

Eco-evolutionary dynamics of mutualisms

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Abstract

Mutualism has long been studied as a conundrum for evolutionary theory. Species that exploit other species would do better than sustaining a long drawn out mutually costly relationship. How such mutualisms are then maintained is a valid question. However studies investigating this question often neglect the importance of within species interactions. Separating inter and intra species interactions may not be always possible especially if the same individuals act within and between species. Feedbacks between inter and intra species interactions are then inevitable and need to be taken into account. Taking into account population dynamics we study the full eco-evolutionary dynamics of mutualism between two species when a variety of different intra species interactions are possible. Our results show that while mutualism can turn into parasitism by overexploitation, for some intra species dynamics, mutualism can be established even while maintaining exploiters in the species composition.

Keywords: mutualism, evolutionary game theory, multiple players

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32 **1 Introduction**

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

48 A well studied example of a one-to-many interaction is that of the plant-microbe mutual-
 49 ism wherein leguminous hosts prefer rhizobial symbionts that fix more nitrogen ([Kiers et al.,](#)
 50 [2003](#)), or where plants provide more carbon resources to fungal strains that are providing
 51 better access to nutrients ([Kiers et al., 2011](#)). As an example of an animal host, mutualistic
 52 relationship between the bioluminescent bacteria *Vibrio fischeri* and *Euprymna scolopes*, the
 53 bobtail squid ([McFall-Ngai, 2014](#)) is a paradigm. Numerous bacteria are hosted in the crypts
 54 of the squid's light organ, where they produce light despite it being costly. The bacteria mature
 55 and develop within the squid, however those that fail to produce bioluminescence are evicted.
 56 While the variation in the phenotypes of the interacting partners has been acknowledged, the
 57 usual analysis focuses on the interaction between the two species without addressing this ad-

58 ditional complexity. The classic example of ants and aphids or butterfly larvae (Pierce et al.,
59 Hölldobler and Wilson, 1990) is an excellent exposition of many player interactions.
60 Numerous ants tend to each of the soft bodied creatures, providing them with shelter and pro-
61 tection from predation and parasites, in exchange for honeydew, a rich source of food for the
62 ants (Hill and Pierce, 1989; Stadler and Dixon, 2008). This is a one-to-many interaction from
63 the perspective of the larva.

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

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

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

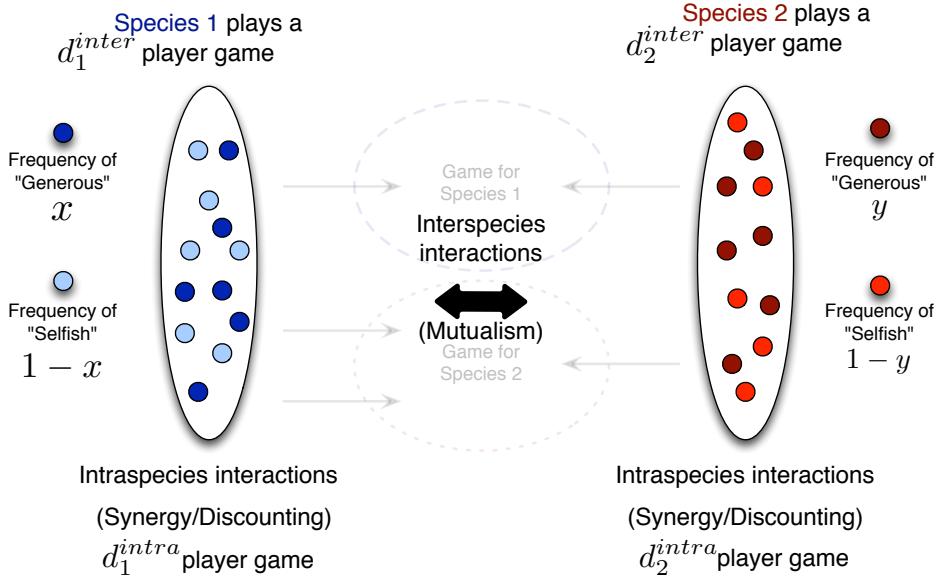


Figure 1: **Evolutionary dynamics with combined inter-intra species dynamics.** We assume the interactions between species to be mutualistic described by the snowdrift game (Bergstrom and Lachmann, 2003; Souza et al., 2009; Gokhale and Traulsen, 2012). Species 1 plays a d_1^{inter} player game with Species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

ics, population dynamics and seasonality. The rich dynamics observed provides us with novel insights about the immense asymmetries in mutualisms and the fragility of such delicately balanced interactions.

