

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 (Aristotle
26 (Translator - Allan Gotthelf), 1991). Formally the Belgian zoologist Pierre van Beneden
27 coined the term mutualism in 1873 (Bronstein, 2003). The study of mutualistic relationships,
28 interspecific interactions that benefit both species, is rich in empirical as well as theoretical
29 understanding (Boucher, 1985; Hinton, 1951; Wilson, 1983; Bronstein, 1994; Pierce et al.,
30 2002; Kiers et al., 2003; Bshary and Bronstein, 2004) (Poulin and Vickery, 1995; Doebeli and
31 Knowlton, 1998; Noë, 2001; Johnstone and Bshary, 2002; Bergstrom and Lachmann, 2003;
32 Hoeksema and Kummel, 2003; Akçay and Roughgarden, 2007; Bshary et al., 2008) - (Need
33 to rewrite). Most examples of mutualisms lend themselves to the idea of direct reciprocity
34 (Trivers, 1971) and have thus been extensively studied using evolutionary game theory. Clas-
35 sical evolutionary games are usually limited to dyadic the fundamental interaction is between
36 two individuals, one from each species, and the sum of many such interactions determines
37 the evolutionary dynamics. However, this is clearly a simplification as has been shown by
38 numerous studies (Noë and Hammerstein, 1995; Noë, 2001; Kiers et al., 2003; Stanton, 2003;
39 Stadler and Dixon, 2008).

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

56 While inferring the particular type of interspecific symbiosis (mutualism, parasitism or

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

68 Mutualistic relationships are, by definition, between species, and timing may be crucial
69 for their maintenance. (this next sentence is awkward but I haven't fixed it) It is natural to
70 imagine that the observed mutualism may be seasonal and the interactions as not a continuous
71 feature of the evolutionary trajectory of a single species. A wildly changing ecology can affect
72 the flowering time of some plants and the maturation of the dispersers they depend on, easily
73 disrupting such delicately balanced mutualistic interactions. Unless both interacting species
74 can respond in a similar fashion such a mutualism will break down (Warren and Bradford,
75 2014).

76 We tackle this seasonality by varying the duration of the impact of intraspecies and in-
77 terspecies dynamics. (do we? not obvious where the duration enters - we have p but that's
78 not a duration.)(Done) To complete the ecological picture we include population dynamics to
79 the evolutionary process of the mutualists. Such dynamics informs us about the population
80 densities we might expect to find the interactors to evolve to. (??) (better?) We demon-
81 strate the crucial nature of the feedback between population and evolutionary dynamics which
82 can maintain mutualisms preventing either or both species from going extinct. We make use
83 of evolutionary game theory to analyze how benefits are shared between the two mutualis-
84 tic species (Weibull, 1995; Hofbauer, 1996; Hofbauer and Sigmund, 1998). Beginning with
85 the previously studied interspecies dynamics as the foundational framework (Gokhale and
86 Traulsen, 2012) we increase the complexity of the system by including intraspecies dynam-
87 ics, population dynamics and seasonality. The rich dynamics observed provides us with novel
88 insights about the immense asymmetries in mutualisms and the fragility of such delicately
89 balanced interactions.

