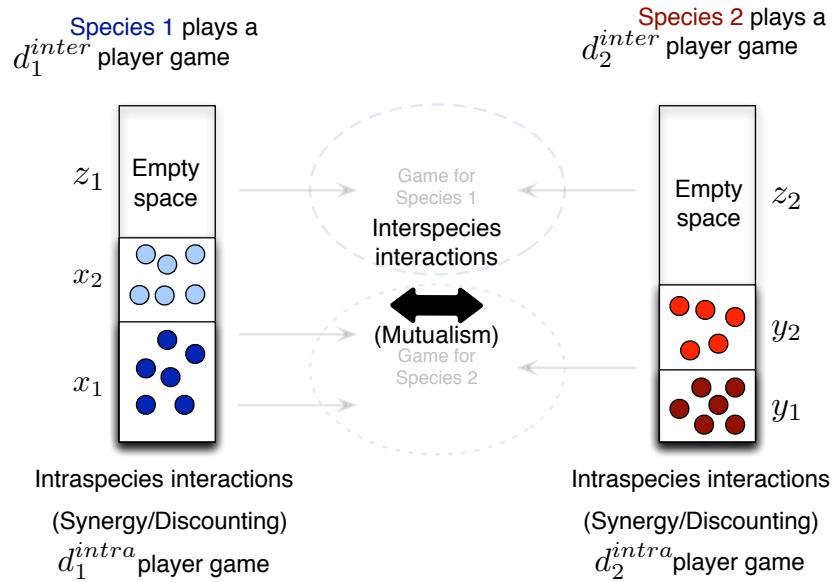


Figure 2: **Change in evolutionary dynamics due to inclusion of intraspecies dynamics.** When the fitness of the “Generous” and “Selfish” types in both the species is solely determined by the interactions which occur between species (in this case mutualism,  $p = 1$ ) then we recover the dynamics as studied previously in (Gokhale and Traulsen, 2012). The colours represent the initial states which result in an outcome favourable for Species 1 (blue leading to  $(S_1, G_2)$ ) and Species 2 (red, leading to  $(G_1, S_2)$ ). This can result in the red King effect and other possible complexities as discussed recently in (Gao et al., 2015). However when we start including intraspecies dynamics the picture can be very different. Even when the impact of intraspecies dynamics is only a  $1/3$  on the total fitness of the “Generous” and “Selfish” types we see a very qualitatively different picture. Two fixed points are observed where both the “Generous” and “Selfish” types can co-exist in both the species. All initial states in the interior lead to either one of these fixed points (hence the lack of colours). However it is still possible to characterize the “successful” species as one of the equilibrium is favoured by one species than the other. The horizontal isolines are for Species 1 while the vertical ones are for Species 2. The analysis was done for a 5 player game  $d_1^{inter} = d_2^{inter} = d_1^{intra} = d_2^{intra} = 5$ ,  $b = 2$ ,  $c = 1$  and  $r_x = r_y/8$  for the interspecies mutualism game while additionally  $\tilde{b}_1 = \tilde{b}_2 = 10$  and  $\tilde{c}_1 = \tilde{c}_2 = 1$  and  $\omega_1 = \omega_2 = 3/4$  for the two intraspecies games within each species. Note that even with symmetric games within each species we can a qualitatively drastic difference when compared to the dynamics excluding intraspecies interactions. For different intraspecies interactions within each species and for varying  $p$  see SI.



**Figure 3: Population and evolutionary dynamics with combined inter-intra species dynamics.**  
 As with the interactions described in 1 the two species consist of two types of individuals “Generous” and “Selfish”. Since the two species can in principle occupy different environmental niches, they can have non-overlapping population carrying capacities. The normalised carrying capacity in both species is 1 and we have  $x_1 + x_2 + z_1 = 1$  (for Species 1) where  $x_1$  and  $x_2$  are the densities of the “Generous” and “Selfish” types respectively (similarly with  $y$  and  $z_2$  in Species 2). The parameter  $z_1$  represents the remaining space into which the population can still expand into. For  $z_1 = 0$  the Species 1 is at its carrying capacity while for  $z_1 = 0$  it is extinct.

