

1 Eco-evolutionary dynamics of mutualisms

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4 Abstract

5 Mutualism has long been studied as a conundrum for evolutionary theory. In the
6 short run species that exploit other species would have a fitness advantage over a mu-
7 tually costly relationship. How such mutualisms are then maintained in the long run is
8 a valid question. However studies investigating this question often neglect the impor-
9 tance of within species interactions. Separating inter and intraspecies interactions may
10 not be always possible especially if the same individuals act within and between species.
11 Feedbacks between inter and intraspecies interactions are then inevitable and need to be
12 taken into account. Including population dynamics adds an ecological component to the
13 study. Herein we study the full eco-evolutionary dynamics of mutualism between two
14 species when a variety of intraspecies interactions are possible. Our results show that
15 while mutualism can turn into parasitism by overexploitation, for some intraspecies dy-
16 namics, mutualism can be maintained even while maintaining exploiters in the species
17 composition.

18 Keywords: mutualism, evolutionary game theory, multiple players, population dynamics, sea-
19 sonality

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34 **1 Introduction**

35 "Is there anything left to say about mutualisms The authors of this volume apparently think
 36 there is something to say, but I wonder if we are not beating a dead horse." - Janzen (1985).

37 Mutualisms have been debated over for a long time. As with many concepts, we can
 38 trace back the study of mutualism to Aristotle (Aristotle (Translator - Allan Gotthelf), 1991).
 39 Formally the Belgian zoologist Pierre van Beneden coined the term mutualism in 1873 (Bron-
 40 stein, 2003). The study of mutualistic relationships, interspecific interactions that benefit both
 41 species, is rich in empirical as well as theoretical understanding (Boucher, 1985; Hinton, 1951;
 42 Wilson, 1983; Bronstein, 1994; Pierce et al., 2002; Kiers et al., 2003; Bshary and Bronstein,
 43 2004) (Poulin and Vickery, 1995; Doebeli and Knowlton, 1998; Noë, 2001; Johnstone and
 44 Bshary, 2002; Bergstrom and Lachmann, 2003; Hoeksema and Kummel, 2003; Akçay and
 45 Roughgarden, 2007; Bshary et al., 2008). Most examples of mutualisms lend themselves to
 46 the idea of direct reciprocity (Trivers, 1971) and have thus been extensively studied using evo-
 47 lutionary game theory. Classical evolutionary games are usually limited to dyadic interactions
 48 (Weibull, 1995; Hofbauer, 1996; Hofbauer and Sigmund, 1998). Between two species then,
 49 the fundamental interaction is between two individuals, one from each species, and the sum
 50 of many such interactions determines the evolutionary dynamics. However, this is clearly a
 51 simplification as has been shown by numerous studies (Noë and Hammerstein, 1995; Noë,
 52 2001; Kiers et al., 2003; Stanton, 2003; Stadler and Dixon, 2008).

53 A well studied example of a one-to-many interaction is that of the plant-microbe mutual-
 54 ism wherein leguminous hosts prefer rhizobial symbionts that fix more nitrogen (Kiers et al.,
 55 2003), or where plants provide more carbon resources to fungal strains that are providing
 56 better access to nutrients (Kiers et al., 2011). As an example of an animal host, mutualis-
 57 tic relationship between the bioluminescent bacteria *Vibrio fischeri* and *Euprymna scolopes*,

58 the bobtail squid (McFall-Ngai, 2014) is a paradigm. Numerous bacteria are hosted in the
59 crypts of the squid’s light organ, where they produce light despite it being costly to do so.
60 The bacteria mature and develop within the squid, however those that fail to produce bio-
61 luminescence are evicted. While the variation in the phenotypes of the interacting partners
62 has been acknowledged, the usual analysis focuses on the interaction between the two species
63 without addressing this additional complexity. The classic example of ants and aphids or but-
64 terfly larvae (Pierce et al., 1987; Hölldobler and Wilson, 1990) is an excellent exposition of
65 many player interactions. Numerous ants tend to each of the soft bodied creatures, providing
66 them with shelter and protection from predation and parasites, in exchange for honeydew, a
67 rich source of food for the ants (Hill and Pierce, 1989; Stadler and Dixon, 2008). This is a
68 one-to-many interaction from the perspective of the larva.

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

80 Mutualistic relationships are, by definition, between species, and timing may be crucial for
81 their maintenance. It is natural to imagine that the observed mutualism may be seasonal and
82 the interactions are not a continuous feature of the evolutionary trajectory of a species. Three
83 species of spiderhunter sunbirds, *Arachnothera*, pollinate the evergreen subtropical “lipstick
84 plant”, *Aeschynanthus speciosus*, only twice a year. A wildly changing ecology can affect
85 the flowering time of some plants and the maturation of the dispersers they depend on, easily
86 disrupting such delicately balanced mutualistic interactions. Unless both interacting species
87 can respond in a similar fashion such a mutualism will break down (Warren and Bradford,
88 2014). We tackle this seasonality by varying the duration of the impact of intraspecies and
89 interspecies dynamics.

90 To complete the ecological picture we include population dynamics to the evolutionary
91 process of the mutualists. The two species can often occupy different niches and Such dy-
92 namics informs us about the population densities we might expect to find the interactors to
93 evolve to. We demonstrate the crucial nature of the feedback between population and evo-