97 2 Model and Results

98 2.1 Interaction dynamics

99 2.1.1 Interspecies

100 Focusing on mutualism, the interspecies dynamics is given by the multiplayer version of the
101 snowdrift game (Bergstrom and Lachmann, 2003; Souza et al., 2009; Gokhale and Traulsen,

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

119 2.1.2 Intraspecies

120 For intraspecies dynamics we do not restrict ourselves to any particular interaction structure
121 and thus make use of the general multiplayer evolutionary games framework (Gokhale and
122 Traulsen, 2010, 2014). Moving from the interspecies dynamics, the two types already de-
123 scribed are "Generous" and "Selfish". Thus we already have each species containing two
124 different types of individuals. It is possible that a different categorisation exists within a
125 species. Thus if the interactions within a Species are say between "Cooperators" and "Defec-
126 tors", these types could be made up of a combination of "Generous" and "Selfish" individuals.
127 However for the sake of simplicity we study the dynamics between "Generous" and "Selfish"
128 types within a species where the types are defined at the interspecies level. The cost benefit
129 framework described in (Eshel and Motro, 1988; Hauert et al., 2006b) allows us to transition
130 between four classic scenarios of evolutionary dynamics (Nowak and Sigmund, 2004). For
131 example in our case we can have a dominance of the "Generous" type or the "Selfish" type
132 or both the types can invade from rare resulting in a co-existence or bistability if both pure
133 strategies are mutually non-invasive. For the intra species interactions the fitness of a G_1 is
134 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"
135 types.

136 2.2 Combined dynamics

137 Putting together intra and interspecific dynamics provides a complete picture of the possible
 138 interactions occurring. While we are interested in mutualism at the level of the interspecies
 139 interactions there are four possible interactions within each species (Nowak and Sigmund,
 140 2004; Hauert et al., 2006b) (dominance of either type, coexistence or bistability). Since the
 141 within species interactions for the two different species do not need to be the same, there are
 142 in all sixteen different possible combinations. Assuming additivity in the fitnesses of inter
 143 and intraspecies fitnesses, the combined fitness of each of the two types in the two species are
 144 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 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,

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

145 This approach provides us with a powerful method to incorporate a multitude of realistic con-
 146 cepts in the analysis. For example the number of players involved in a game, which has been
 147 shown to be a crucial factor in determining the evolutionary dynamics could be different for
 148 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 a given set of parameter
 159 values but the the full spectrum of possible dynamics, see Figure A.1. Even under a large
 160 number of assumptions and even if the intraspecies dynamics accounts for only 33% ($1 - p$) of
 161 the cumulative fitness, we can see drastically different qualitative dynamics which is capable
 162 of explaining the persistence of exploiters Fig. 2.

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 can
 168 happen at fast timescales, comparable to those of the ecological dynamics (Post and Palko-
 169 vacs, 2009; Beaumont et al., 2009; Hanski, 2011; Sanchez and Gore, 2013). Hence we need
 170 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,

