

A general model for the evolution of mutualisms

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Abstract

The evolution of mutualisms presents a puzzle. Why does selection favour cooperation among species rather than cheaters that accept benefits but provide nothing in return? Here we present a general model that predicts three key factors will be important in mutualism evolution: (i) high benefit to cost ratio, (ii) high within-species relatedness and (iii) high between-species fidelity. These factors operate by moderating three types of feedback benefit from mutualism: *cooperator association*, *partner-fidelity feedback* and *partner choice*. In defining the relationship between these processes, our model also allows an assessment of their relative importance. Importantly, the model suggests that phenotypic feedbacks (partner-fidelity feedback, partner choice) are a more important explanation for between-species cooperation than the development of genetic correlations among species (cooperator association). We explain the relationship of our model to existing theories and discuss the empirical evidence for our predictions.

Introduction

...there is no general theory of mutualism that approaches the explanatory power that 'Hamilton's rule' appears to hold for the understanding of within-species interactions. (Herre *et al.*, 1999)

Mutualisms are widespread and ecologically important but, like within-species cooperation, their evolution represents a challenge for evolutionary theory (Herre *et al.*, 1999; Bronstein, 2003; Sachs *et al.*, 2004). Trivers (1971) showed that mutualism resembles the Prisoner's dilemma, where two players can benefit from cooperation but gain most from cheating their partners. This raises the question of how selection favours cooperation among species rather than cheaters that accept the benefits from their partner species without providing anything in return.

A number of factors have been suggested to explain mutualism (reviewed in Bergstrom *et al.*, 2003; Sachs *et al.*, 2004). Axelrod & Hamilton (1981) showed that cooperation is favoured in the Prisoner's dilemma when

there are repeated interactions and when cooperation is conditional upon the other partner's behaviour. More recently, a spatial version of the prisoner's dilemma has shown that local interactions can produce cooperation among species without conditional behaviour (Doebeli & Knowlton, 1998; Yamamura *et al.*, 2004). Frank (1994) also emphasized the potential for local interactions to favour mutualism when it generates a genetic correlation between species, which was likened to a form of *between-species relatedness*. *Within-species relatedness* has also been shown to promote mutualism (Frank, 1994; West *et al.*, 2002b).

Other approaches have separated Axelrod and Hamilton's two themes of repeated interactions and conditional responses (Sachs *et al.*, 2004). First, the idea of repeated interactions has been developed into the notion of partner-fidelity feedback (Bull & Rice, 1991; Sachs *et al.*, 2004), which argues that cooperation will be favoured when species stay together in stable associations that align their fitness interests. Secondly, conditional responses are central to the idea of partner choice, where one species interacts preferentially with the more cooperative members of the partner species (Bull & Rice, 1991; Noe & Hammerstein, 1994; Johnstone & Bshary, 2002; Sachs *et al.*, 2004). Similarly, in partner sanctions noncooperative partners are sanctioned and receive less mutualistic aid (West *et al.*, 2002a; Kiers *et al.*, 2003). Normally sanctions are considered to be enforced by only

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one party but mutualism is also promoted if both partner species preferentially direct aid to more cooperative members of the other species (Ferriere *et al.*, 2002). Finally, it has been suggested that there may often simply be no incentive to cheat a mutualism if cooperation carries no energetic cost (Connor, 1986, 1995; Sachs *et al.*, 2004). Such 'byproduct mutualisms' can easily evolve and it has been suggested that in many mutualisms one of the partners may be largely passive and bear no costs from the interaction (pseudoreciprocity, Connor, 1986).

Several factors, therefore, have been proposed to facilitate the evolution of cooperation between species and Sachs *et al.* (2004) recently proposed a useful verbal classification of some of the ideas. However, the theory is characterized by studies that focus upon one or a few factors in isolation and the formal relationship between the major ideas is unclear. For example, what is the relationship between the partner-fidelity feedback and the evolution of genetic correlations among species? How general are the effects of within-species relatedness? And how does byproduct mutualism interact with other mechanisms of mutualism evolution? As such, we lack a general theory of mutualism (Herre *et al.*, 1999; West *et al.*, 2002a; Bergstrom *et al.*, 2003; Sachs *et al.*, 2004). Here we present a simple model that captures the key processes in mutualism evolution with the aim of uniting the existing ideas in a single framework. The result identifies three major factors important in the evolution of mutualisms: (i) benefit to cost ratio, (ii) within-species relatedness and (iii) between-species fidelity, which operate through three distinct feedback mechanisms: cooperator association, partner-fidelity feedback and partner choice. In defining the relationship between these processes, our model also allows their relative importance in mutualism evolution to be assessed. Importantly, the model suggests that phenotypic feedbacks (partner-fidelity feedback, partner choice) will typically be more important in between-species cooperation than the genetic correlations (cooperator association) that have been emphasized by previous theory (Frank, 1994; Doebeli & Knowlton, 1998; Yamamura *et al.*, 2004).