differential equations,

$$\begin{aligned}\dot{x}_1 &= r_x x_1 (z_1 f_{G_1} - e_1) \\ \dot{x}_2 &= r_x x_2 (z_1 f_{S_1} - e_1) \\ \dot{z}_1 &= -\dot{x}_1 - \dot{x}_2\end{aligned}\tag{3}$$

and for species 2

$$\begin{aligned}\dot{y}_1 &= r_y y_1 (z_2 f_{G_2} - e_2) \\ \dot{y}_2 &= r_y y_2 (z_2 f_{S_2} - e_2) \\ \dot{z}_2 &= -\dot{y}_1 - \dot{y}_2\end{aligned}\tag{4}$$

where we have introduced  $e_1$  and  $e_2$  as the death rates of 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. 2 (For the sake of brevity we avoid showing the fitnesses in their the functional forms). In this setup however the fitnesses need to be re-evaluated as now we need to account for the presence of empty spaces (See SI). The dynamics is simplified by focusing on the proportion of “Generous” types in both the species thus  $g_1 = x_1/(1 - z_1)$  and  $g_2 = y_1/(1 - z_2)$  whose time evolution is given by,

$$\begin{aligned}\dot{g}_1 &= r_x z_1 g_1 (1 - g_1) (f_{G_1} - f_{S_1}) \\ \dot{z}_1 &= e_1 (1 - z_1) - r_x z_1 (1 - z_1) (g_1 f_{G_1} - (1 - g_1) f_{S_1})\end{aligned}\tag{5}$$

and

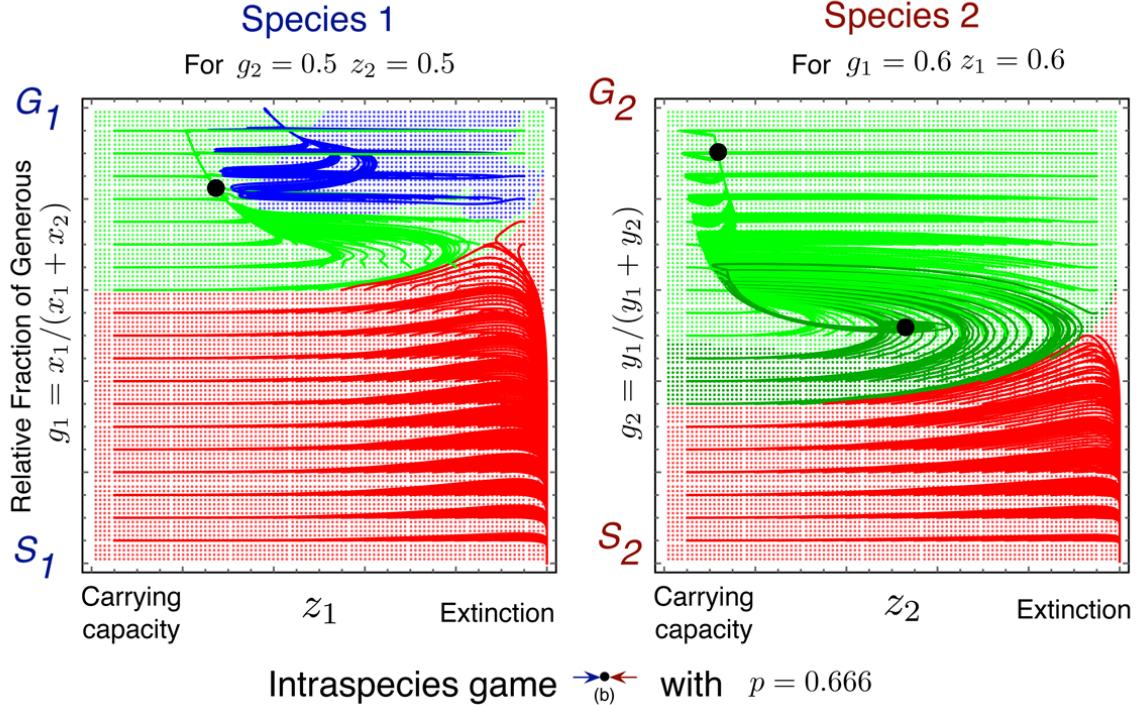
$$\begin{aligned}\dot{g}_2 &= r_y z_2 g_2 (1 - g_2) (f_{G_2} - f_{S_2}) \\ \dot{z}_2 &= e_2 (1 - z_2) - r_y z_2 (1 - z_2) (g_2 f_{G_2} - (1 - g_2) f_{S_2})\end{aligned}\tag{6}$$