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

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

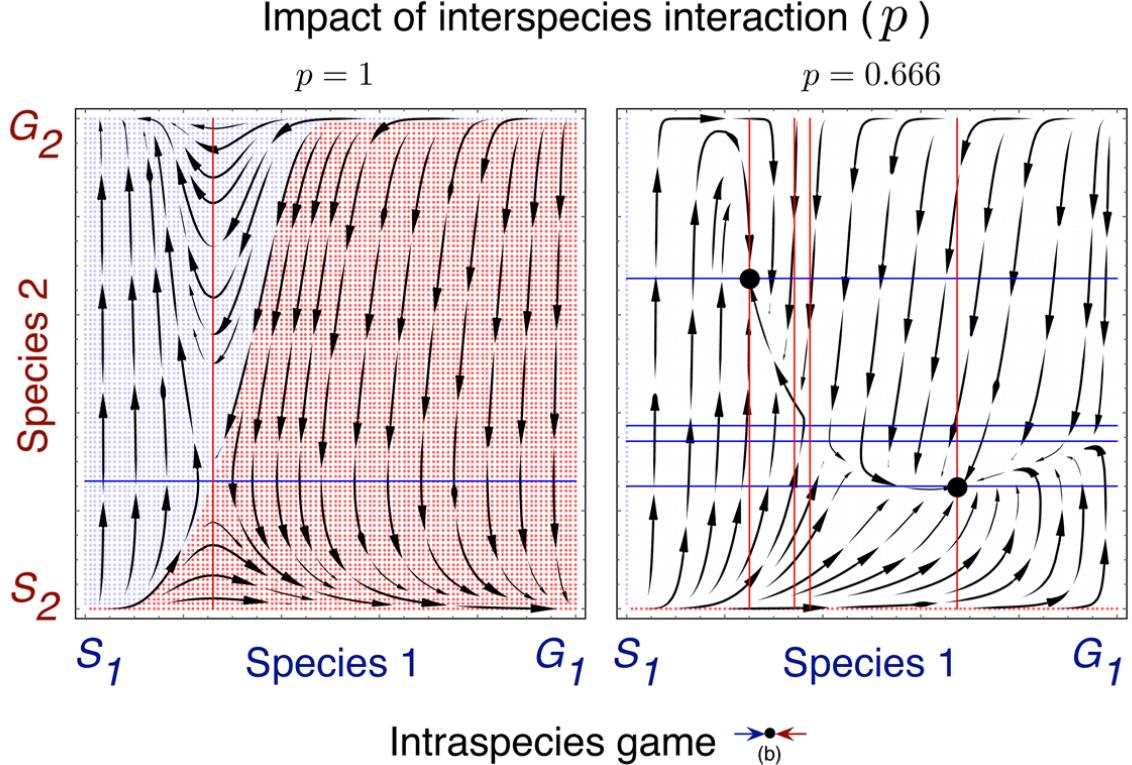


Figure 2: **Change in evolutionary dynamics due to inclusion of intraspecies dynamics.** When the fitness of the “Generous” and “Selfish” types in both the species is solely determined by the interactions which occur between species (in this case mutualism, $p = 1$) then we recover the dynamics as studied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

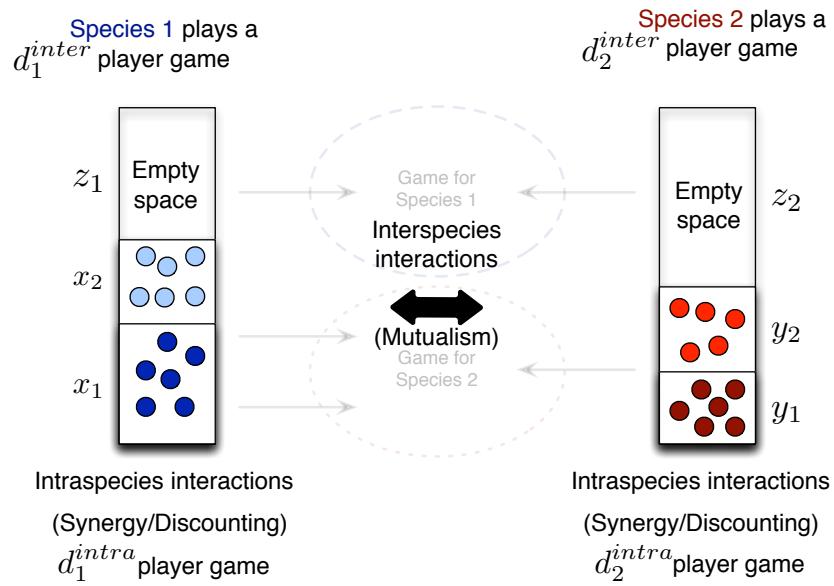


Figure 3: Population and evolutionary dynamics with combined inter-intra species dynamics.
 As with the interactions described in 1 the two species consist of two types of individuals “Generous” and “Selfish”. Since the two species can in principle occupy different environmental niches, they can have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

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,

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

and

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

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 summarised 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) .