The model

We consider two species, A and B, which can increase each other's fitness (Fig. 1), e.g. microbe species in a biofilm that exchange compounds to mutual advantage (Kuhl *et al.*, 1996) or a cleaner fish that removes parasites from a client fish that allows the cleaner to leave its mouth unharmed (Grutter, 1999; Bshary & Grutter, 2002). We adopt a general approach because we are interested in the factors common to all mutualisms. General models can be criticized for removing much of the complexity of biological systems but their value lies in highlighting the fundamental processes of evolution

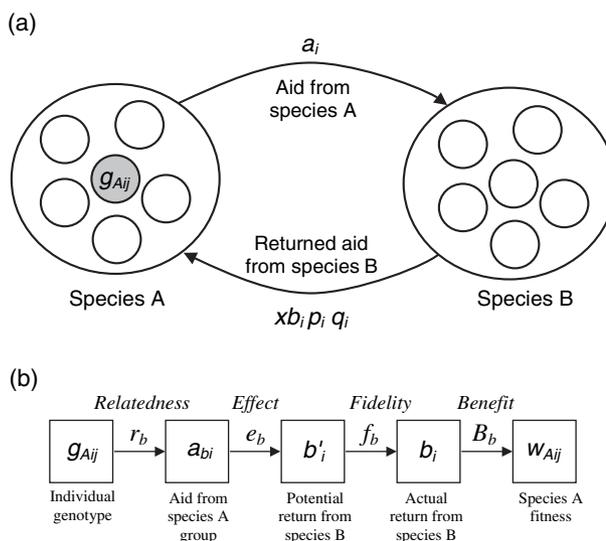


Fig. 1 (a) Diagram of model scenario. The focal individual of species A (shaded) invests a_{ij} in mutual aid for species B, in a group of species A that invests an average of a_i . This benefits species B, which in turn may provide a return-benefit to species A. In the model, the return-benefit can be modulated by (i) the evolved level of cooperation of species B (b_i), (ii) a passive phenotypic response in species B (p_i) (e.g. its growth or survival), and (iii) a behavioural response of species B (q_i), which drive the three feedbacks shown in Fig. 3. (b) The processes important in determining the feedback benefit to species A from being mutualistic. We use the effect of mutualism by species A on the level of cooperation of species B (b_i) as an example but equivalent diagrams can be made for the other two feedbacks (p_i , q_i).

(Hamilton, 1964; Frank, 1998; West *et al.*, 2002a; West & Buckling, 2003; Foster, 2004). Our goal is to develop a framework that identifies the key processes and forms a basis to compare the huge diversity of mutualisms. We follow a direct fitness perspective that captures the fitness effects of a social action through its effects on a focal individual, which can also be used to derive Hamilton's rule (Appendix; Frank, 1998).

We derive the model for an interaction between a group of each species, which we illustrate with a biofilm in which blue-green algae (cyanobacteria) release organic carbon and oxygen that benefits bacteria, which in return provide the algae with *inorganic* carbon (Kuhl *et al.*, 1996). This includes an interaction between individuals (e.g. client and cleaner fish) as a special case. As with most evolutionary models of mutualism (Axelrod & Hamilton, 1981; Frank, 1994; Doebeli & Knowlton, 1998; Yamamura *et al.*, 2004), the analysis is phrased as a two-species interaction but the general conclusions do not rely upon this assumption and the framework is extendable to additional species. We capture the effects of mutualistic behaviour by a focal individual of species A on its own fitness (w_{Aij}) with five terms (Fig. 1a, Table 1):

Table 1 Summary of the main notations

Notation	Definition
w_{Aij}	Fitness of focal individual of species A
a_{ij}	Evolved investment in cooperation/mutualism by focal individual of species A
g_{Aij}	Genotype of focal individual of species A at the locus for cooperation
x	Benefit weighting of receiving mutualistic aid
a_i	Mean evolved cooperation in species A group
b_i	Mean evolved cooperation in species B group
p_i	Passive phenotypic response of species B to species A cooperation
q_i	Behavioural response of species B to species A cooperation, e.g. partner choice
C	Cost of mutualistic action
B_b, B_p, B_q	Benefit of mutualism from evolved cooperativity (b_i), passive phenotypic response (p_i) and behavioural response (q_i) in partner species.
F_b, F_p, F_q	Degree of feedback effect from evolved cooperativity, passive phenotypic response and behavioural response in partner species
r_b, r_p, r_q	Relatedness among species A individuals at the spatial scale at which the feedbacks F_b, F_p, F_q function
e_b, e_p, e_q	Maximum potential effect of mutualism in species A upon evolved cooperativity, passive phenotypic response and behavioural response in partner species
f_b, f_p, f_q	Fidelity between species A and B in group over time relative to the rate that the feedbacks F_b, F_p, F_q function

$$w_{Aij} = f(a_{ij}, x, b_i, p_i, q_i) \quad (1a)$$

where a simple illustrative form of this equation is:

$$w_{Aij} = (1 - a_{ij}) + \frac{\text{Cost}}{\text{Feedback benefit from Species B}} \quad (1b)$$

and a_{ij} is the aid provided by the j th individual of species A that benefits species B in the i th group, e.g. the amount of energy that a focal alga cell (species A) invests in organic carbon that benefits the bacteria (species B). The weighting term x determines the benefit to species A of receiving aid from species B. For example, x will be large if a small amount of inorganic carbon greatly benefits species A algae. We consider three properties of species B that may be affected by mutualism in species A. First is b_i , which is the genetically determined level of return aid by species B in the group e.g. inorganic carbon release in the bacteria group. We also consider two possible phenotypic effects of species A mutualism on species B. If mutualism by the algae increases the numbers, resources or survival of the bacteria in the group, this may increase the level of returned inorganic carbon. The effect of such a 'passive' phenotypic response in the bacteria on the aid they return is accounted for by p_i . Second, we consider a coercive adaptation of species B to favour more cooperative members of species A (q_i), e.g. a behavioural response by the bacteria to the level of organic carbon provided by the algae, such as association with those alga that produce more carbon (sanctions or partner choice, Bull & Rice, 1991; Noe & Hammerstein, 1994; West *et al.*, 2002a; Kiers *et al.*, 2003; Sachs *et al.*, 2004). We focus on the evolution of cooperative traits here and do not track the evolution of such partner choice itself. However, other models suggest that partner choice and sanctioning will often be selected (West *et al.*, 2002a) because it enables a mutualist to avoid exploitative cheaters in a partner species.