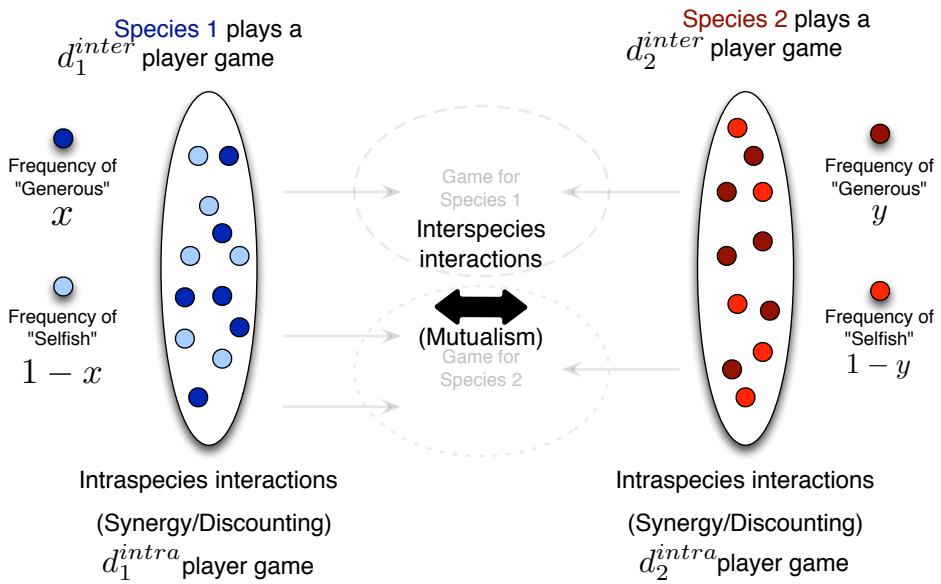


Figure 1: Evolutionary dynamics with combined inter-intra species dynamics. We assume the interactions between species to be mutualistic described by the snowdrift game (Bergstrom and Lachmann, 2003; Souza et al., 2009; Gokhale and Traulsen, 2012). Species 1 plays a d_1^{inter} player game with Species 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)

90 **2 Model and Results**

91 **2.1 Interaction dynamics**

92 **2.1.1 Interspecies**

93 Focusing on mutualism, the interspecies dynamics is given by the multiplayer version of the
94 snowdrift game (Bergstrom and Lachmann, 2003; Souza et al., 2009; Gokhale and Traulsen,
95 2012) (also known as hawk-dove, or chicken). In this, a common benefit is possible but there
96 is a cost to contributing and species do not need to contribute equally. However the individuals
97 in each species could get away with contributing a bit less than other individuals. (Awkward
98 wording I think, but I haven't fixed yet.) Hence for example if producing brighter light comes
99 at a premium for the *Vibrio* in the squid then the dimmer *Vibrio* would be better off (Not
100 producing any light is not an option as the squid then actively evicts these bacteria) (McFall-
101 Ngai, 2014). We assume that each species consists of two types of individuals "Generous"
102 G and "Selfish" S . If enough individuals are "Generous" and contributing to the generation
103 of mutual benefits then other individuals can get away with being selfish (not contributing).
104 But all individuals in the game lose out if not enough are generous. Hence both species
105 cannot be completely "selfish", as per the definition of mutualism. This interaction framework
106 corresponds to that of a multi player version of a snowdrift game and is discussed in detail
107 in the Supplementary Material (SI). Hence the pressure is on a species to make the partner
108 "Generous" while getting away itself by being "Selfish". The fitness of each of the types
109 within a species thus depends on the composition of the other species. Denoting the frequency
110 of the "Generous" types in Species 1 (G_1) as x , and that in Species 2 (G_2) as y , the fitness of
111 G_1 is given by $f_{G_1}^{inter}(y)$ and that of G_2 as $f_{G_2}^{inter}(x)$.

112 **2.1.2 Intraspecies**

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

123 Motro, 1988; Hauert et al., 2006b) allows us to transition between four classic scenarios of
 124 evolutionary dynamics (Nowak and Sigmund, 2004). For example in our case we can have a
 125 dominance of the “Generous” type or the “Selfish” type or both the types can invade from rare
 126 resulting in a co-existence or bistability if both pure strategies are mutually non-invasive. For
 127 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
 128 given by $f_{G_2}^{intra}(y)$ and similarly for the “Selfish” types.

129 2.2 Combined dynamics

130 Putting together intra and interspecific dynamics provides a complete picture of the possible
 131 interactions occurring. While we are interested in mutualism at the level of the interspecies
 132 interactions there are four possible interactions within each species (Nowak and Sigmund,
 133 2004; Hauert et al., 2006b) (dominance of either type, coexistence or bistability). Since the
 134 within species interactions for the two different species do not need to be the same, there are
 135 in all sixteen different possible combinations. Assuming additivity in the fitnesses of inter-
 136 and intraspecies fitnesses, the combined fitness of each of the two types in the two species are
 137 given by,

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

The parameter p tunes the impact of each of the interactions on the final 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), while for $p = 0$ the dynamics of the two species are decoupled and can be individually studied by the synergy/discounting framework of nonlinear social dilemmas (Hauert et al., 2006b). Of interest here is the continuum described by 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 0 to 1 (Appendix C). The time evolution of the “Generous” types in both species is then given by,