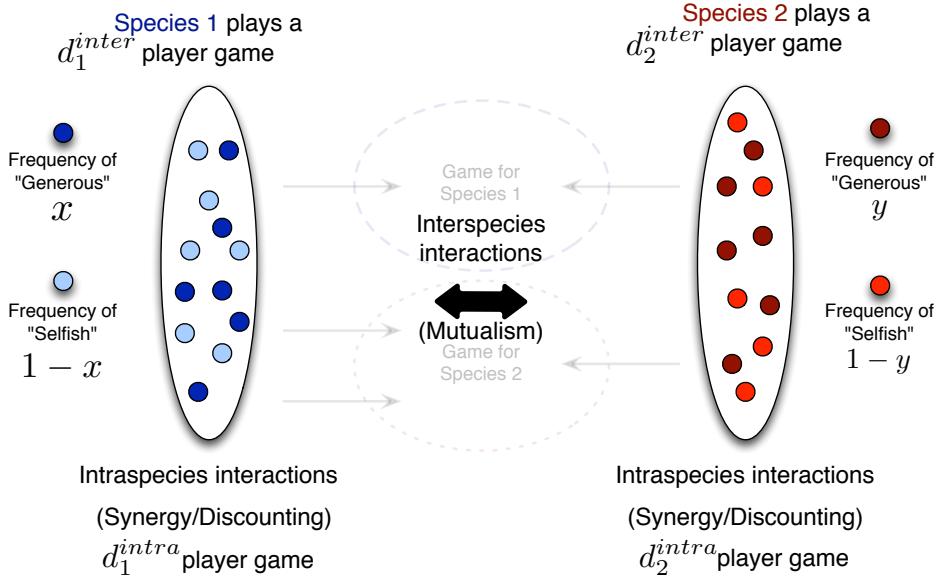


Figure 1: Evolutionary dynamics with combined inter-intra-species dynamics. We assume the interactions between species to be mutualistic described by the snowdrift game (Bergstrom and Lachmann, 2003; Souza et al., 2009; Gokhale and Traulsen, 2012). Species 1 plays a d_1^{inter} player game with species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

lutionary dynamics which can maintain mutualisms preventing either or both species from going extinct. Beginning with the previously studied interspecies dynamics as the foundational framework (Gokhale and Traulsen, 2012) we increase the complexity of the system by including intraspecies dynamics, and then seasonality. For the complete eco-evolutionary picture to emerge we include population dynamics next. The rich dynamics observed provides us with novel insights about the immense asymmetries in mutualisms and the fragility of such delicately balanced interactions.

101 **2 Model and Results**

102 **2.1 Interaction dynamics**

103 **2.1.1 Interspecies**

104 Focusing on mutualism, the interspecies dynamics is given by the multiplayer version of the
105 snowdrift game (Bergstrom and Lachmann, 2003; Souza et al., 2009; Gokhale and Traulsen,
106 2012) (also known as hawk-dove, or chicken). A common benefit is generated by contributions
107 from both species but there is a cost involved to it and species do not need to contribute
108 equally. However the individuals in each species could get away with contributing a bit less
109 than other individuals. Hence for example if producing brighter light comes at a premium for
110 the *Vibrio* in the squid then the dimmer *Vibrio* would be better off (Not producing any light
111 is not an option as the squid then actively evicts these bacteria) (McFall-Ngai, 2014). We
112 assume that each species consists of two types of individuals “Generous” G and “Selfish” S .
113 If enough individuals are “Generous” and contributing to the generation of mutual benefits
114 then other individuals can get away with being selfish (not contributing). But all individuals
115 in the game lose out if not enough are generous. Hence both species cannot be completely
116 “selfish”, as per the definition of mutualism. This interaction framework corresponds to that
117 of a multiplayer version of a snowdrift game and is discussed in detail in the Supplementary
118 Material (SI). Hence the pressure is on a species to make the partner “Generous” while itself
119 being “Selfish”. The fitness of each of the types within a species depends on the composition
120 of the other species. Denoting the frequency of the “Generous” types in species 1 (G_1) as
121 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 G_2 as
122 $f_{G_2}^{inter}(x)$.

123 **2.1.2 Intraspecies**

124 For intraspecies dynamics we do not restrict ourselves to any particular interaction structure
125 and thus make use of the general multiplayer evolutionary games framework (Gokhale and
126 Traulsen, 2010, 2014). Moving from the interspecies dynamics, the two types already de-
127 scribed are “Generous” and “Selfish”. Thus we already have each species containing two
128 different types of individuals. It is possible that a different categorisation exists within a
129 species. Thus if the interactions within a species are say between “Cooperators” and “Defec-
130 tors”, these types could be made up of a combination of “Generous” and “Selfish” individuals.
131 However for the sake of simplicity we study the dynamics between “Generous” and “Selfish”
132 types within a species where the types are defined at the interspecies level. The cost benefit
133 framework described in (Eshel and Motro, 1988; Hauert et al., 2006b) allows us to transition

134 between four classic scenarios of evolutionary dynamics (Nowak and Sigmund, 2004). For
 135 example in our case we can have a dominance of the “Generous” type or the “Selfish” type
 136 or both the types can invade from rare resulting in a co-existence or bistability if both pure
 137 strategies are mutually non-invasive. For the intraspecies interactions the fitness of a G_1 is
 138 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”
 139 types.

140 2.2 Combined dynamics

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

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

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,

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

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

151 shown to be a crucial factor in determining the evolutionary dynamics could be different for
152 each interactions, inter and intraspecies interactions for species 1 (d_1^{inter} , d_1^{intra}) and simi-
153 larly for species 2 (d_2^{inter} , d_2^{intra}). The interspecies interactions are proxied by the multiplayer
154 snowdrift game which can incorporate threshold effects. For example a certain number of
155 “Generous” cleaner fish may be required to clean the host or a certain number of “Generous”
156 ants required to protect larva from predators. We can have M_1 and M_2 as the thresholds in the
157 two species. Since the interaction matrices for the inter and intraspecies dynamics are com-
158 pletely different, in principle, we can have different costs and benefits for the four games (two
159 snowdrift games from the perspective of each species and the intragames within each species).

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

166 2.3 Seasonality

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

175 To analyse such episodic mutualistic events, instead of a static variable p measuring the
176 impact of interspecific interaction on fitness we make use of a time-dependent function $p(t) =$
177 $(1 + \sin(at))/2$. For the particular parameter set used in Fig. 2 ($p = 0.666$ panel), introducing
178 seasonality still maintains the two interior fixed points (they are closer to each other for $p =$
179 0.5), but this is seen only when the oscillations in $p(t)$ are comparable, $a = 1$, or faster, $a = 10$,
180 with respect to the evolutionary timescale. For slower oscillations $a = 0.1$ we see cyclic
181 behaviour which is prominent in species 2 more than in species 1. Very slow oscillations mean
182 that the system spends longer close to the starting value of $p(t)$ and hence the phase in which
183 $p(t)$ starts becomes more and more important for smaller and smaller a . This is especially
184 interesting if the stability of the system is qualitatively affected over the p continuum.