We investigate when an increase in mutualistic aid by the focal individual of species A is favoured (Frank, 1998). There is an equivalent equation for species B,

which we later consider in the interaction between the two species (Fig. 2). If g_{Aij} is the genotype (or breeding value, Frank, 1998) that determines investment in mutualistic aid and w_{Aij} the fitness of a focal individual of species A (eqn 1), then mutualistic aid is favoured when dw_{Aij}/dg_{Aij} is positive (Appendix; Price, 1970, 1972; Frank, 1998). This simply says that increased organic carbon release is selected for when algal genotypes with increased release have increased fitness. Differentiating eqn 1a using the chain rule gives:

$$\frac{dw_{Aij}}{dg_{Aij}} = \frac{\partial w_{Aij}}{\partial a_{ij}} \cdot \frac{da_{ij}}{dg_{Aij}} + \frac{\partial w_{Aij}}{\partial x} \cdot \frac{dx}{dg_{Aij}} + \frac{\partial w_{Aij}}{\partial b_i} \cdot \frac{db_i}{dg_{Aij}} + \frac{\partial w_{Aij}}{\partial p_i} \cdot \frac{dp_i}{dg_{Aij}} + \frac{\partial w_{Aij}}{\partial q_i} \cdot \frac{dq_i}{dg_{Aij}} \quad (2)$$

This partitions the relationship between fitness and mutual aid genotype (dw_{Aij}/dg_{Aij}) into a sum of five terms, which are functions of a_{ij} , x , b_i , p_i and q_i respectively. Each term includes a partial differential and a full differential. The partial differentials capture the effect of each factor upon the focal individual's fitness (w_{Aij}) in the absence of other effects, which correspond to costs and benefits (Appendix, eqn 3 below).

The full differentials describe the effect of the focal individual's genotype (g_{Aij}) on the five terms of interest. We assume a direct correspondence between the genotype and phenotype of the focal individual so that $da_{ij}/dg_{Aij} = 1$ (Frank, 1998), and that the weighting term x is a constant so $dx/dg_{Aij} = 0$ and the terms containing x drop out. The last three full differentials capture the potential feedback effects of species B (db_i/dg_{Aij} , dp_i/dg_{Aij} , dq_i/dg_{Aij}), which we term F_b , F_p , F_q . Substituting back into eqn 2, this gives:

$$\frac{dw_{Aij}}{dg_{Aij}} = -C + B_b F_b + B_p F_p + B_q F_q \quad (3a)$$

where, in our example, C is the personal cost to the algae of releasing organic carbon, B_b , B_p and B_q assess the benefits to the algae from the evolved cooperativity (b_i),

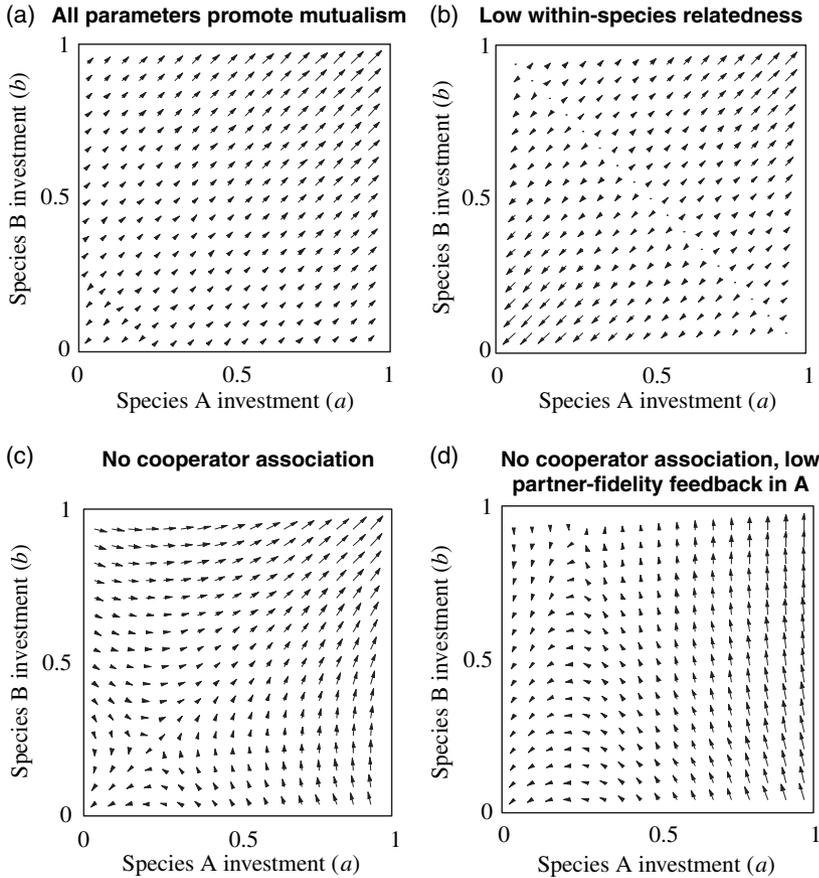


Fig. 2 The evolution of mutualism between two species. The phase plots show the direction of evolutionary change in both species as a function of their level of mutualism, for a simple illustrative form of eqn 1 (see text). Parameters are explained in Table 1, with the addition of subscripts *A* and *B* to denote effects from the perspective of each of the two species *A* and *B*. (a) *Mutualism promoted by all parameters* ($r_A = r_B = 1$, $f_{Ab} = f_{Ba} = 1$, $f_{Ap} = f_{Bp} = 1$, $x_A = x_B = 5$). (b) *Low within-species relatedness* ($r_A = r_B = 0.2$), strongly reduces the scope for mutualism. (c) *No cooperator association* ($f_{Ab} = f_{Ba} = 0$) has less impact than relatedness because benefits still return through partner-fidelity feedback. (d) *No cooperator association, low partner-fidelity feedback in one species* ($f_{Ab} = f_{Ba} = 0$, $f_{Ap} = 0.2$, $f_{Bp} = 1$) destabilizes mutualism in both species. This could occur if the rate of feedback to one species is very slow. Unless stated, the parameters in figures (b), (c) and (d) are the same as (a).