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

138 This approach provides us with a powerful method to incorporate a multitude of realistic con-
 139 cepts in the analysis. For example the number of players involved in a game, which has been

140 shown to be a crucial factor in determining the evolutionary dynamics could be different for
 141 each interactions, inter and intra species interactions for Species 1 (d_1^{inter} , d_1^{intra}) and simi-
 142 larly for Species 2 (d_2^{inter} , d_2^{intra}). The interspecies interactions are proxied by the multiplayer
 143 snowdrift game which can incorporate threshold effects. For example a certain number of
 144 “Generous” cleaner fish may be required to clean the host or a certain number of “Generous”
 145 ants required to protect larva from predators. We can have M_1 and M_2 as the thresholds in
 146 the two species. Since the interaction matrices for the inter and intra species dynamics are
 147 completely different in principle we can have different costs and benefits for the four games
 148 (Two snowdrift games from the perspective of each species and the intragames within each
 149 species).

150 We can have a diverse and rich set of dynamics possible which brings into question the
 151 study of coevolution based on only interspecies interactions. For a given set of parameter
 152 values but the the full spectrum of possible dynamics, see Figure A.1. Even under a large
 153 number of assumptions and even if the intraspecies dynamics accounts for only 33% ($1 - p$) of
 154 the cumulative fitness, we can see drastically different qualitative dynamics which is capable
 155 of explaining the persistence of exploiters Fig. 2.

156 2.3 Population dynamics

157 Until now we have considered that each species consists of two types of individuals and they
 158 make up the population of that species. However populations sizes change over time. As-
 159 suming that ecological changes are fast enough that they can be averaged out, we can usually
 160 ignore their effect on the evolutionary dynamics. It is now possible to show that evolution can
 161 happen at fast timescales, comparable to those of the ecological dynamics (Post and Palko-
 162 vacs, 2009; Beaumont et al., 2009; Hanski, 2011; Sanchez and Gore, 2013). Hence we need
 163 to tackle not just evolutionary but eco-evolutionary dynamics 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. Further 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 two species and hence now the dynamics of this complete system is determined by the following set of differential equations,