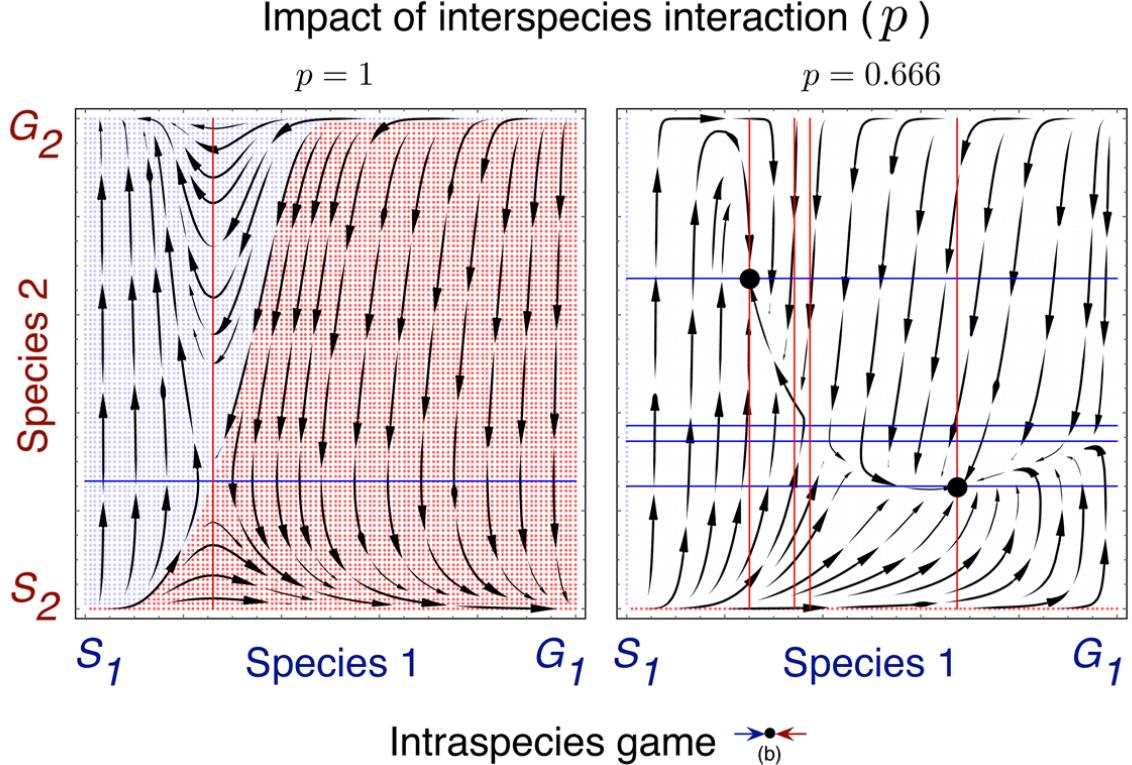


Figure 2: **Change in evolutionary dynamics due to inclusion of intraspecies dynamics.** When the fitness of the “Generous” and “Selfish” types in both the species is solely determined by the interactions which occur between species (in this case mutualism, $p = 1$) then we recover the dynamics as studied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

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

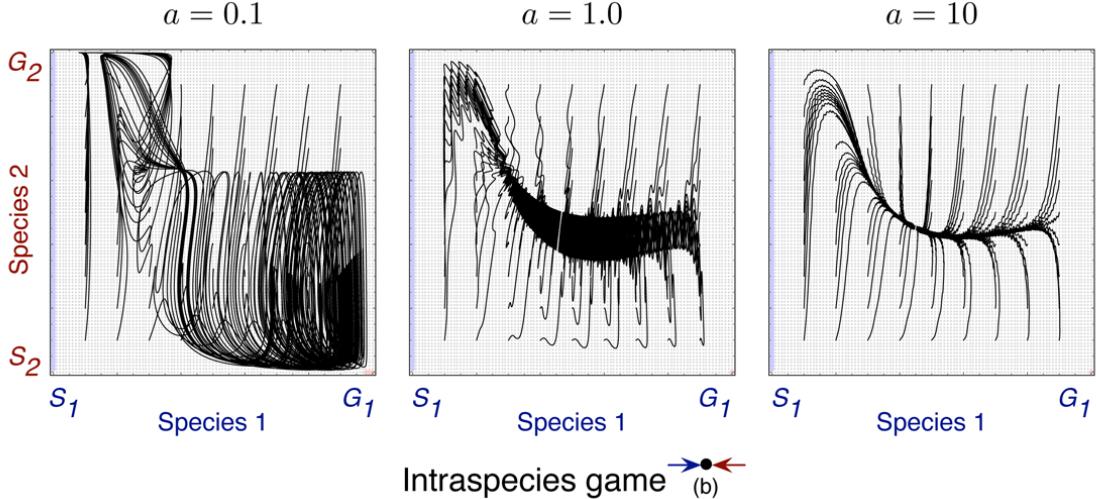


Figure 3: Seasonal changes in the interspecies interactions affecting the evolutionary dynamics within species. We model the impact of the interspecies interaction on the fitness of the different types as in Eqs. 1 however instead of a static value for p we introduce seasonality via a simple sine function 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).