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 $(1 + \sin(at))/2$. For the particular parameter set used in Fig.2, introducing seasonality still

Evolutionary and population dynamics

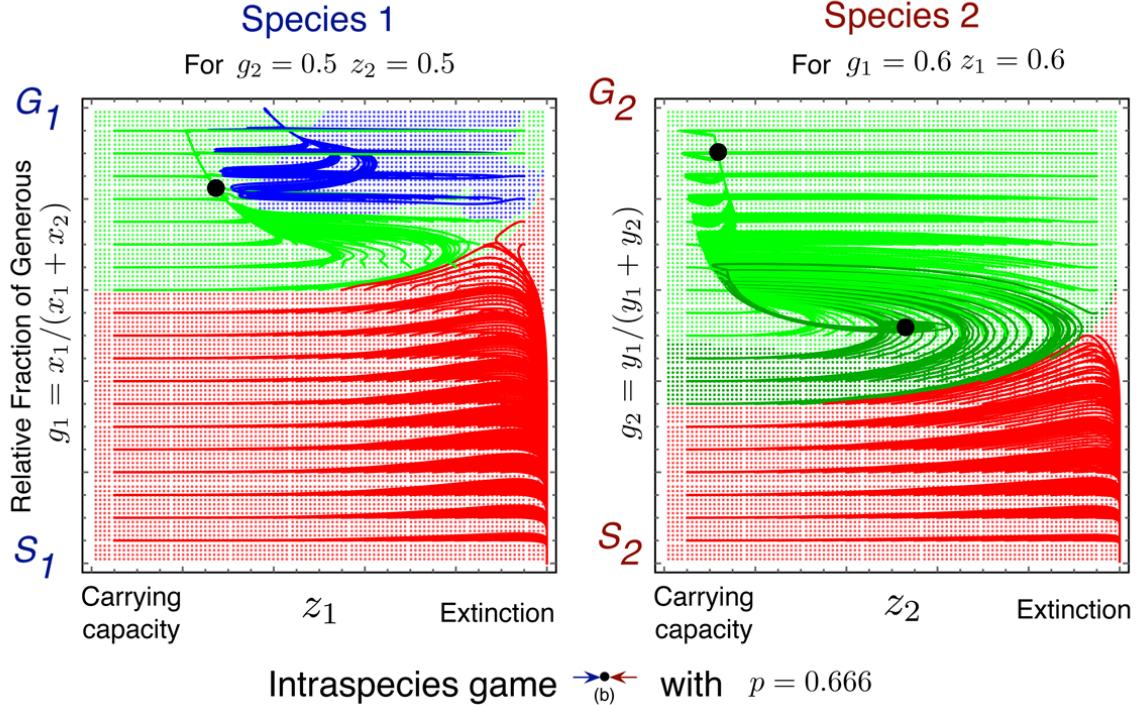


Figure 4: Dynamics of evolutionary strategies and population density for an intraspecies coexistence game with interspecies mutualism. With exactly the same parameters as that of Figure 2 with symmetric death rates $e_1 = e_2 = 0.05$ we show two different numerically evaluated examples. Left Panel: shows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

193 maintains the two interior fixed points (they are closer to each other for $p = 0.5$), but this
194 is seen only when the oscillations in $p(t)$ are comparable, $a = 1$, or faster, $a = 10$, with
195 respect to the evolutionary timescale. For slower oscillations $a = 0.1$ we see cyclic behaviour
196 which is prominent in Species 2 more than in Species 1. very slow oscillations mean that the
197 system spends longer close to the starting value of $p(t)$ and hence the phase in which $p(t)$ starts
198 becomes more and more important for smaller and smaller a . This is especially interesting if
199 the stability of the system is qualitatively affected over the p continuum.