passive phenotypic (p_i) or behavioural response (q_i) of the bacteria, and F_b , F_p and F_q capture the extent to which benefits from these effects feedback upon the focal alga. As for Hamilton’s rule (Hamilton, 1964; Price, 1970, 1972; Frank, 1998; Appendix), selection favours the focal trait (carbon release) when $dw_{Aij}/dg_{Aij} > 0$, and mutualistic aid is predicted to evolve when:

$$C < B_b F_b + B_p F_p + B_q F_q \quad (3b)$$

Feedback effects

The degree to which mutualistic benefits feedback upon the focal individual is captured by F_b , F_p and F_q . We expand these to capture three processes that determine the degree of each feedback, taking feedback from the cooperation genotype of species *B* (F_b) as an example (Fig. 1b):

$$F_b = \frac{db_i}{dg_{Aij}} = \frac{db_i}{db'_i} \cdot \frac{db'_i}{da_{bi}} \cdot \frac{da_{bi}}{dg_{Aij}} = f_b e_b r_b \quad (4)$$

This breaks F_b into three processes:

- (i) *Within-species relatedness* ($da_{bi}/dg_{Aij} = r_b$; Frank, 1998; Pepper, 2000; Foster, 2004): the association between focal individual’s genotype (g_{Aij}) and group phenotype for cooperation (a_{bi} ; within-group relatedness,

Appendix). The subscript b in r_b and a_{bi} allows for feedback benefits (F_b , F_p , F_q) that return at different spatial scales. For example, the mutualistic benefit of changing species *B* genotype might be diffuse and shared by all species *A* in the population giving $r_b = 0$ (relatedness to population) whereas the benefit from altering species *B* phenotype may feedback on the focal *A* individual alone giving $r_q = 1$ (relatedness to self).

- (ii) *Potential effect* ($db'_i/da_{bi} = e_b$): the maximum effect of a change in the level of aid by species *A* in the group (a_i) on the level of aid provided by species *B* (b'_i). The simplest case is that a change in species *A* causes a proportional change in species *B* and so $e_b = 1$.
- (iii) *Between-species fidelity* ($db_i/db'_i = f_b$): The fidelity term defines whether the two species stay associated for long enough for potential benefits (b'_i) to feedback as actual benefits (b_i) and increase the focal individual’s fitness. Fidelity captures any dilution of the feedback benefit over time, whereas relatedness captures any dilution over space. In a clonal group, fidelity corresponds to the proportion of the feedback effect that returns to the acting genotype. This will decrease if members of either species leave the group in the time it takes the feedback benefit to

occur: if a group completely turns over before feedback occurs then $f = 0$, whereas no group turnover means $f = 1$. Fidelity values are likely to be lowest for feedbacks that take multiple generations to return: dispersal and, in sexuals, outbreeding in each generation will tend to cause turnover in the genotypes present and reduce the likelihood that a feedback benefits the actor genotype. As for relatedness, the use of subscript b in f_b allows for the possibility that the different feedback effects (F_b , F_p , F_q) may occur at different rates and so have different fidelity values (f_b , f_p , f_q).

Applying these expansions to F_b , F_p and F_q gives an expanded form of eqn 3:

$$\frac{dw_{Aij}}{dg_{Aij}} = -C + B_b f_b e_b r_b + B_p f_p e_p r_p + B_q f_q e_q r_q \quad (5)$$

where terms are defined as above and in Table 1. This equation is very general: it applies to any situations where two species provide mutual aid and, importantly, it is general for all functional forms of the original equation (eqn 1a). For example, we only assume that the relationship between species B cooperation (b_i) and species A fitness (w_{Aij}) is positive, and whether it is linear, accelerating or decelerating function does not affect the model's predictions. However, our model also forms a basis for more specific analyses, which we illustrate for a simple case in Fig. 2. The equations used in the figure are $w_{Aij} = (1-a_{ij}) + b_i p_{Ai} x_A$ (species A) and $w_{Bij} = (1-b_{ij}) + a_i p_{Bi} x_B$ (species B), where the parameters have subscripts A and B added to denote effects in each species. We assume no partner choice, that all feedbacks return at the same spatial scale: $r_{Ab} = r_{Ap} = r_A$, $r_{Ba} = r_{Bp} = r_B$, and a direct correspondence between mutualistic investment and the maximum benefit received: $e_{Ab} = e_{Ap} = 1$, and $e_{Ba} = e_{Bp} = 1$. Differentiating gives dw_{Aij}/dg_{Aij} and dw_{Bij}/dg_{Bij} (see Frank, 1998; Foster, 2004), which are plotted in phase plots as a function of evolved cooperativity in each species, a and b (Fig. 2). The solution assumes gradual evolution with small changes in investment in mutualism (a_{ij} , b_{ij} ; Frank, 1998) and that individuals of a species at any moment have near-identical phenotypes: $a_{ij} = a_i = a$, $b_{ij} = b_i = b$, $p_{Ai} = p_A$, $p_{Bi} = p_B$. Note that this makes the effects of cooperator association, which acts through variation within species, approximations only. Finally, we exploit the fact that the passive phenotypic feedback from a partner species (p_A , p_B) is a function of the mutualistic investment of a focal species (a , b) i.e. $p_A = g(a)$ and $p_B = h(b)$ and take the simplest case of a direct correspondence between investment and the effect on the other species: $p_A = g(a) = a$ and $p_B = h(b) = b$. This gives the plotted equations:

$$\begin{aligned} dw_{Aij}/dg_{Aij} &= -1 + ax_A f_{Ab} r_A + bx_A f_{Ap} r_A, \quad \text{and} \quad dw_{Bij}/dg_{Bij} \\ &= -1 + bx_B f_{Ba} r_B + ax_B f_{Bp} r_B. \end{aligned}$$