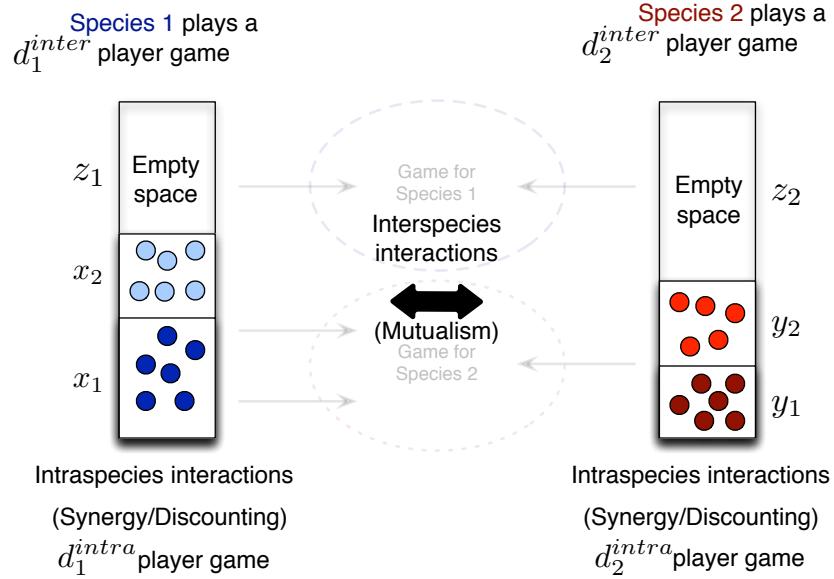


Figure 4: Population and evolutionary dynamics with combined inter-intra-species dynamics. As with the interactions described in Fig. 1 the two species consist of two types of individuals “Generous” and “Selfish”. Since the two species can in principle occupy different environmental niches, they can 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.

185 2.4 Population dynamics

186 Until now we have considered that each species consists of two types of individuals and they
 187 make up the population of that species. However populations sizes change over time. As-
 188 suming that ecological changes are fast enough that they can be averaged out, we can usually
 189 ignore their effect on the evolutionary dynamics. It is now possible to show that evolution can
 190 happen at fast timescales, comparable to those of the ecological dynamics ([Post and Palko-](#)
 191 [vacs, 2009; Beaumont et al., 2009; Hanski, 2011; Sanchez and Gore, 2013](#)). Hence we need
 192 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. 4). 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,

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

for species 1, and

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

for species 2. 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

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

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

195 Interactions at varying population densities affect the group size formation which now
196 includes the possibilities of player positions being left empty. Thus for smaller population
197 densities the interactions groups are small and vice versa for lager densities. Effect of group
198 size on the evolutionary dynamics is a well documented phenomena which can potentially
199 change the results qualitatively (Pacheco et al., 2009; Souza et al., 2009). Such a two species
200 multi-type interaction system is a complicated as well as a realistic depiction of most of the
201 mutualisms observed in nature. However given this complexity, we need to look at the dy-
202 namics within the two species simultaneously.

203 We take the most stable situation observed in the dynamics when population dynamics is
204 absent (Fig. 2) which shows two internal stable equilibria and add population dynamics to it.
205 The results are summarised in Figure 5 where we plot the evolutionary parameter (fraction of
206 “Generous” in each species) against the ecological parameter, the population density (or rather
207 in this case the empty spaces) .

208 3 Discussion

209 Mutualistic interactions have been implicated as one possible mechanism facilitating the suc-
210 cess of invasive species (Richardson et al., 2000). However mutualism based invasions also
211 have the possibility to change the composition of the supporting local species. About 150
212 ant species have been found invading new habitats mostly by forming mutualistic associations
213 with honeydew producers (McGlynn, 1999).

214 Usually when interspecies relationships such as mutualism (or antagonist relationships as
215 in predator-prey) are considered, the within species interactions are ignored for the sake of
216 convenience. The converse is the case when the intraspecies interactions are of interest. The
217 major body of work focusing on within population social dilemmas between “Cooperators” and
218 “Defectors” is an example of the same. Obviously, this is an assumption which is very useful
219 when distilling the interactions at different community scales. However when the inter and
220 intraspecies interactions are interdependent then the feedbacks between the two levels cannot
221 be ignored (Schluter and Foster, 2012).

222 In principle the framework developed herein is capable of handling a diverse array of inter-
223 and intraspecific interactions. For interspecific interactions our focus is on mutualism. Mu-
224 tualistic interactions between two species can be represented by a bimatrix game. The compo-
225 nents of each of the two game matrices need not be correlated as long as they independently
226 satisfy the inequalities leading to a Snowdrift games. Including realistic phenomena such as
227 intraspecies interactions, population dynamics and seasonality we show that maintenance of
228 mutualism is possible. A fragile balance of parameters maintains mutualism. If within each
229 species the “Generous” and “Selfish” interactions result in coexistence then it can outweigh the
230 competition which they experience at the interspecies level. Note however that at the inter-
231 species level the competition of a “Generous” individuals is with the “Selfish” individuals from
232 the other species. While the “Selfish” individuals from the other species can drive “Generous”
233 individuals within a species extinct, co-existence between “Generous” and “Selfish” within the
234 same species can overcome the pressure for extinction. In this way mutualism can be main-
235 tained but it comes at a cost of also maintaining a significant level of exploiters. In fact the
236 coevolutionary dynamics between the two species is determined together by the inter as well