200 3 Discussion

201 Usually when interspecies relationships such as mutualism (or antagonist relationships as in
202 predator-prey) are considered, the within species interactions are ignored for the sake of con-
203 venience. The converse is the case when the intra species interactions are of interest. The
204 major body of work focusing on social dilemmas between “Cooperators” and “Defectors” is
205 a glaring example of the same. Obviously this is an assumption which is very useful when
206 distilling the interactions at different community scales. However when the inter and intra
207 species interactions are interdependent then the feedbacks between the two levels cannot be
208 ignored ([Schluter and Foster, 2012](#)).

209 In principle the framework developed herein is capable of handling a diverse array of inter
210 and intraspecific interactions. For interspecific interactions our focus is on mutualism. Mu-
211 tualistic interactions between two species can be represented by a bimatrix game. The com-
212 ponents of each of the two game matrices need not be correlated as long as they satisfy the
213 inequalities leading to a Snowdrift games. Including realistic phenomena such as intraspecies
214 interactions, population dynamics and seasonality we show that maintenance of mutualism is
215 possible. A fragile balance of parameters maintains mutualism. If within each Species the
216 “Generous” and “Selfish” interactions result in coexistence then it can outweigh the compe-
217 tition which they experience at the inter species level. Note however that at the interspecies
218 level the competition of a “Generous” individuals is with the “Selfish” individuals from the
219 other Species. While the “Selfish” individuals from the other Species can drive “Generous”
220 individuals within a Species extinct, co-existence between “Generous” and “Selfish” within
221 the same Species can overcome the pressure for extinction. In this way mutualism can be
222 maintained but it comes at a cost of also maintaining a significant level of exploiters. In fact
223 the coevolutionary dynamics between the two species is determined together by the inter as
224 well as the intraspecific interactions.

225 While the simple case makes predictions possible, including seasonality inserts a time
226 dependent factor which makes analytical reasoning difficult. However given the patterns of

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

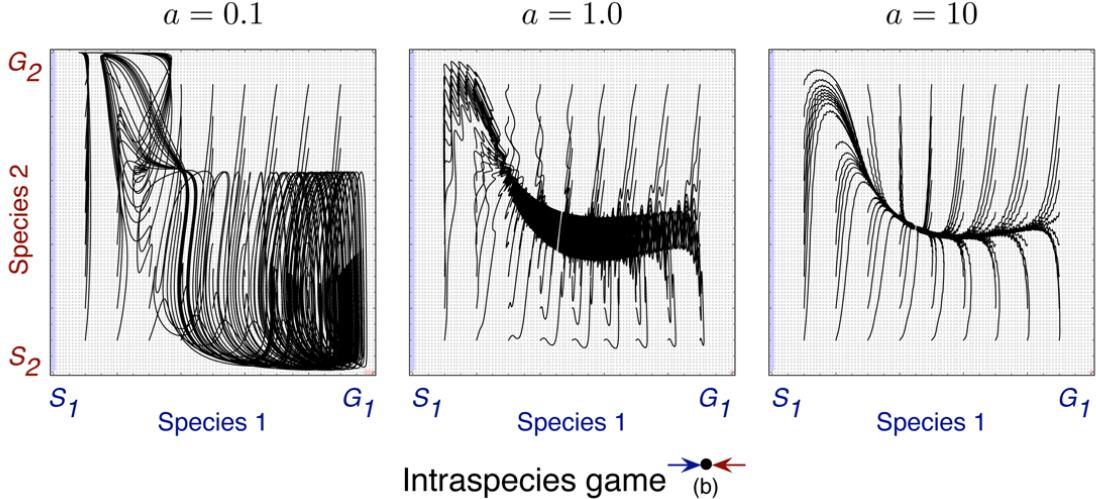


Figure 5: Seasonal changes in the interspecies interactions affecting the evolutionary dynamics within species. We model the impact of the interspecies interaction on the fitness of the different types as in Eqs. 1 however instead of a static value for p we introduce seasonality via a simple sine function as $p(t) = (1 + \sin(at))/2$. Here, a denotes how the seasonality time scale relates to the inter-intra-species interactions 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. The trajectories shown in the panels are obtained by numerical interactions with initial conditions $x = y = \{0.1, 0.9\}$ and a step size of $\Delta x = \Delta y = 0.1$. The background colour is obtained by a finer grain of $\Delta x = \Delta y = 0.01$ and depict the same outcomes as in Fig. 2, with gray representing the outcome that none of the edge equilibria are reached. 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 smaller a especially if the stability of the fixed points changes as p changes (see Fig. A.1 panel (b) x (b) across the p continuum).