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

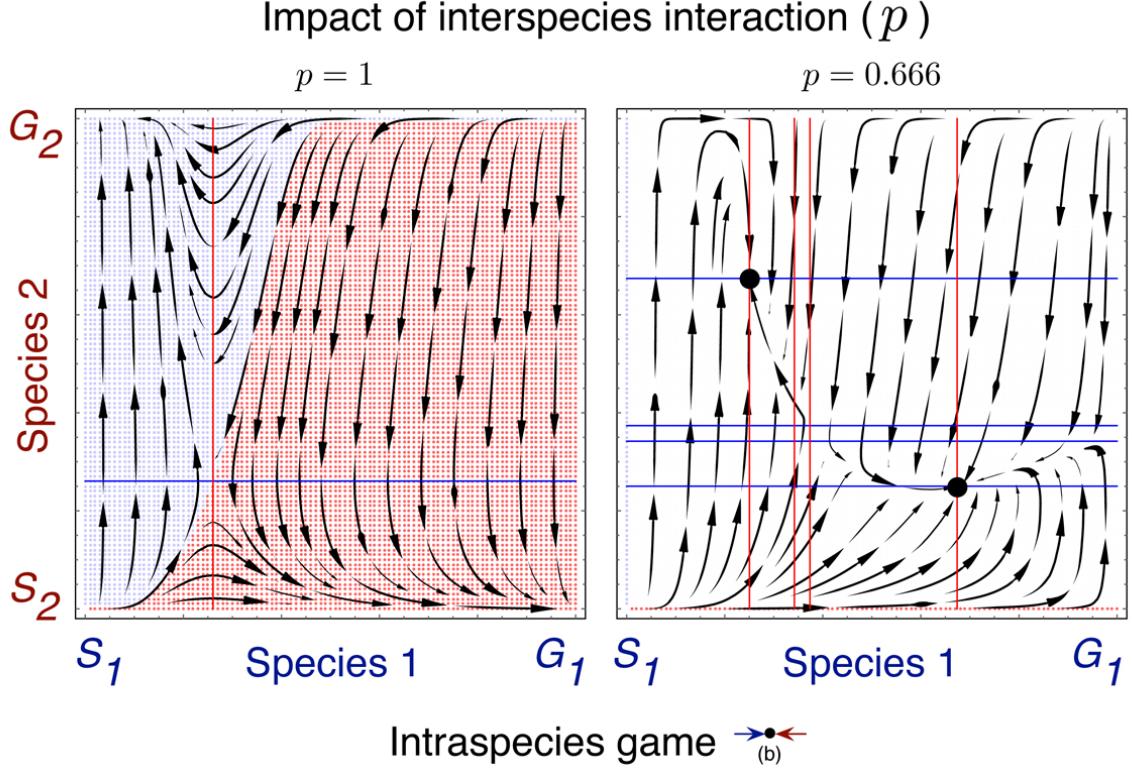


Figure 2: **Change in evolutionary dynamics due to inclusion of intraspecies dynamics.** When the fitness of the “Generous” and “Selfish” types in both the species is solely determined by the interactions which occur between species (in this case mutualism, $p = 1$) then we recover the dynamics as studied 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 isoclines 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.

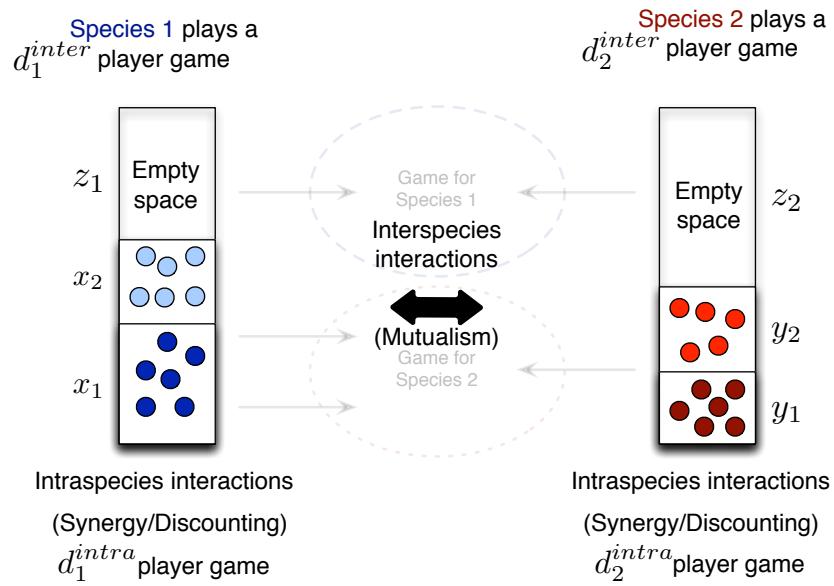


Figure 3: Population and evolutionary dynamics with combined inter-intra species dynamics.
As with the interactions described in 1 the two species consist of two types of individuals “Generous” and “Selfish”. Since the two species can in principle occupy different environmental niches, they can have 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.

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

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

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

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

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

174 2.4 Seasonality

175 Many mutualisms are observed only during certain periods of a year. Such seasonal or episodic
176 mutualism run a high risk of phenological partner mismatch as a result of climate change
177 (Rafferty et al., 2015). While tropical species, such as the various varieties of fig (*Ficus*)