Evolutionary and population dynamics

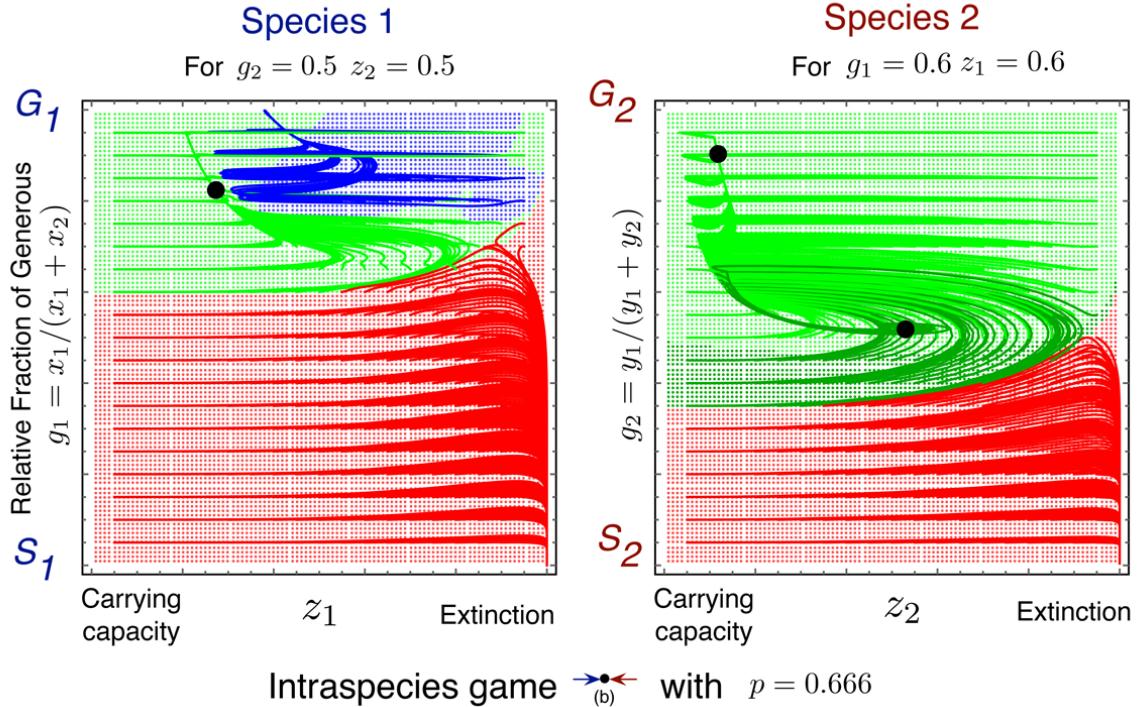


Figure 5: **Dynamics of evolutionary strategies and population density for an intraspecies coexistence game with interspecies mutualism.** With exactly the same parameters as that of Figure 2 with symmetric death rates $e_1 = e_2 = 0.05$ we show two different numerically evaluated examples. Left Panel: 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.

237 as the intraspecific interactions.

238 While the simple case makes predictions possible, including seasonality inserts a time
239 dependent factor which makes analytical reasoning difficult. However given the patterns of
240 episodic interactions and studies of mutualistic relationship obtained from field studies over
241 the decades it might be possible to include the seasonal component in future analysis on re-
242 alistic systems to see how the interactions are going to change under drastic climate change.
243 Including this feature informs us of the dependence of the mutualism on environmental fac-
244 tors. This is particularly important as species specific mutualisms are at a high risk of being
245 destabilised. For example bird pollinators of numerous plants are sensitive to the environmen-
246 tal and ecological changes which can occur naturally or catalysed by anthropogenic activity.
247 The difference in the timescales of the evolutionary process and environmental fluctuations
248 highlights the fact that averaging out the environmental effects might not always be possible.
249 The system can show qualitatively different behaviour from the average dynamics depending
250 on the kind of interactions initially involved within and between species.

251 An ecologically important example of species specific mutualism is that of sunbirds, par-
252 ticularly the Malachite Sunbird (*Nectarinia famosa*) and the geophyte *Brunsvigia littoralis*.
253 Besides being sensitive to the environmental variation, *B. littoralis* it furthermore suffers from
254 low population densities (Geerts and Pauw, 2012) and threatened by rapid urbanisation. An
255 example more economically connected to humans comes from the honeybee, *Apis mellifera*.
256 A species of immense capital importance, the colony collapse of this pollinator has been at-
257 tributed to numerous causes ranging from the pesticides to biological interference from para-
258 sites and pathogens as well as a change in the environment (Nazzi et al., 2012). Our framework
259 incorporates exactly these essential elements of interspecies interactions and changing envi-
260 ronments, predicting a deep impact on population dynamics of the interactors. While our
261 focus is currently on mutualism, it is easy to change the interactions by changing/modifying
262 the game defining the interspecies interactions. Including population dynamics and the real
263 threat of extinction needs to be acknowledged when modelling such scenarios. Only then can
264 better conservation tactics be formulated which are not solely based on evolutionary predic-
265 tions but eco-evolutionary dynamics.

266 Going back to one of the most well studied examples of mutualism, the squid-vibrio sym-
267 biosis, it is hard to exclude population dynamics at least from one of the interacting species
268 (Nyholm and McFall-Ngai, 2004). The diel pattern of the host squid is associated with oscil-
269 lations in the population density of the symbiont *Vibrio fiscerei*. Since the growth rates of the
270 two species differ vastly, the population size turnover inside the squid needs to be managed.
271 While the squid makes use of the full light organ at night camouflaging itself from predators,
272 at dawn it expels almost 95% of the bacteria. The squid lies buried underground during the

273 day and the remaining 5% of the bacteria repopulate the light organ again reaching saturation
274 by mid-afternoon. While in our model the population dynamics of the mutualists are driven
275 by the empty spaces in their own niches, this particular example beckons a specific modeling
276 approach where the host itself acts as the niche environment of the symbiont and controls the
277 population density too. Our framework comes with the capability of including such specific
278 examples and can be modified to suit particular examples. It thus helps in not only elucidating
279 the interactions which might be involved in generating the dynamics which we observe in na-
280 ture but rather provide the criteria under which the observed dynamics are being maintained
281 and ways to explore their stability under varying crucial parameters.

282 Our study shows the critical nature of mutualism and the sliver of parameter space where
283 they are maintained. A slight change in the values can either end up in a system where one of
284 the mutualist is completely exploited by the other species or even leads to extinction of both
285 types in case of obligate mutualisms. Going back to [Janzen \(1985\)](#) an appropriately succinct
286 summary would be, ‘A mutualist today may be a parasite of the mutualism tomorrow’.

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289 References

- 290 E. Akçay and J. Roughgarden. Negotiation of mutualism: rhizobia and legumes. *Proceedings*
291 *of the Royal Society B*, 274:25–32, 2007.
- 292 Aristotle (Translator - Allan Gotthelf). *History of Animals*. Number Books VII-X. No - 439
293 in Loeb Classical Library. Harvard University Press, 1991.
- 294 H. J. E. Beaumont, J. Gallie, C. Kost, G. C. Ferguson, and P. B. Rainey. Experimental evolution
295 of bet hedging. *Nature*, 462:90–93, 2009.
- 296 Jocelyn E Behm and E Toby Kiers. A phenotypic plasticity framework for assessing intraspe-
297 cific variation in arbuscular mycorrhizal fungal traits. *Journal of Ecology*, 102(2):315–327,
298 2014.
- 299 C. T. Bergstrom and M. Lachmann. The Red King Effect: When the slowest runner wins the
300 coevolutionary race. *Proceedings of the National Academy of Sciences USA*, 100:593–598,
301 2003.
- 302 D. H. Boucher. The idea of mutualism, past and future. In D. H. Boucher, editor, *The Biology*
303 *of Mutualism*, pages 1–28. Oxford University Press, New York, 1985.