Consistent with the predictions of the general model (eqn 5), the analysis predicts that mutualism will

evolve when relatedness and fidelity are sufficient for feedback benefits through either cooperator association or partner fidelity to occur. Modelling both species together also highlights the interaction between the two species' levels of mutualism. That is, a critical level of mutualistic aid must be provided by one partner before mutualism can evolve in the other. This is consistent with the intuitive idea that selection will not favour investment in a partner species that provides little or no return aid. Related to this, the model shows that low feedback benefits to mutualism in any one species is sufficient to prevent mutualism because as one provides less aid, the other is also favoured to be more selfish (Fig. 2d).

Discussion

The model predicts that three key factors will be important in the evolution of mutualism: costs to benefit ratio, relatedness, and fidelity, which function by moderating the importance of three feedback benefits (below, Fig. 3). Most fundamentally, mutualism is favoured when the cost are low relative to the benefits, as in Hamilton's rule (Appendix). This can result from the basic ecology of a mutualism but, interestingly, may also occur due to coercive adaptations in the partner species that restrict the potential for cheating (Yu et al., 2004). Costs and benefits are also central to the suggestion that cooperation often evolves between species through 'byproduct mutualism', where a trait evolves in one species for purely selfish reasons that happens to benefit another species (West-Eberhard, 1975; Brown, 1983; Connor, 1986, 1995; Sachs et al., 2004). A hypothetical example from Connor (1986) is a plant in a hot environment whose leaves happen to shade a bird's nest and keeps it cool.

The benefit and cost terms in eqn 3 formally define byproduct mutualism: the cost of the trait (growing leaves) on individual fitness C is negative (i.e. it has a benefit), and there are no benefits through aid provided to the other species ($B_b = B_p = B_q = 0$). Equation 3 also makes it clear that traits can evolve for a combination of byproduct benefits and feedbacks from the partner species when some benefit terms (B_b , B_p , B_q) are positive in addition to C being negative, e.g. the plant may be selected to grow more foliage in the bird's presence than in its absence if the bird provides some return benefit. This shows that byproduct benefits are not a discrete category of mutualism but can exist alongside the other feedback mechanisms, such as partner fidelity or partner choice (below). Interestingly, this nonexclusivity of byproduct effects is analogous to the argument that individual and group selection are not mutually exclusive but rather positive selection can occur at both levels, where again the relative importance of the two selective forces can be assessed by partial differentials (Goodnight et al., 1992).

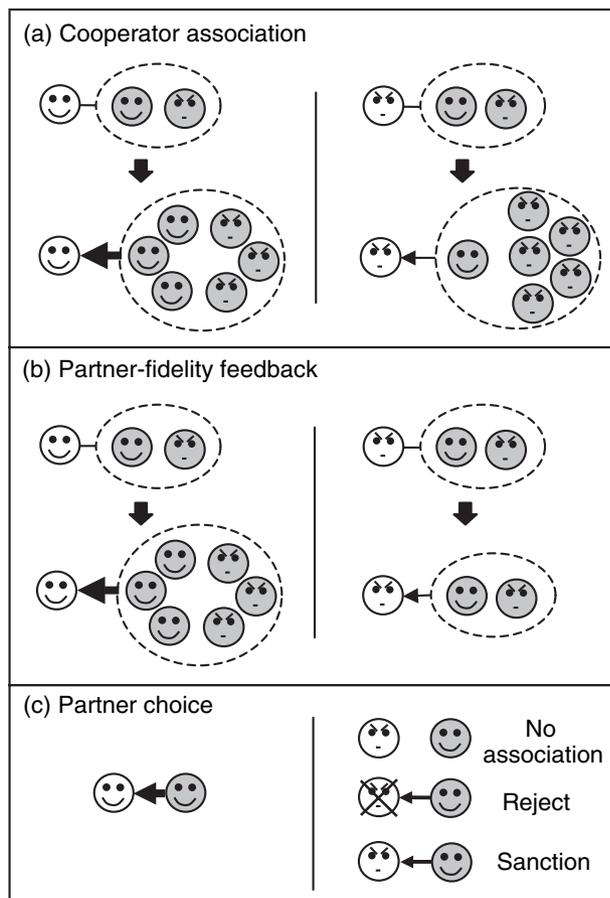


Fig. 3 Illustration of the three feedback benefits in the model. (a) *Cooperator association* – cooperative genotypes of one species (white smiling faces) tend to occur with cooperative genotypes of the other species (grey smiling faces). The figure shows one way this association may be generated (Yamamura *et al.*, 2004): when cooperation in one species (white) provides large benefits and compensates for the cost of cooperation by the other (grey), which better allows cooperative genotypes to persist. Other ways cooperator association may occur are discussed in the text. (b) *Partner-fidelity feedback* – when cooperation by one species (white) has a positive phenotypic effect on the other species (e.g. abundance, survival, growth, reproduction) that provides a feedback benefit. (c) *Partner choice* – an active behavioural response in one species (grey) that favours cooperation in the other. Three mechanisms are shown (i) No association – choosing species interacts more with cooperators in the other species, e.g. client's choosing cleaner fish. (ii) Rejection – choosing species interacts randomly but rejects noncooperators, e.g. yuccas dropping fruit with many moth eggs. (iii) Sanctions – choosing species interacts randomly but supplies less aid to noncooperators, e.g. legumes regulating nutrients to rhizobia.