227 episodic interactions and studies of mutualistic relationship obtained from field studies over
228 the decades it might be possible to include the seasonal component in future analysis on re-
229 alistic systems to see how the interactions are going to change under drastic climate change.
230 Including this feature informs us of the dependence of the mutualism on environmental fac-
231 tors. The difference in the timescales of the eco-evolutionary process and environmental fluc-
232 tuations highlights the fact that averaging out the environmental effects might not always be
233 possible. The system can show qualitatively different behaviour from the average dynamics
234 depending on the kind of interactions initially involved within and between species.

235 Using this framework it is easy to incorporate the natural complexities of inter as well as
236 intraspecies dynamics elucidating the final outcome on an evolutionary trajectory.

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

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360 A Interspecies Evolutionary Dynamics

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

365 The snowdrift game

366 Two player setting

367 Two drivers are stuck in a snowdrift. They must shovel away the snow (paying the cost c)
368 to reach home (benefit b) but there are three possible outcomes to this scenario. One of the
369 driver shovels while the other stays warm in the care ($b - c$ and b), both the drivers share the
370 workload and shovel away the snow ($b - c/2$ and $b - c/2$) or none of them gets out of the care
371 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 |

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

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

382 Multiplayer setting

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

$$\begin{aligned} \Pi_{G_1}(k) &= \begin{cases} b - \frac{c}{k} & \text{if } k \geq M \\ -\frac{c}{M} & \text{if } k < M \end{cases} \\ \Pi_{S_1}(k) &= \begin{cases} b & \text{if } k \geq M \\ 0 & \text{if } k < M. \end{cases} \end{aligned} \quad (\text{A.1})$$

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?) (So below the threshold all cooperators are trying their best by putting in c/M as M
 is the threshold but as soon as the threshold is crossed then they can put in less c/k as k will
 be larger than M) 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,

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

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

and similarly $f_{G_2}^{inter}$ and $f_{S_2}^{inter}$ for Species 2.

Note that here for the sake of notation we have assumed the same values of benefits and costs, thresholds for the two species. However along with the number of player d_1^{inter} and d_2^{inter} , these parameters could be very well different for the two Species. For asymmetric bi-matrix games there is a difference in the dynamics between the standard replicator dynamics and the alternative dynamics put forward by Maynard-Smith (?). In this case the replicator equations cannot be simplified by removing the average fitness from the denominator and can give rise to qualitatively different dynamics.

393 B Intraspecies Evolutionary Dynamics

For elucidating the intraspecies dynamics we will focus on Species 1 as the analysis is analogous for Species 2. Within species dynamics can in principle be completely different from the between species interactions. We can have a multistrategy multiplayer game within a Species but to keep things simple we assume a two strategy multiplayer game. The partitioning of the individuals into two strategies follows the same partitioning as in the inter species interactions as of “Generous” and “Selfish”. In principle we could have two different labels for the strategies in the intraspecies interactions and the “Generous” and “Selfish” categories could be split into them. However for the sake of simplicity we assume the same categorisation as at the inter species level.