- 304 J. L. Bronstein. Our current understanding of mutualism. *The Quarterly Review of Biology*,
305 69:31–51, 1994.
- 306 J. L. Bronstein. Exploitation within mutualistic interactions. In Peter Hammerstein, editor,
307 *Genetic and Cultural Evolution of Cooperation*. MIT Press, 2003.
- 308 R. Bshary and D. Schäffer. Choosy reef fish select cleaner fish that provide high-quality
309 service. *Animal Behaviour*, 63:557–564, 2002.
- 310 R. Bshary, A. S. Grutter, A. S. T. Willener, and O. Leimar. Pairs of cooperating cleaner fish
311 provide better service quality than singletons. *Nature*, 455:964–967, 2008.
- 312 R. S. Bshary and J. L. Bronstein. Game structures in mutualisms: what can the evidence tell
313 us about the kinds of models we need? *Advances in the Study of Behavior*, 34:59–104,
314 2004.
- 315 R. S. Bshary and R. Noë. Biological markets: the ubiquitous influence of partner choice on the
316 dynamics of cleaner fish-client reef fish interactions. In Peter Hammerstein, editor, *Genetic*
317 and *Cultural Evolution of Cooperation*, pages 167–184. MIT Press, 2003.
- 318 M. Doebeli and N. Knowlton. The evolution of interspecific mutualisms. *Proceedings of the*
319 *National Academy of Sciences USA*, 95:8676–8680, 1998.
- 320 I Eshel and U Motro. The three brothers' problem: kin selection with more than one potential
321 helper. 1. The case of immediate help. *American Naturalist*, pages 550–566, 1988.
- 322 Lei Gao, Yao-Tang Li, and Rui-Wu Wang. The shift between the Red Queen and the Red King
323 effects in mutualisms. *Scientific reports*, 5:8237, 2015.
- 324 S Geerts and A Pauw. The cost of being specialized: Pollinator limitation in the endan-
325 gered geophyte Brunsvigia litoralis (Amaryllidaceae) in the Cape Floristic Region of South
326 Africa. *South African Journal of Botany*, 78:159–164, 2012.
- 327 C. S. Gokhale and A. Traulsen. Evolutionary games in the multiverse. *Proceedings of the*
328 *National Academy of Sciences USA*, 107:5500–5504, 2010.
- 329 C. S. Gokhale and A. Traulsen. Mutualism and evolutionary multiplayer games: revisiting the
330 Red King. *Proceedings of the Royal Society B*, 279:4611–4616, 2012.
- 331 C. S. Gokhale and A. Traulsen. Evolutionary multiplayer games. *Dynamic Games and Appli-*
332 *cations*, 4:468–488, 2014.

- 333 I A Hanski. Eco-evolutionary spatial dynamics in the Glanville fritillary butterfly. *Proceedings*
334 *of the National Academy of Sciences USA*, 108(35):14397–14404, 2011.
- 335 C. Hauert, M. Holmes, and M. Doebeli. Evolutionary games and population dynamics: main-
336 tenance of cooperation in public goods games. *Proceedings of the Royal Society B*, 273:
337 2565–2570, 2006a.
- 338 C. Hauert, F. Michor, M. A. Nowak, and M. Doebeli. Synergy and discounting of cooperation
339 in social dilemmas. *Journal of Theoretical Biology*, 239:195–202, 2006b.
- 340 C. J. Hill and N. E. Pierce. The effect of adult diet on the biology of butterflies 1. the common
341 imperial blue, *Jalmenus evagoras*. *Oecologia*, 81:249–257, 1989.
- 342 H. E. Hinton. Myrmecophilous lycaenidae and other lepidoptera - a summary. *Proc. Trans. S.*
343 *London Entomol. Nat. Hist. Soc.*, 1949-50:111–175, 1951.
- 344 J. D. Hoeksema and M. Kummel. Ecological persistence of the plant-mycorrhizal mutualism:
345 A hypothesis from species coexistence theory. *The American Naturalist*, 162:S40–S50,
346 2003.
- 347 J. Hofbauer. Evolutionary dynamics for bimatrix games: A Hamiltonian system? *Journal of*
348 *Mathematical Biology*, 34:675–688, 1996.
- 349 J. Hofbauer and K. Sigmund. *Evolutionary Games and Population Dynamics*. Cambridge
350 University Press, Cambridge, UK, 1998.
- 351 B. Hölldobler and E. O. Wilson. *The Ants*. Belknap Press, 1990.
- 352 D. H. Janzen. The natural history of mutualisms. In D. H. Boucher, editor, *The Biology of*
353 *Mutualism*, pages 1–28. Oxford University Press, New York, 1985.
- 354 R. A. Johnstone and R. Bshary. From parasitism to mutualism: partner control in asymmetric
355 interactions. *Ecology Letters*, 5:634–639, 2002.
- 356 E. T. Kiers, R. A. Rousseau, S. A. West, and R. F. Denison. Host sanctions and the legume-
357 rhizobium mutualism. *Nature*, 425:78–81, 2003.
- 358 E Toby Kiers, Marie Duhamel, Yugandhar Beesetty, Jerry A Mensah, Oscar Franken, Erik Ver-
359 bruggen, Carl R Fellbaum, Georg A Kowalchuk, Miranda M Hart, Alberto Bago, Todd M
360 Palmer, Stuart A West, Philippe Vandenkoornhuyse, Jan Jansa, and Heike Bücking. Recip-
361 rocal rewards stabilize cooperation in the mycorrhizal symbiosis. *Science*, 333:880–882,
362 Jan 2011.