171 where everywhere we have  $x_1 = g_1(1 - z_1)$  (with  $x_2 = (1 - g_1)(1 - z_1)$ ) and  $y_1 = g_2(1 - z_2)$   
172 (with  $y_2 = (1 - g_2)(1 - z_2)$ ) in the fitnesses as well.

173 Such a two species multi-type interaction system is a complicated as well as a realistic  
174 depiction of most of the mutualisms observed in nature. However given this complexity, we  
175 need to look at the dynamics within the two Species simultaneously.

176 We take the most stable situation observed in the dynamics when population dynamics is  
177 absent (Fig. 2) which shows two internal stable equilibria and add population dynamics to it.  
178 The results are summarized in Figure 4 where we plot the evolutionary parameter (fraction of  
179 “Generous” in each species) against the ecological parameter, the population density (or rather  
180 in this case the empty spaces) .

## Evolutionary and population dynamics



**Figure 4: Dynamics of evolutionary strategies and population density for an intraspecies coexistence game with interspecies mutualism.** With exactly the same parameters as that of Figure 2 with symmetric death rates  $e_1 = e_2 = 0.05$  we show two different numerically evaluated examples. Left Panel: shows the outcomes in Species 1 when starting from 0.5 fraction of “Generous” individuals in Species 2 at half carrying capacity  $z_2 = 0.5$ . While most of the initial conditions lead to an extinction of Species 1 (red), there exists a fixed point which can be reached when most of Species 1 is “Generous” and close to carrying capacity (green). For the same or higher fraction of  $G_1$  but lower population density, Species 1 can end up being completely “Generous” (blue). Right Panel: shows the outcomes in Species 2 when starting from 0.6 fraction of “Generous” individuals in Species 1 with empty spaces proportion of  $z_1 = 0.6$ . When Species 2 is mostly made up of “Selfish” types then it leads to species extinction (red), For intermediate levels of “Generous” individuals there exists an internal equilibrium (dark green). However another stable equilibrium exists as well as even higher densities of “Generous” types closer to full carrying capacity (green). Equilibrium selection is thus possible for Species 2 in this case where it is preferable to have an intermediate number of “Selfish” types.

181 **2.4 Seasonality**

182 Many mutualisms are observed only during certain periods of a year. Such seasonal or episodic  
183 mutualism run a high risk of phenological partner mismatch as a result of climate change  
184 (Rafferty et al., 2015). While tropical species, such as the various varieties of fig (*Ficus*)  
185 can flower all year round, their mutualistic relationships (with wasps) run a lower risk. For  
186 example in the ant-aphid mutualism, the number of attending ants was seen to increase till  
187 June and declined after late July and the aphid colonies went rapidly (within a month) extinct  
188 in the absence of attending ants (Yao et al., 2000; Yao and Akimoto, 2009). For the evolution  
189 of a species this means that the effect of interspecific interaction changes over time.

190 To analyse such episodic mutualistic events, instead of a static variable  $p$  measuring the  
191 impact of interspecific interaction on fitness we make use of a time-dependent function  $p(t) =$   
192  $(1 + \sin(at))/2$ . (Discuss 5)

193 **3 Discussion**

194 Usually when interspecies relationships such as mutualism (or antagonist relationships as in  
195 predator-prey) are considered, the within species interactions are ignored for the sake of con-  
196 venience. Obviously this is an assumption which is very useful when distilling the interactions  
197 at different community scales. However when such interactions are interdependent then the  
198 connectivity between the different levels cannot be ignored Schluter and Foster (2012). As  
199 an example we focus on mutualism. A fragile balance of parameters maintains mutualism.  
200 Including realistic phenomena such as intraspecies interactions, population dynamics and sea-  
201 sonality we show that maintenance of mutualism is possible. However often it can come at  
202 a cost of maintaining a significant level of exploiters as well. In fact the coevolutionary dy-  
203 namics between the two species is determined together by the inter as well as the intraspecific  
204 interactions.