Evolutionary and population dynamics

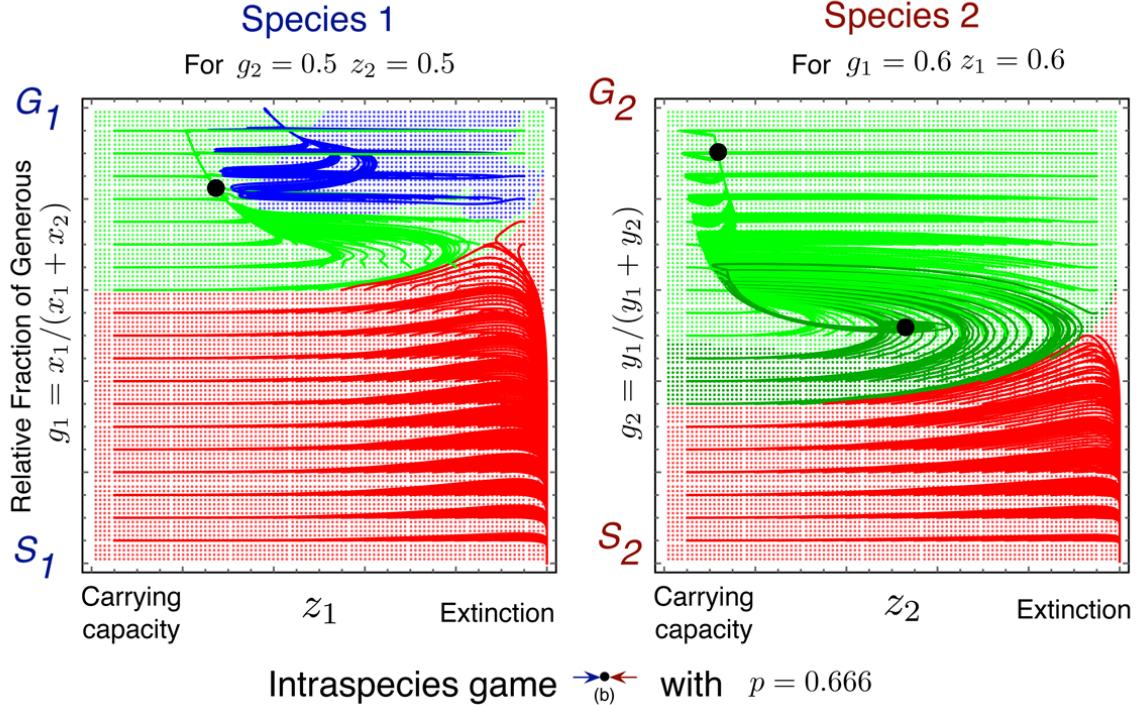


Figure 4: **Dynamics of evolutionary strategies and population density for an intraspecies coexistence game with interspecies mutualism.** With exactly the same parameters as that of Figure 2 with symmetric death rates $e_1 = e_2 = 0.05$ we show two different numerically evaluated examples. Left Panel: 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.

178 can flower all year round, their mutualistic relationships (with wasps) run a lower risk. For
179 example in the ant-aphid mutualism, the number of attending ants was seen to increase till
180 June and declined after late July and the aphid colonies went rapidly (within a month) extinct
181 in the absence of attending ants (Yao et al., 2000; Yao and Akimoto, 2009). For the evolution
182 of a species this means that the effect of interspecific interaction changes over time.

183 To analyse such episodic mutualistic events, instead of a static variable p measuring the
184 impact of interspecific interaction on fitness we make use of a time-dependent function $p(t) =$
185 $(1 + \sin(at))/2$. For the particular parameter set used in Fig.2, introducing seasonality still
186 maintains the two interior fixed points (they are closer to each other for $p = 0.5$), but this
187 is seen only when the oscillations in $p(t)$ are comparable, $a = 1$, or faster, $a = 10$, with
188 respect to the evolutionary timescale. For slower oscillations $a = 0.1$ we see cyclic behaviour
189 which is prominent in Species 2 more than in Species 1. very slow oscillations mean that the
190 system spends longer close to the starting value of $p(t)$ and hence the phase in which $p(t)$ starts
191 becomes more and more important for smaller and smaller a . This is especially interesting if
192 the stability of the system is qualitatively affected over the p continuum.

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. The converse is the case when the intra species interactions are of interest. The
197 major body of work focusing on social dilemmas between “Cooperators” and “Defectors” is
198 a glaring example of the same. Obviously this is an assumption which is very useful when
199 distilling the interactions at different community scales. However when extra-species interac-
200 tions are interdependent then the connectivity between the different levels cannot be ignored
201 (Schluter and Foster, 2012).