- 363 J. Maynard Smith. *Evolution and the Theory of Games*. Cambridge University Press, Cam-
364 bridge, 1982.
- 365 Margaret McFall-Ngai. Divining the Essence of Symbiosis: Insights from the Squid-Vibrio
366 Model. *PLoS Biology*, 12(2), 2014.
- 367 Terrence P McGlynn. The Worldwide Transfer of Ants: Geographical Distribution and Eco-
368 logical Invasions. *Journal of Biogeography*, 26(3):535–548, 1999.
- 369 Francesco Nazzi, Sam P Brown, Desiderato Annoscia, Fabio Del Piccolo, Gennaro Di Prisco,
370 Paola Varricchio, Giorgio Della Vedova, Federica Cattonaro, Emilio Caprio, and Francesco
371 Pennacchio. Synergistic Parasite-Pathogen Interactions Mediated by Host Immunity Can
372 Drive the Collapse of Honeybee Colonies. *PLoS Pathogens*, 8(6):e1002735, 2012.
- 373 R. Noë. Biological markets: partner choice as the driving force behind the evolution of
374 mutualisms. In Ronald Noë, Jan A.R.A.M. van Hooff, and Peter Hammerstein, editors,
375 *Economics in Nature: Social Dilemmas, Mate Choice and Biological Markets*. Cambridge
376 University Press, 2001.
- 377 Ronald Noë and Peter Hammerstein. Biological markets. *Trends in Ecology and Evolution*,
378 10(8):336–339, August 1995.
- 379 M. A. Nowak. *Evolutionary Dynamics*. Harvard University Press, Cambridge MA, 2006.
- 380 M. A. Nowak and K. Sigmund. Evolutionary dynamics of biological games. *Science*, 303:
381 793–799, 2004.
- 382 Spencer V Nyholm and Margaret McFall-Ngai. The winnowing: establishing the
383 squid—[ndash]—vibrio symbiosis. *Nature Reviews Microbiology*, 2(8):632–642, 2004.
- 384 J. M. Pacheco, F. C. Santos, M. O. Souza, and B. Skyrms. Evolutionary dynamics of collective
385 action in n-person stag hunt dilemmas. *Proceedings of the Royal Society B*, 276:315–321,
386 2009.
- 387 N. E. Pierce, M. F. Braby, A. Heath, D. J. Lohman, J. Mathew, D. B. Rand, and M. A. Travas-
388 sos. The Ecology and Evolution of Ant Association in the Lycaenidae (Lepidoptera). *An-
389 nual Review of Entomology*, 47:733–770, 2002.
- 390 Naomi E Pierce, R L Kitching, R C Buckley, M F J Taylor, and K F Benbow. The costs and
391 benefits of cooperation between the australian lycaenid butterfly, *Jalmenus evagoras*, and
392 its attendant ants. *Behavioral Ecology and Sociobiology*, 21:237–248, Jun 1987.

- 393 D M Post and E P Palkovacs. Eco-evolutionary feedbacks in community and ecosystem ecology: interactions between the ecological theatre and the evolutionary play. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1523):1629–1640, 2009.
- 396 R. Poulin and W. L. Vickery. Cleaning symbiosis as an evolutionary game: to cheat or not to cheat? *Journal of Theoretical Biology*, 175:63–70, 1995.
- 398 Nicole E Rafferty, Paul J CaraDonna, and Judith L Bronstein. Phenological shifts and the fate 399 of mutualisms. *Oikos*, 124(1):14–21, 2015.
- 400 D M Richardson, N Allsopp, C M D’Antonio, S J Milton, and M Rejmánek. Plant invasions— 401 the role of mutualisms. *Biological Reviews*, 75(1):65–93, 2000.
- 402 J. Roughgarden. Resource partitioning among competing species - a coevolutionary approach. 403 *Theoretical Population Biology*, 9:288–424, 1976.
- 404 J. Roughgarden, D. Heckel, and E. Fuentes. *Lizard Ecology: Studies of a Model Organism*, 405 chapter Coevolutionary theory and the biogeography and community structure of *Anolis*., 406 pages 371–410. Harvard University Press, 1983.
- 407 A Sanchez and J Gore. Feedback between Population and Evolutionary Dynamics Determines 408 the Fate of Social Microbial Populations. *PLoS Biology*, 11(4):e1001547, 2013.
- 409 Jonas Schluter and Kevin R Foster. The evolution of mutualism in gut microbiota via host 410 epithelial selection. *PLoS Biology*, 10(11):e1001424, 2012.
- 411 M. O. Souza, J. M. Pacheco, and F. C. Santos. Evolution of cooperation under n-person 412 snowdrift games. *Journal of Theoretical Biology*, 260:581–588, 2009.
- 413 B. Stadler and A. F. G. Dixon. *Mutualism: Ants and their Insect partners*. Cambridge Uni- 414 versity Press, 2008.
- 415 Maureen L Stanton. Interacting Guilds: Moving beyond the Pairwise Perspective on Mutual- 416 alisms. *The American Naturalist*, 162(s4):S10–S23, 2003.
- 417 R. L. Trivers. The evolution of reciprocal altruism. *The Quarterly Review of Biology*, 46: 418 35–57, 1971.
- 419 Robert J II Warren and Mark A Bradford. Mutualism fails when climate response differs 420 between interacting species. *Global Change Biology*, 20(2):466–474, 2014.
- 421 J. W. Weibull. *Evolutionary Game Theory*. MIT Press, Cambridge, 1995.

422 D. S. Wilson. The effect of population structure on the evolution of mutualism: A field test
423 involving burying beetles and their phoretic mites. *The American Naturalist*, 121(6):851–
424 870, 1983.

425 Izumi Yao and Shin-Ichi Akimoto. Seasonal changes in the genetic structure of an aphid-ant
426 mutualism as revealed using microsatellite analysis of the aphid *Tuberculatus quercicola*
427 and the ant *Formica yessensis*. *Journal of Insect Science*, 9(1):9–18, 2009.

428 Izumi Yao, Harunobu Shibao, and Shin-Ichi Akimoto. Costs and Benefits of Ant Attendance
429 to the Drepanosiphid Aphid *Tuberculatus quercicola*. *Oikos*, 89(1):3–10, 2000.

