



A mechanistic model of a mutualism and its ecological and evolutionary dynamics

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Abstract

This paper develops a mechanistic model of the population dynamics and coevolution of mutualisms such as plants and mycorrhizae where one resource is traded for another resource. The mechanism is based on limiting resources and is derived from von Liebig's law of the minimum [von Liebig, 1862, *Die Chemie in ihrer Anwendung auf Agricultur und Physiologie*, 7e ed. F. Vieweg und Sohn, Braunschweig] and Tilman's R^* [Tilman, D., 1980, *Resources: a graphical-mechanistic approach to competition and predation*, *Am. Nat.* 116, 362–393]. The model makes several predictions: (1) resource limitations cause mutualisms to have stable population dynamics, despite previous predictions to the contrary, (2) game-theory based models of evolution show that potential coevolving mutualists face a Prisoner's-dilemma-like paradox, rigorously confirming the intuition of many people and (3) a mechanism which enforces fair-trade will eliminate the dilemma and a mutualism will evolve, despite having no gene flow between the species.

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1. Introduction

Mutualism is a type of interaction between two species. Specifically, mutualism occurs when one species provides some benefit that it has in abundance (relative to the other species) in exchange for some benefit that the other species has in relative abundance (see similar definition in Bronstein, 1994a). The bene-

fit exchanged might be good (e.g., some nutrient) or a service (e.g., pollination, protection). For example, in insect-mediated pollination, a plant exchanges carbon energy in the form of nectar or pollen which it has in relative abundance due to photosynthesis with a bee which provides directed dispersal (of pollen), something which it has in relative abundance due to its mobility. In this case, a resource is traded for a service. This idea of trading goods with differing availability to different species is very similar to the economic concept of comparative advantage (Noe and Hammerstein, 1995; Schwartz and Hoeksema, 1998; Holland, 2002; Hoeksema and Schwartz, 2003), which has been applied by

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economists to trade between nations (Ricardo, 1821) and to specialization of labor (Smith, 1776).

This complex idea of comparative advantage has often been reduced to simply saying mutualisms are a +/+ interaction (Begon et al., 1986; Bronstein, 1994b). The definition of mutualism as a +/+ interaction has resulted in repeated attempts to model mutualism population dynamics using the classic Lotka–Volterra models, which have proved so durable in modeling competition and predation. The first such model was by Gause and Witt (1935) who merely converted the interspecific interaction coefficients from negative to positive in the Lotka–Volterra competition model. The problem with their model was that it predicted strong mutualisms would be unstable, with both populations racing off to infinity. Many later models of mutualism dynamics also resulted in infinite populations (see Boucher, 1985 for a review of this phenomenon). Eventually however, modelers developed models that had both stable population dynamics and a mechanistic basis albeit for the specific case of handling time of pollinators or ant farmers (Pierce and Young, 1986; Wright, 1989; Holland et al., 2002). Other researchers noticed that a third species that was competitive (Heithaus et al., 1980) or exploitative (Rai et al., 1983; Tonkyn, 1986; Ringel et al., 1996) to one of the mutualistic partners could limit the populations.

A third and perhaps most fundamental biological reason that mutualistic species populations do not go to infinity is that they face resource limitations. This has been modeled as a limit on mutualisms phenomenologically. For example, some of the above models incorporate a phenomenological self-regulation, i.e. a density dependent term commonly called *K*. In this paper, I implemented a model based specifically on the mechanism of limiting resources by implementing a model of Liebig's law of the minimum (von Liebig, 1862).

2. Mechanism behind mutualism

In the rest of this paper, I will focus on one specific subcategory of mutualisms: facultative, bitrophic mutualisms. Facultative mutualisms are those in which each individual is capable of living and reproducing without the other individual. A bitrophic mutualism is defined here as one in which each species is providing some form of foodstuff to the other. Three well-studied

examples of this type of mutualism are:

- legumes and rhizobium bacteria (the legumes provide carbon energy in exchange for nitrogen in a usable form) (Martin, 1984);
- plants and mycorrhizal fungi (the plants provide carbon energy in exchange for a variety of mineral nutrients, especially phosphorous) (Allen and Allen, 1990);
- coral coelenterates and zooxanthellae (algae that live symbiotically inside the coral animals, receiving protection and mineral nutrients in exchange for carbon energy) (Battey, 1992; Rowan, 1998).

The pollinator mutualism given as an example in the introduction would not be in this subset of bitrophic mutualisms. By dealing with a specific subset of mutualisms, I will be able to make the model more mechanistic.

The effect of limiting resources has been well studied, especially in plants. Liebig's law of the minimum (von Liebig, 1862) states that population growth will be constrained by whatever resource is most limiting. Tilman (1980, 1988) developed this into an isocline-based model of plant population dynamics. Inherent in the idea that there is one limiting resource is the idea that the plant has excess capacity for capture of other resources. This returns us to the idea that mutualism is the exchange of goods in excess (in this case non-limiting resources) for goods that are limiting (the Liebig limiting resource) or in economic terms "comparative advantage." Schwartz and Hoeksema have explored the idea of comparative advantage in relation to mutualisms (Schwartz et al., 2002; Hoeksema and Schwartz, 2003). However, their methodology based on economics techniques can only show when it would be optimal to engage in a mutualism. It is well known that organisms do not always evolve to beneficial scenarios (Williams, 1966). In this paper, I extend Schwartz and Hoeksema's work on comparative advantage by using game theory to explore whether a mutualism will evolve when it is beneficial.