202 In principle the framework developed herein is capable of handling a diverse array of inter-
203 and intraspecific interactions. Our focus on mutualism. Mutualistic interactions between two
204 species can be represented by a bimatrix game. The components of each of the two game
205 matrices need not be correlated as long as they satisfy the inequalities leading to a Snowdrift
206 games. Including realistic phenomena such as intraspecies interactions, population dynamics
207 and seasonality we show that maintenance of mutualism is possible. A fragile balance of
208 parameters maintains mutualism. However often it can come at a cost of also maintaining a
209 significant level of exploiters. In fact the coevolutionary dynamics between the two species is
210 determined together by the inter as well as the intraspecific interactions.

211 Using this framework it is easy to incorporate the natural complexities of inter as well

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

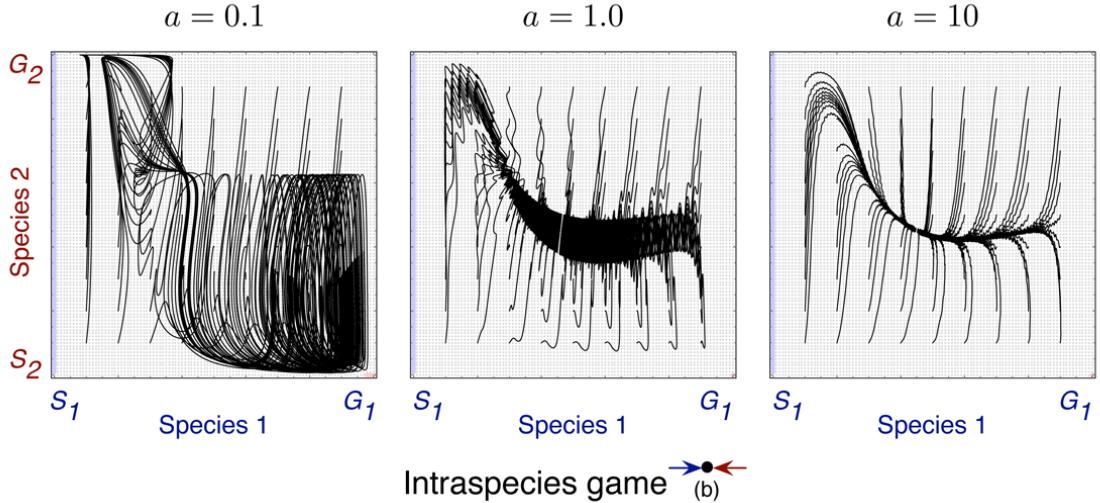


Figure 5: Seasonal changes in the interspecies interactions affecting the evolutionary dynamics within species. We model the impact of the interspecies interaction on the fitness of the different types as in Eqs. 1 however instead of a static value for p we introduce seasonality via a simple sine function as $p(t) = (1 + \sin(at))/2$. Here, 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. For comparable or 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 larger a especially if the stability of the internal (or edge) fixed points changes as p changes (see Fig. A.1 panel (b) x (b) across the p continuum).

212 as intraspecies dynamics elucidating the final outcome on an evolutionary trajectory. While
213 the simple case makes predictions possible, including seasonality inserts a time dependent
214 factor which makes analytical reasoning difficult. However given the patterns of episodic
215 interactions and studies of mutualistic relationship obtained from field studies over the decades
216 it might be possible to include the seasonal component in future analysis on realistic systems
217 to see how the interactions are going to change under drastic climate change.

218 **Acknowledgements.** (CSG acknowledges funding from the New Zealand Institute for
219 Advanced Study and time spent at Victoria University of Wellington. . . .)

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341 **A Interspecies Evolutionary Dynamics**

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

346 **The snowdrift game**

347 **Two player setting**

348 Two drivers are stuck in a snowdrift. They must shovel away the snow (paying the cost c)
349 to reach home (benefit b) but there are three possible outcomes to this scenario. One of the
350 driver shovels while the other stays warm in the care ($b - c$ and b), both the drivers share the
351 workload and shovel away the snow ($b - c/2$ and $b - c/2$) or none of them gets out of the care
352 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:				
		Species 2			Species 1		
		G_2	S_2			G_1	S_1
Species 1	G_1	$b - c/2$	$b - c$	Species 2	G_2	$b - c/2$	$b - c$
	S_1	b	0		S_2	b	0

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

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

363 Multiplayer setting

364 Following Souza et al. (Souza et al., 2009), a multiplayer snowdrift game can be described by
 365 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,

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

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

366 B Intraspecies Evolutionary Dynamics

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

378 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,

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

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

379 Thus the defectors get a fraction of the benefit which is scaled by the factor ω , which de-
 380 termes whether the benefits are linearly accumulating ($\omega = 1$) for increasing number of
 381 cooperators, synergistically enhanced ($\omega > 1$) or saturating ($\omega < 1$). Note that the costs and
 382 benefits in the within species game need not be the same as in between species ($b \neq \tilde{b}$ and
 383 $c \neq \tilde{c}$).