430 **A Interspecies Evolutionary Dynamics**

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

435 **The snowdrift game**

436 **Two player setting**

437 Two drivers are stuck in a snowdrift. They must shovel away the snow (paying the cost c)
438 to reach home (benefit b) but there are three possible outcomes to this scenario. One of the
439 driver shovels while the other stays warm in the care ($b - c$ and b), both the drivers share the
440 workload and shovel away the snow ($b - c/2$ and $b - c/2$) or none of them gets out of the care
441 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

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

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

452 Multiplayer setting

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

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

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,

$$\begin{aligned}f_{G_1}^{inter}(y) &= \sum_{k=0}^{d_1^{inter}-1} \binom{d_1^{inter}-1}{k} y^k (1-y)^{d_1^{inter}-1-k} \Pi_{G_1}(k+1) \\ f_{S_1}^{inter}(y) &= \sum_{k=0}^{d_1^{inter}-1} \binom{d_1^{inter}-1}{k} y^k (1-y)^{d_1^{inter}-1-k} \Pi_{S_1}(k),\end{aligned}\tag{A.2}$$

455 and similarly $f_{G_2}^i$ nter and $f_{S_2}^i$ nter for species 2.

456 Note that here for the sake of notation we have assumed the same values of benefits and
457 costs, thresholds for the two species. However along with the number of player d_1^{inter} and
458 d_2^{inter} , these parameters could be very well different for the two species. For asymmetric bi-
459 matrix games there is a difference in the dynamics between the standard replicator dynamics
460 and the alternative dynamics put forward by Maynard-Smith ([Maynard Smith, 1982](#)). In this
461 case the replicator equations cannot be simplified by removing the average fitness from the
462 denominator and can give rise to qualitatively different dynamics. Then one has to resort to
463 difference rather than differential equations.

464 **B Intraspecies Evolutionary Dynamics**

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

474 **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. Since the categorisation of the strategies at the intraspecies 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?) (Yes. Now described above) 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),

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

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

where the payoffs are given by,

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

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

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

480 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,

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

$$\dot{y} = r_y y (f_{G_2}(x, y) - \bar{f}_2(x, y)). \quad (\text{A.7})$$

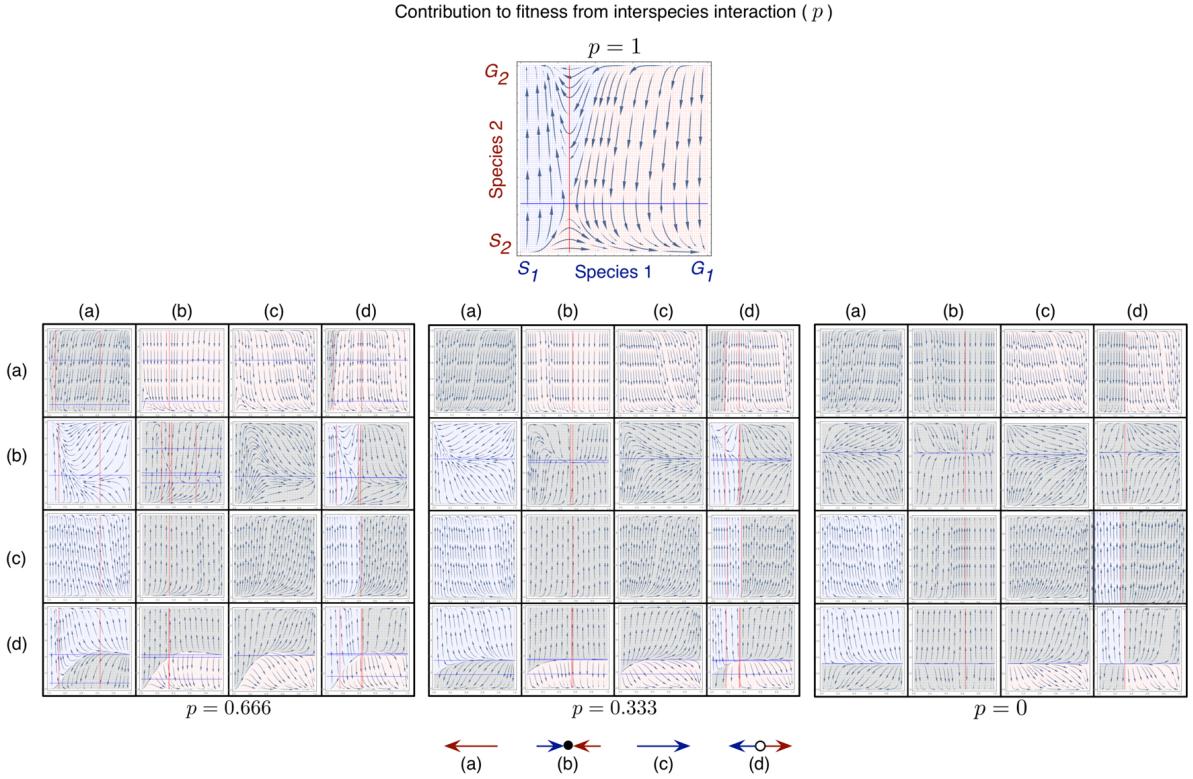


Figure A.1: $d_1^{inter} = d_2^{inter} = 5$, $b = 2$, $r_x = r_y/8$, $M_1 = M_2 = 1$ and $c = 1$ for the interspecies game. As for the intraspecies games we have $d_1^{intra} = d_2^{intra} = 5$ and $\tilde{b} = 10$ with (a) $\tilde{c} = 3$, $\omega = 3/4$, (b) $\tilde{c} = 1$, $\omega = 3/4$, (c) $\tilde{c}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

481 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. 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,

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

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

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

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

⁴⁸² where $V(S, p, q, r) = \binom{S-1}{k} \left(\frac{p}{1-r}\right)^k \left(\frac{q}{1-r}\right)^{S-1-k}$ is the probability of having a k “Generous”(Cooperator) individuals and $S - 1 - k$ “Selfish”(Defector) individuals in the inter(intra) species game. and the actual payoffs are calculated as per Eqs. A.1 and A.4.