403 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), i.e., dominance of either type, coexistence and bistability (Perhaps good to

list the 4 types). Since the categorisation of the strategies at the intra species level is the same as that of the inter species level, for Species 1, x and $1 - x$, are the frequencies of “Generous” and “Selfish” type. (Q: is this because they are the very same players? i.e. are we assuming a Generous player in the inter is a Cooperative one in the intra?) The “Generous” and “Selfish” in Species 1 play a d_1^{intra} player game. Thus the fitnesses of of the two types are defined as (Hauert et al., 2006b),

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

$$f_{S_1}^{intra}(x) = \sum_{k=0}^{d_1-1} \binom{d_1^{intra}-1}{k} x^k (1-x)^{d_1^{intra}-1-k} \Gamma_{S_1}(k). \quad (\text{A.3})$$

where the payoffs are given by,

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

$$\Gamma_{G_1}(k) = \Gamma_{S_1}(k) - \tilde{c}. \quad (\text{A.4})$$

404 Thus the “Selfish” get a fraction of the benefit which is scaled by the factor ω , which de-
 405 termines whether the benefits are linearly accumulating ($\omega = 1$) for increasing number of
 406 “Generous” individuals, synergistically enhanced ($\omega > 1$) or saturating ($\omega < 1$). Note that
 407 the costs and benefits in the within species game need not be the same as in between species
 408 ($b \neq \tilde{b}$ and $c \neq \tilde{c}$).

409 C Combined Evolutionary Dynamics

The average payoffs are then assumed to be a linear combination of the interspecies and in-
 traspecies interactions where the parameter p determines the strength of each of the interac-
 tions such that,

$$f_{G_1}(x, y) = p f_{G_1}^{inter}(y) + (1-p) f_{G_1}^{intra}(x)$$

$$f_{S_1}(x, y) = p f_{S_1}^{inter}(y) + (1-p) f_{S_1}^{intra}(x). \quad (\text{A.5})$$

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

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

$$\bar{f}_2(x, y) = y f_{G_2}(x, y) + (1-y) f_{S_2}(x, y). \quad (\text{A.6})$$

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,

$$\begin{aligned}\dot{x} &= r_x x \left(f_{G_1}(x, y) - \bar{f}_1(x, y) \right) \\ \dot{y} &= r_y y \left(f_{G_2}(x, y) - \bar{f}_2(x, y) \right).\end{aligned}\quad (\text{A.7})$$