As in the analyses of Frank (1994) and West *et al.* (2002b), our model predicts that within-species relatedness in groups will promote among-species cooperation. More generally, our model shows that relatedness is essential for all feedback benefits (Fig. 3), and, unless

there are byproduct effects, a group will only provide mutual aid to another species if there is positive relatedness in the group. It is important to note, however, that relatedness in our model is 'within-group' relatedness: the regression of group phenotype on individual genotype (Appendix). This encompasses both the effect of pairwise relatedness among group member (e.g. if they are kin) and the direct effect of the focal individual on the group phenotype. The latter is important when groups are small because each individual can directly influence group phenotype and a significant proportion of mutualistic investments will feedback upon the actor ($1/n$, where n is group size). This effect generates within-group relatedness that can select for mutualism without pairwise relatedness ('weak altruism', Wilson, 1990; Foster *et al.*, 2006). To take the extreme case, mutualistic aid can return to a single individual, such as when the bobtail squid, *Euprymna scolopes*, directs nutrients to the bioluminescent bacteria, *Vibrio fischeri*, that live in its light organ (Visick *et al.*, 2000; Sachs *et al.*, 2004). Here, investments only benefit the focal squid and relatedness to the 'group' that benefits from the mutualism is simply the relatedness of the squid to itself i.e. $r_{ap} = 1$. By contrast, in a large group of unrelated individuals, the focal individual carries the cost of providing aid to the other species but nonrelatives share the benefits, which prevents mutualism and is an example of the evolutionary 'tragedy of the commons' (Hardin, 1968; Leigh, 1977; Frank, 1998; Michod, 1999; Foster, 2004; Wenseleers *et al.*, 2004). Relatedness in our model also captures the effect of multiple species on one side (or guild) of a mutualism (Stanton, 2003), where increasing species in a guild will have the same effect as reducing within-species relatedness.

High fidelity between the members of each species promotes the evolution of mutualism. Investment in a partner species will only be selected if species stay together long enough for feedbacks to benefit those that caused them. This is consistent with several models that have emphasized the importance of spatial structure and population viscosity, which function to keep members of the two species together over time (Frank, 1994; Doebeli & Knowlton, 1998; Yamamura *et al.*, 2004). Both fidelity and relatedness need to be positive for a feedback to provide a benefit to a mutualist. Furthermore, the model predicts that the levels of fidelity and relatedness associated with a particular feedback benefit (Fig. 3) will be central to whether it selects for mutualism. We now discuss each of the feedback benefits in turn.

Cooperator association

Mutualism will be promoted when cooperation by a species A individual (a_{ij}) increases the evolved level of cooperation in species B (b_i). That is, when the genotypes at the locus for cooperation correlate across the two species (*cooperator association*; Fig. 3a). This effect was

described by Frank (1994) and the term $F_b = f_b e_b r_b$ in eqn 3 corresponds to his 'between-species relatedness' (r_{ji} in Frank, 1994). Frank showed that local selection can generate this correlation whenever mutualist genotypes tend to stay together across generations. Such local selection was also central to the evolution of mutualism in the spatial simulations of Doebeli & Knowlton (1998) and Yamamura *et al.* (2004) (see Fig. 3b in the latter paper). In the simulations, local pockets of mutualism formed between the two species where mutualistic genotypes in species A favoured mutualistic genotypes in the other species ($e_b > 0$), and spatial structure meant that the species A genotypes could benefit in the next generation from the local increase in species B cooperation ($f_b > 0$, $r_b > 0$) (see also Wilkinson & Sherratt, 2001). Hypothetically, cooperator association might also occur through a phenotype-matching mechanism analogous to the 'greenbeard' mechanism for within-species cooperation (Hamilton, 1964; Dawkins, 1976) or if more cooperative individuals of each species tend to occur in the same environment.

Examples: little is known empirically about cooperator association. A first step is to quantify natural genetic variation in the levels of mutualism, which is required for cooperator association to occur. Evidence for this variation comes from mutualisms with 'cheater' individuals, including yucca plants that do not sustain yucca moth larvae in their fruits (Bao & Addicott, 1998), some nectarless plants in populations of honey mesquite (Golubov *et al.*, 1999), nonfixing strains of rhizobial bacteria of legumes (Thrall *et al.*, 2000) and strains of the symbiotic algae of the upside-down jellyfish that invest little in their host (Sachs and Wilcox, 2006). However, to the best of our knowledge, there is no evidence as yet that the genetic component of this variation correlates among mutualist species.

Partner-fidelity feedback

Mutualism is favoured by positive effects upon the phenotype of the partner species, such as its abundance or survival, which provide feedback benefits to the mutualist. Like cooperator association, this effect is promoted by group fidelity ($f_p > 0$). That is, spatial structure and low group turnover relative to the rate of feedback benefits. As a result, such effects have been termed 'partner-fidelity feedback' (Bull & Rice, 1991; Sachs *et al.*, 2004), although fidelity is important for all of the feedbacks (above). Our model shows it is important to distinguish partner-fidelity feedback from cooperator association. Cooperator association occurs when increased mutualism affects the genetics of the partner species and selects for more cooperative genotypes (Fig. 3a), whereas partner-fidelity feedback is purely phenotypic (Fig. 3b).

Partner-fidelity feedback is present in some models (Frank, 1994; Doebeli & Knowlton, 1998) but cooperator

association is often emphasized (Doebeli & Knowlton, 1998; Wilkinson & Sherratt, 2001; Yamamura *et al.*, 2004). In contrast, our model suggests that partner-fidelity feedback will typically be more important than cooperator association, because fidelity values are likely to be much higher for the former ($f_p > f_b$). Phenotypic effects can be much more rapid than genetic changes and, particularly, do not require that species associate across generations. Furthermore, although the effects of mutualism upon a partner's phenotype can potentially be very great ($0 \leq e_p < \infty$), cooperator association can at best cause an equivalent response in the partner species ($0 \leq e_b \leq 1$).