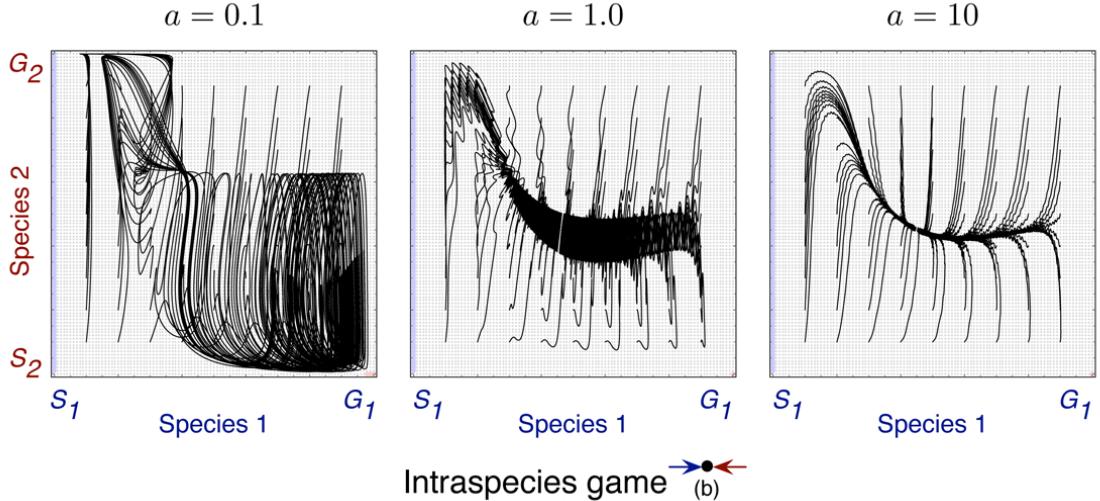
205 In our study we have mutualistic interactions between two species. This can be represented  
206 by a bimatrix game. The components of each of the bimatrix game need not be correlated as  
207 long as they satisfy the inequalities leading to a Snowdrift games.

208 **Acknowledgements.** Thanks for all the fish.

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211 *of the Royal Society B*, 274:25–32, 2007.

**Impact of interspecies interaction,**  $p(t) = \frac{1 + \sin(at)}{2}$



**Figure 5: Seasonal changes in the interspecies interactions affecting the evolutionary dynamics within species.** We model the impact of the interspecies interaction on the fitness of the different types as in Eqs.?? however instead of a static value for  $p$  we introduce seasonality via a simple sine function as  $p(t) = (1+\sin(at))/2$ .  $a$  denotes how the evolutionary time scale relates to the mutualism timescale. A large  $a$  denotes multiple bouts of mutualism affecting fitness for a given evolutionary time step while a small  $a$  denotes fewer of such bouts within the same evolutionary time step. While for comparable  $a$  larger  $a$  the dynamics under oscillations can be captured by the average dynamics (at  $p = 0.5$ ) however for small  $a$  we see qualitatively different outcome. Furthermore the phase in which the oscillating function begins is more important for smaller and smaller  $a$  especially if the stability of the internal (or edge) fixed points changes as  $p$  changes (see Fig.A.1 panel (b) x (b) as  $p$  changes).

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## 317 A Interspecies Evolutionary Dynamics

318 Traditional coevolutionary models consider interspecific dependence only (Roughgarden, 1976;  
319 Roughgarden et al., 1983). Since in our case each the interactions between the Species are mu-  
320 tualistic and each Species consists of two types of individuals “Generous” and “Selfish”, the  
321 following Snowdrift game is an appropriate representation of the interactions.