384 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,

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

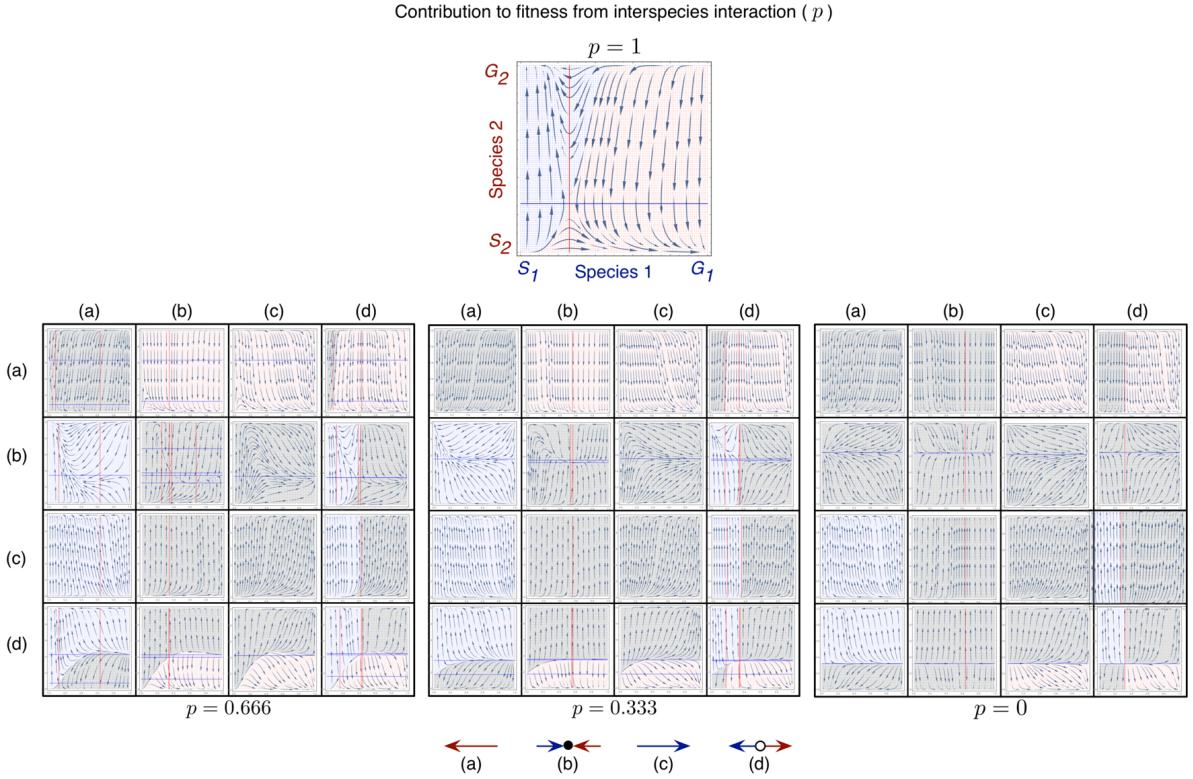


Figure A.1: $d_1^{inter} = d_2^{inter} = 5$, $b = 2$, $r_x = r_y/8$, $M_1 = M_2 = 1$ and $c = 1$ for the interspecies game. As for the intraspecies games (a), (b), (c) and (d) the exact same parameter values as in (Hauert et al., 2006b). (We need to spell out those 4 games at some point.)

386 Asymmetries

387)

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

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

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

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

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

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

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

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

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

390 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,

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

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

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

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

391 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)
392 species game. and the actual payoffs are calculated as per Eqs. ?? and A.8.
393