Examples: Partner-fidelity feedback was shown by Agrawal & Karban (1997) who by adding leaf domatia to cotton plants, were able to increase the number of predatory arthropods that protect the plant from herbivores, which increased fruit production (Agrawal & Karban, 1997). Such abundance benefits to a host are likely whenever a symbiont lives on or in a partner species (Fig. 3b), including examples such as the gut flora of animals (Frank, 1996a; Backhed *et al.*, 2005), rhizobia and mycorrhiza on or in the roots of plants (Strack *et al.*, 2003), and the fluorescent bacteria *Vibrio fischeri* that live in the bobtail squid (Visick *et al.*, 2000). Feedback benefits from increasing partner abundance will also be important in multispecies biofilms (Stoodley *et al.*, 2002), including the blue-green algae and bacterial example discussed above (Kuhl *et al.*, 1996), and dental biofilms where some species of bacteria require each other to colonize the surface of a tooth (Palmer *et al.*, 2001). Switching to the symbiont perspective, symbionts can benefit from partner-fidelity feedback when mutualism improves the growth and survival of their hosts, e.g. *V. fischeri* bacteria will benefit from keeping their squid host alive (Visick *et al.*, 2000).

Strong selection for mutualism will result when there is a feedback benefit from a partner species' reproduction, because this can align the fitness interests of the two partners. This feedback occurs in vertically transmitted symbionts including the garden fungi of leafcutter ants (Mueller, 2002), and termites (Korb & Aanen, 2003) whose reproduction is limited by dispersing sexuals in some species; viruses carried by some parasitoid wasps that inactivate the immune system of the wasp's caterpillar host (Whitfield, 2002); and the transport of scale insects by dispersing ant gynes to a new plant, where upon arrival the scale insects will provide the ants with honeydew in return for protection (Gullan & Kosztarab, 1997).

Partner choice and sanctions

Mutualism will be favoured if one species actively increases the return benefits to more mutualistic members of the other species. Several behaviours can cause this effect, including interacting more with cooperators in

the other species, interacting randomly but later rejecting noncooperators and interacting randomly but sanctioning or punishing noncooperators (Fig. 3c; Bull & Rice, 1991; Noe & Hammerstein, 1994; Johnstone & Bshary, 2002; West *et al.*, 2002a; Kiers *et al.*, 2003; Sachs *et al.*, 2004). All these mechanisms result in increased benefits being provided to the more cooperative members of the other species ($F_q > 0$). Our model predicts that partner choice mechanisms will select strongly for mutualism. For example, if pollinators avoid plants with low nectar then this will be a strong, rapid and relatively local effect (partner choice: high f_q , r_q) compared to the negative effect of low nectar on pollinator population size, which is likely to be weaker, delayed and affect many more plants (partner-fidelity feedback: low f_p , r_p). This said, partner choice is typically only found in one of the species in mutualisms (Sachs *et al.*, 2004) and, therefore, cannot explain the mutualism in the choosing species itself.

Examples: Consistent with the prediction that partner choice is a highly effective way to promote mutualism, there is growing evidence for partner choice in many mutualisms. A nice example comes from some yucca species (Pellmyr & Huth, 1994; Marr & Pellmyr, 2003) and the Senita cactus (Holland *et al.*, 2004) that abort fruit containing too many eggs of their pollinating moths. Yuccas also create 'damage zones' around eggs that inflict disproportionate harm when many eggs are laid in a fruit (Addicott & Bao, 1999; Shapiro & Addicott, 2003). Other plants with partner choice include some ant plants, where the domatia for the ants only develop properly if the plant's leaves are protected (Yu, 2001), and legumes that direct more resources to root nodules containing cooperative rhizobial bacteria (Kiers *et al.*, 2003). Partner choice has also been found in the leaf cutter ant and fungus mutualism where ants act to remove parasitic and foreign fungi (Currie & Stuart, 2001; Mueller *et al.*, 2004; Poulsen & Boomsma, 2005); in client fish that return to cleaner fish that provide the best service (Bshary & Grutter, 2002; Bshary & Schaffer, 2002) or leave cleaner fish that bite them (Johnstone & Bshary, 2002); in ants that preferentially attend aphids and lycaenid caterpillars that produce the sweetest honeydew (Volkl *et al.*, 1999; Agrawal & Fordyce, 2000; Mailleux *et al.*, 2003); in the bobtail squid that poisons nonfluorescent bacteria in its light organ (Visick *et al.*, 2000); in frugivores that only ingest and disperse the seeds of plants that provide nutritious fruit (Howe & Smallwood, 1982) and in pollinators that reject plants with low nectar (Smithson & Gjord, 2003).

Conclusions

The model shows that mutualism will evolve when costs are low relative to feedback benefits (Fig. 3). In addition, it predicts that those feedbacks benefits which are associated with high within-species relatedness and

between-species fidelity will be most important in mutualism evolution. This suggests that partner choice, which can act locally (high relatedness) and quickly (high fidelity), will provide a powerful incentive for mutualism. In addition, the relative rapidity with which partner-fidelity feedback can operate suggests that it too will often be important. In contrast, the development of genetic associations among species (cooperator association) is predicted to be the least important feedback, because of the likely requirement that mutualists associate across generations. Consistent with these predictions, there is good empirical evidence for the role of partner-fidelity feedback and partner choice whereas the present role of cooperator association is much less clear, although it is important in several models (Frank, 1994; Doebeli & Knowlton, 1998; Yamamura *et al.*, 2004). It is also the case that cooperator association has received less attention empirically and dedicated studies are now desirable. In addition, there is a broad scope for interesting studies into the role of within-species relatedness, which is a central factor in within species cooperation (Ratnieks *et al.*, 2006) but has been little studied in mutualisms (one notable exception is the fig wasps (Frank, 1985; Herre, 1985).