### 322 The snowdrift game

#### 323 Two player setting

324 Two drivers are stuck in a snowdrift. They must shovel away the snow (paying the cost  $c$ )  
325 to reach home (benefit  $b$ ) but there are three possible outcomes to this scenario. One of the  
326 driver shovels while the other stays warm in the care ( $b - c$  and  $b$ ), both the drivers share the

327 workload and shovel away the snow ( $b - c/2$  and  $b - c/2$ ) or none of them gets out of the car  
 328 and they both remain stuck (0 and 0).

Putting this game in perspective of the two species (i.e. the two drivers represent the two different species) we get the matrix,

		Species 1 payoff:				Species 2 payoff:	
		G <sub>2</sub>	S <sub>2</sub>			G <sub>1</sub>	S <sub>1</sub>
Species 1	G <sub>1</sub>	b - c/2	b - c	Species 2	G <sub>2</sub>	b - c/2	b - c
	S <sub>1</sub>	b	0		S <sub>2</sub>	b	0

329 where strategy  $G$  stands for being “*Generous*” and shoveling the snow while  $S$  stands for  
 330 being “*Selfish*” and just sitting in the car. For  $b = 2$  and  $c = 1$  we recover the matrix used in  
 331 (Bergstrom and Lachmann, 2003).

332 For the snowdrift game in a single population for which the pairings are formed at ran-  
 333 dom, there exists a single, stable internal equilibrium. Hence the population will evolve to a  
 334 polymorphism which is a combination of “*Generous*” and “*Selfish*” individuals. But in a two  
 335 species system (pairs still random, but one from each species), this stable equilibrium turns  
 336 into a saddle point: a small deviation from this fixed point leads the system to one of the stable  
 337 fixed point where one of the species is completely “*Generous*” and the other one is completely  
 338 “*Selfish*”.

### 339 Multiplayer setting

340 Following Souza et al. (Souza et al., 2009), a multiplayer snowdrift game can be described by  
 341 the payoff entries

$$\Pi_{G_1}(k) = \begin{cases} b - \frac{c}{k} & \text{if } k \geq M \\ -\frac{c}{M} & \text{if } k < M \end{cases} \quad (\text{A.1})$$

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

All 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 is in vain  
 for  $k < M$ . (I'm confused here: why is  $\frac{c}{k}$  lost if above the threshold but  $\frac{c}{M}$  lost if not?) For  
 two player games we had  $k = 1$  but multiplayer games provide the possibility of exploring this

threshold aspect of collective action games. From these payoff entries we need to calculate the average fitnesses. For simplicity we just illustrate the fitnesses of the strategies in Species 1. For a  $d_1^{inter}$  player game for Species 1 we need to pick  $d_1^{inter} - 1$  other individuals from Species 2. Assuming random sampling the composition of the formed groups is given by a binomial distribution. Summing over all possible compositions of groups we arrive at the average fitnesses of the two strategies in species 1,

$$f_{G_1}^{inter}(y) = \sum_{k=0}^{d_1^{inter}-1} \binom{d_1^{inter}-1}{k} y^k (1-y)^{d_1^{inter}-1-k} \Pi_{G_1}(k+1) \quad (\text{A.3})$$

$$f_{S_1}^{inter}(y) = \sum_{k=0}^{d_1^{inter}-1} \binom{d_1^{inter}-1}{k} y^k (1-y)^{d_1^{inter}-1-k} \Pi_{S_1}(k). \quad (\text{A.4})$$

## 342 B Intraspecies Evolutionary Dynamics

343 For elucidating the intraspecies dynamics we will focus on Species 1 as the analysis is anal-  
 344 ogous for Species 2. Within species dynamics can in principle be completely different from  
 345 the between species interactions. We can have a multistrategy multiplayer game within a  
 346 Species but to keep things simple we assume a two strategy multiplayer game. The partition-  
 347 ing of the individuals into two strategies follows the same partitioning as in the inter species  
 348 interactions as of “Generous” and “Selfish”. However we can relabel them as “Cooperators”  
 349 and “Defector” for the sake of the interactions structure which we will be making use of. Note  
 350 that the “Generous” in the interspecies interactions need not always be the “Cooperators” for  
 351 the within species interaction but again for the sake of simplicity we will assume it to be so.  
 352 (Ah! now I get it. I guess we need to highlight this earlier on, as it's a strong condition: I  
 353 found myself wondering whether Generous in inter  $\leftrightarrow$  Cooperator in intra, or not...)