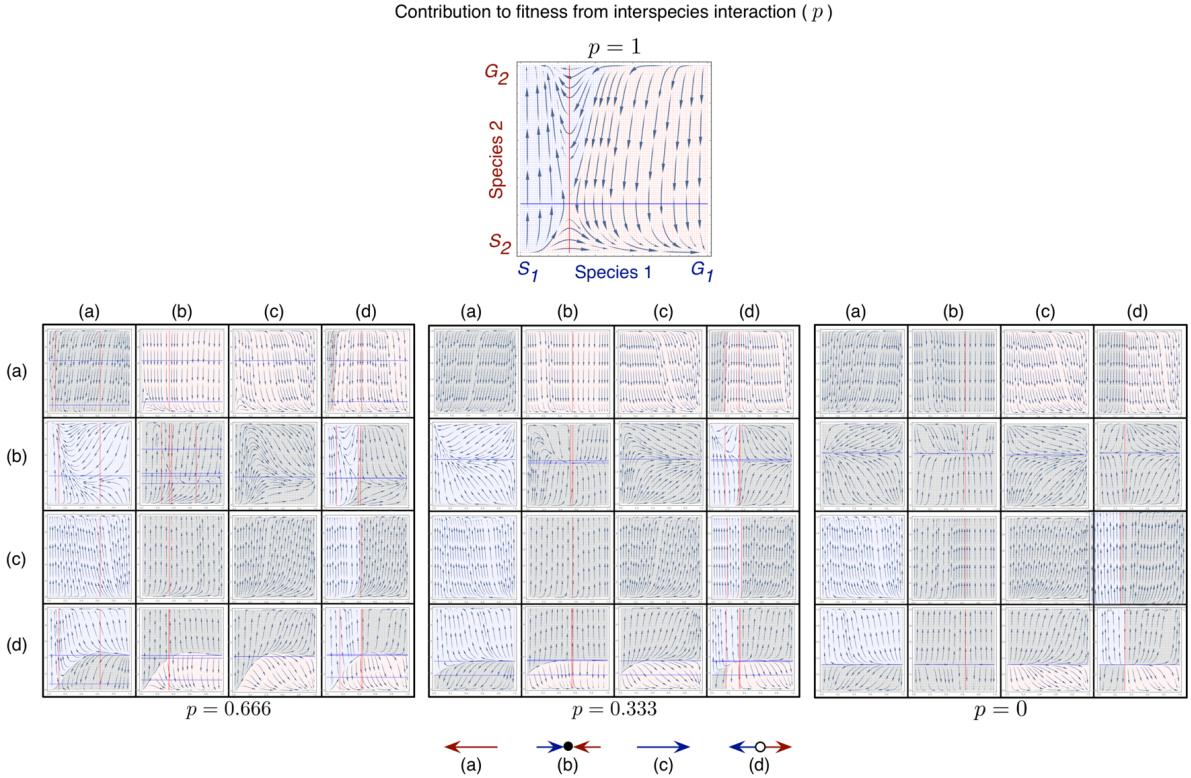


Figure A.1: $d_1^{inter} = d_2^{inter} = 5$, $b = 2$, $r_x = r_y/8$, $M_1 = M_2 = 1$ and $c = 1$ for the interspecies game. As for the intraspecies games we have $d_1^{intra} = d_2^{intra} = 5$ and $\tilde{b} = 10$ with (a) $\tilde{c} = 3$, $\omega = 3/4$, (b) $\tilde{c} = 1$, $\omega = 3/4$, (c) $\tilde{c} = 1$, $\omega = 4/3$ and (d) $\tilde{c} = 3$, $\omega = 4/3$, the exact same parameter values as in (Hauert et al., 2006b).

410 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,

$$\begin{aligned}\dot{x}_1 &= r_x x_1 (z_1 f_{G_1} - e_1) \\ \dot{x}_2 &= r_x x_2 (z_1 f_{S_1} - e_1) \\ \dot{z}_1 &= -\dot{x}_1 - \dot{x}_2\end{aligned}\tag{A.8}$$

and for species 2

$$\begin{aligned}\dot{y}_1 &= r_y y_1 (z_2 f_{G_2} - e_2) \\ \dot{y}_2 &= r_y y_2 (z_2 f_{S_2} - e_2) \\ \dot{z}_2 &= -\dot{y}_1 - \dot{y}_2\end{aligned}\tag{A.9}$$

We have e_1 and e_2 as the death rates for the two species. For the special case of $e_1 = \frac{z_1(x_1 f_{x_1} + x_2 f_{x_2})}{x_1 + x_2}$ 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.7. (This comes across as a special case only - justified? - or rephrase.) (Done) The fitnesses however need to be reevaluated in this setup. For example in Species 1 the fitness for type G_1 is,

$$\begin{aligned}f_{G_1}^{inter} &= \sum_{S=2}^{d_1} \binom{d_1 - 1}{S - 1} z_2^{d_1 - S} (1 - z_2)^{S-1} P_G^{inter}(S, y_1, y_2, z_2) \\ f_{G_1}^{intra} &= \sum_{S=2}^{d_1} \binom{d_1 - 1}{S - 1} z_1^{d_1 - S} (1 - z_1)^{S-1} P_G^{intra}(S, x_1, x_2, z_1)\end{aligned}\tag{A.10}$$

$$f_{G_1} = f_{G_1}^{inter} + f_{G_1}^{intra}\tag{A.11}$$

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

$$P_G^{inter}(S, p, q, r) = \sum_{k=0}^{S-1} V(S, p, q, r) \Pi_{G_1}(k+1)\tag{A.12}$$

$$P_G^{intra}(S, p, q, r) = \sum_{k=0}^{S-1} V(S, p, q, r) \Gamma_{G_1}(k+1)\tag{A.13}$$

$$P_S^{inter}(S, p, q, r) = \sum_{k=0}^{S-1} V(S, p, q, r) \Pi_{S_1}(k)\tag{A.14}$$

$$P_S^{intra}(S, p, q, r) = \sum_{k=0}^{S-1} V(S, p, q, r) \Gamma_{S_1}(k)\tag{A.15}$$

⁴¹¹ 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)
⁴¹² species game. and the actual payoffs are calculated as per Eqs. A.1 and A.4.
⁴¹³