Our model does not capture many of the interesting details and idiosyncrasies of individual mutualisms, and there is a broad scope for more specific analyses (e.g. West *et al.*, 2002b). The utility of our model we hope lies in the ability to capture the key processes in a single model and facilitate comparisons across the huge diversity of mutualisms. That said, there are some processes that we did not consider. Firstly, our analysis is phrased in terms of two interacting species although many mutualisms, such as any pollinators and plants, occur between two guilds each containing multiple species, where each guild will often contain both mutualist and 'cheater' species (Ferriere *et al.*, 2002; Bronstein, 2003; Wilson *et al.*, 2003). The conclusions of our model certainly apply to such systems but we recognize that explicit models of such multiple species guilds may reveal additional factors important in mutualism evolution. Our model also focused upon the origin and evolution of mutualistic traits (gene or individual-level selection) rather than the ecological stability of the resulting mutualism, which is the question of whether species with particular traits would persist over evolutionary time (species-level selection, e.g. Wilson *et al.*, 2003). Combining these two forms of selection remains a challenge for the future but the general prediction is that species-level selection will favour mutualisms with properties that prevent the evolution of cheaters, such as pleiotropic links between potential cheating strategies and a personal cost (Foster *et al.*, 2004).

The evolution of cooperation *within* species has been intensely studied (Hamilton, 1964; Wilson, 1975; Maynard Smith & Szathmáry, 1995; Frank, 1998, 2003; Foster, 2004; Sachs *et al.*, 2004). Our model shows that,

although undoubtedly more complex, the evolution of mutualisms is amenable to the same kinds of analysis, and similar factors are important for within and between-species cooperation (costs and benefits, relatedness, fidelity). Importantly, the model suggests that mutualism can often provide selfish benefits and helps to explain the puzzle of cooperation between species.

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Appendix

Deriving a direct fitness Hamilton's rule

This appendix summarizes Frank's (1998, p. 38) method for deriving Hamilton's rule from a direct fitness perspective, in order to show the similarity to the derivation used in the paper. The direct fitness perspective captures the fitness effects of a social action entirely through its effects on a focal individual. This contrasts with an inclusive fitness approach (Hamilton, 1964), where the focal individual is viewed as an actor only and the recipients are the other individuals (relatives) in the group (Frank, 1998). Ultimately, the two approaches are equivalent for most problems and both can be used to derive Hamilton's rule (Hamilton, 1964; Frank, 1998). However, for a model of mutualism, a direct fitness perspective is most appropriate because the recipient is a different species that is not captured by the focal individual's inclusive fitness. That is, one species cannot carry copies of the other species' genes.

The effect of a social action on the fitness of a focal individual (w_{Aij}) can be written as:

$$w_{Aij} = f(a_{ij}, a_i) \quad (\text{A1})$$

where a_{ij} is the phenotypic expression of the social action of the focal individual and a_i is the mean phenotypic expression of the social action in the group. We want to know how these phenotypes affect the focal individual's fitness, which can be examined by differentiating with respect to genotype (g_{ij}), where the genotype corresponds to the focal individual's breeding value (additive genetic value) for the social trait (Price, 1970, 1972; Frank, 1998):

$$\frac{dw_{Aij}}{dg_{ij}} = \frac{\partial w_{ij}}{\partial a_{ij}} \cdot \frac{da_{ij}}{dg_{ij}} + \frac{\partial w_{ij}}{\partial a_i} \cdot \frac{da_i}{dg_{ij}} \quad (\text{A2})$$

In this equation, $da_{ij}/dg_{ij} = 1$, since we assume a direct correspondence between breeding value and phenotype,

and $da_i/dg_{ij} = r$, the within-group relatedness coefficient of kin selection theory (Frank, 1998). Furthermore, the partial differentials $\partial w_{ij}/\partial a_{ij}$ and $\partial w_{ij}/\partial a_i$ measure how the focal individual's fitness is affected by an increase in its own (a_{ij}) and mean group (a_i) level of expression of the social trait. These correspond to the cost ($-C$) and benefit (B) of the social action. This recovers a direct fitness version of Hamilton's rule (Hamilton, 1964; Frank, 1998):

$$\frac{da_{ij}}{dg_{ij}} = -C + B \cdot r \quad (\text{A3})$$

It is a direct fitness formulation because the benefit term (B) is the effect of group phenotype on the focal individual's fitness rather than the effect of individual phenotype on the other group members' fitness, which would be used in an inclusive fitness formulation (see Frank, 1998, p. 72 for an equivalent inclusive fitness derivation).

Note that the measure of relatedness that emerges from the analysis is 'within-group relatedness', which includes the relatedness of the focal individual to themselves (Frank, 1998; Foster, 2004). A more familiar measure of relatedness is 'pairwise relatedness', which is equivalent to average kinship in the group and excludes the relatedness of the actor to themselves where $r = r_p(n-1)/n + 1/n$, where r is within-group relatedness, r_p is mean pairwise relatedness, n is group size (Frank, 1996b; Pepper, 2000). For example, a group of five nonrelatives has pairwise relatedness of zero but within-group relatedness is 0.2 because of the relatedness of the actor to itself. This relatedness-to-self effect is the mechanism by which 'trait-group selection' can drive cooperation in an unrelated group (Wilson, 1990; Foster, 2004). Note that increasing group size decreases within-group relatedness and, all else being equal, cooperation is less likely in large than in small groups (Wilson, 1990; Foster *et al.*, 2006).

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