## 354 Synergy/Discounting Framework

We model the within species interactions by making use of a general framework of costs and non-linear benefits (Eshel and Motro, 1988; Hauert et al., 2006b) which can potentially encompass all different types of (traditionally studied) social interaction structures qualitatively (Nowak, 2006) (Perhaps good to list the 4 types). For Species 1 the frequency of cooperators is just  $x$  and the defectors is  $1 - x$ , the same as the “Generous” and “Selfish”. (Q: is this because they are the very same players? ie. are we assuming a Generous player in the inter is a Cooperative one in the intra?) The “Cooperators” and “Defectors” in Species 1 play a  $d_1^{intra}$  player game. Thus the fitnesses of cooperators and defectors are defined as (Hauert et al.,

2006b),

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

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

where the payoffs are given by,

$$\Gamma_{S_1}(k) = \frac{\tilde{b}}{d_1^{intra}} \sum_{i=0}^{k-1} \omega^i \quad (\text{A.7})$$

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

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

## 360 C Combined Evolutionary 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,

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

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

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

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

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

The time evolution of the “Generous” types in both 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,

$$\begin{aligned} \dot{x} &= r_x x (\bar{f}_1(x, y) - \bar{f}_1(x, y)) \\ \dot{y} &= r_y y (\bar{f}_2(x, y) - \bar{f}_2(x, y)). \end{aligned} \quad (\text{A.13})$$

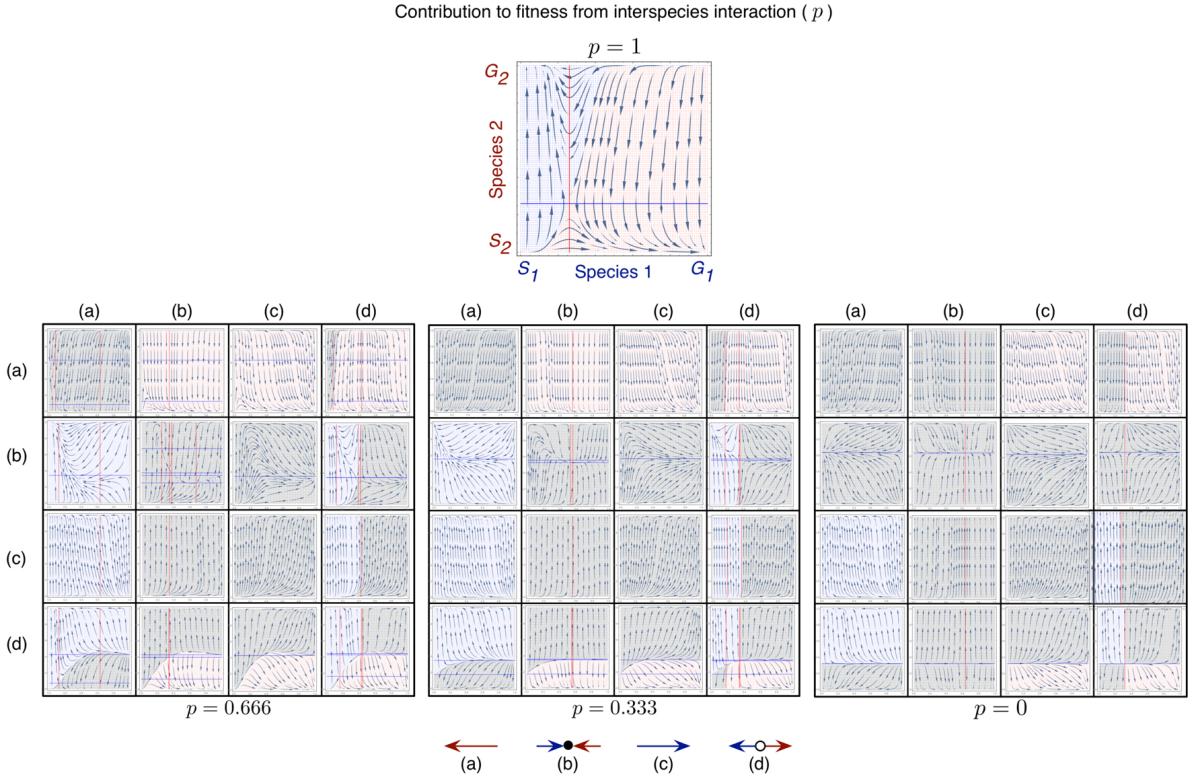


Figure A.1:  $d_1^{inter} = d_2^{inter} = 5$ ,  $b = 2$ ,  $r_x = r_y/8$ ,  $M_1 = M_2 = 1$  and  $c = 1$  for the interspecies game. As for the intraspecies games (a), (b), (c) and (d) the exact same parameter values as in (Hauert et al., 2006b). (We need to spell out those 4 games at some point.)

## 362 Asymmetries

363 )

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

$$d_1 \neq d_2 \quad (\text{A.14})$$

$$d^{inter} \neq d^{intra} \quad (\text{A.15})$$

$$M_1 \neq M_2 \quad (\text{A.16})$$

$$b \neq \tilde{b} \quad (\text{A.17})$$

$$c \neq \tilde{c} \quad (\text{A.18})$$

$$r_x \neq r_y \quad (\text{A.19})$$

$$\vdots \quad (\text{A.20})$$

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

## 366 D 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  $x_1 + x_2 + z_1 = 1$  where  $x_1$  and  $x_2$  are the densities of "Generous" and "Selfish" types. The population dynamics then is dictated by,

$$\dot{x}_1 = r_x x_1 (z_1 f_{G_1} - e_1) \quad (\text{A.21})$$

$$\dot{x}_2 = r_x x_2 (z_1 f_{S_1} - e_1) \quad (\text{A.22})$$

$$\dot{z}_1 = -\dot{x}_1 - \dot{x}_2 \quad (\text{A.23})$$

and for species 2

$$\dot{y}_1 = r_y y_1 (z_2 f_{G_2} - e_2) \quad (\text{A.24})$$

$$\dot{y}_2 = r_y y_2 (z_2 f_{S_2} - e_2) \quad (\text{A.25})$$

$$\dot{z}_2 = -\dot{y}_1 - \dot{y}_2 \quad (\text{A.26})$$

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. A.13. (This comes across as a special case only - justified? - or rephrase.) The fitnesses however need to be reevaluated in this setup. For example in Species 1 the fitness for type  $G_1$  is,

$$f_{G_1}^{inter} = \sum_{S=2}^{d_1} \binom{d_1 - 1}{S - 1} z_2^{d_1 - S} (1 - z_2)^{S-1} P_G^{inter}(S, y_1, y_2, z_2) \quad (\text{A.27})$$

$$f_{G_1}^{intra} = \sum_{S=2}^{d_1} \binom{d_1 - 1}{S - 1} z_1^{d_1 - S} (1 - z_1)^{S-1} P_G^{intra}(S, x_1, x_2, z_1) \quad (\text{A.28})$$

$$f_{G_1} = f_{G_1}^{inter} + f_{G_1}^{intra} \quad (\text{A.29})$$

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

$$P_G^{inter}(S, p, q, r) = \sum_{k=0}^{S-1} V(S, p, q, r) \Pi_{G_1}(k+1) \quad (\text{A.30})$$

$$P_G^{intra}(S, p, q, r) = \sum_{k=0}^{S-1} V(S, p, q, r) \Gamma_{G_1}(k+1) \quad (\text{A.31})$$

$$P_S^{inter}(S, p, q, r) = \sum_{k=0}^{S-1} V(S, p, q, r) \Pi_{S_1}(k) \quad (\text{A.32})$$

$$P_S^{intra}(S, p, q, r) = \sum_{k=0}^{S-1} V(S, p, q, r) \Gamma_{S_1}(k) \quad (\text{A.33})$$

367 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  $k$  “Gener-  
 368 ous”(Cooperator) individuals and  $S - 1 - k$  “Selfish”(Defector) individuals in the inter(intra)  
 369 species game. and the actual payoffs are calculated as per Eqs. ?? and A.8.