3. A mathematical representation (methods)

3.1. Fitness equations

The first step in developing any population model is to write a formula for fitness (per capita growth rate)

as a function of the variables of interest, here the sizes of the two mutualistic populations and the level of resources available to the two species. Once complete, I will extend this to two organisms interacting in a mutualistic fashion.

Assume there are two species whose population sizes are given by N and M . Let R_{1N} denote the amount of resource #1 (e.g., carbon energy) available per unit time to species N . Note that R_{1N} is not the same as R_{1M} because our assumption is that the two species have different comparative advantages, i.e. access to differential amounts of resources. Let u_{1N} be the per capita usage of resource #1 by species N in a unit of time. Thus, all resources will be exactly used if $N = \frac{R_{1N}}{u_{1N}}$, which we may denote as K_{1N} . Similar variables can be defined for resource #2 (e.g., mineral nutrients) and for species M (Table 1).

How can one use these to describe the fitness of a population dependent on these two resources? A few qualitative criteria that one might wish a fitness function to meet are:

1. fitness of the population should be close to r (maximum per capita growth rate) when the population size is close to zero (relative to the resource constraints);

2. fitness should monotonically decrease as the population size N increases (note some argument could be made about fitness increasing at small populations due to the Allee affect but this is not modeled herein);
3. fitness should be at zero (no growth or decline in population) when it hits the first resource constraint. In practice fitness might possibly reach zero slightly before being limited by the most limiting resource if it is also receiving a density dependent depression from nearing the second resource constraint as well;
4. fitness should be negative once population size exceeds the first resource constraint.

A simple implementation of the Liebig minimum principle meets these criteria. The most literal implementation would use a step function (S_a). Let

$$S_a(x) = \begin{cases} 1 & \text{if } x \leq a \\ 0 & \text{if } x > a \end{cases}$$

Then fitness could be written as

$$W(N, R_{1N}, R_{2M}) = r(2 \times S_{\left(\frac{R_{1N}}{u_{1N}}\right)}(N)S_{\left(\frac{R_{2N}}{u_{2N}}\right)}(N) - 1) \tag{1}$$

Table 1
Summary of parameters used in the model

Parameter	Definition	Units
N	Population size of species #1	# of individuals
M	Population size of species #2	# of individuals
R_{ij}	Amount of resource type i (e.g., carbon energy or nitrogen) available per unit time to species j (M or N)	e.g., J/s or Moles/s
u_{ij}	Per capita resource requirement for resource type i to species j	e.g., J/s/individual
k_{ij}	$= R_{ij}/u_{ij}$. The amount of resource available measured in units of individuals (i.e., the carrying capacity)	e.g., J/individual
$W()$	Fitness as a function of various parameters. Here fitness is defined as $1/N \, dN/dt$ (i.e., the per capita growth rate). Fitness is used in a discrete time context and normalized such that $W=0$ gives an unchanging population size	Individuals/individual/time
r	The maximum per-capita growth rate of a species	1/time
c	Strength of Liebig's law. For $c = \infty$, the response is a step function. For $c = 0$, the resource has no effect on fitness.	Dimensionless
p_{ij}	The proportion (ranging from 0 to 1) of the resource requirements for species j for resource type i that species j gives to the other species (hence $(1 + p)uN$ represents the total resources extracted by the species)	Dimensionless
P_{ij}	The proportion of resource (as above) needed by the target individual when playing the field against a population of conspecifics with strategy p_{ij}	Dimensionless
h	Rate of evolution. Usually related to heritability and variability of the trait under study	Dimensionless

where r is the maximal growth rate and the multiplication by 2 and subtraction of 1 causes the range to go from $-r$ to r (instead of 0 to r). Paris (1992) shows that Liebig’s law extended to multiple limiting resources is well modeled by multiplication of the response to individual resources, as I have done above. Aside from the mathematical difficulties of dealing with a discontinuous step function, it is widely recognized in biology that the transition is usually somewhat smoother and more gradual than a pure step function (Paris, 1992; Sinclair and Park, 1993). Thus, I replace the step function $S_a(x)$ with the smooth sigmoid logistic function, $L_a(x) = 1/(1 + \exp(x - a))$. I also add a parameter, c , to control the rate of drop-off ($L_a(x) \rightarrow S_a(x)$ as $c \rightarrow \infty$). This gives:

$$W_N = r \left[2 \frac{1}{1 + \exp[-c(R_{1N} - u_{1N}N)]} \times \frac{1}{1 + \exp[-c(R_{2N} - u_{2N}N)]} - 1 \right] \quad (2)$$

This equation can be parameterized in several ways. For example, the u ’s can be absorbed into the c ’s and the exponential terms can be written as $\exp[-c(K_{1N} - N)]$ instead. See Fig. 1 for a view of the fitness surface as a function of the relative availability of the two resources. This figure is very similar to the isocline figures in Tilman’s R^* theory except that he only draws one

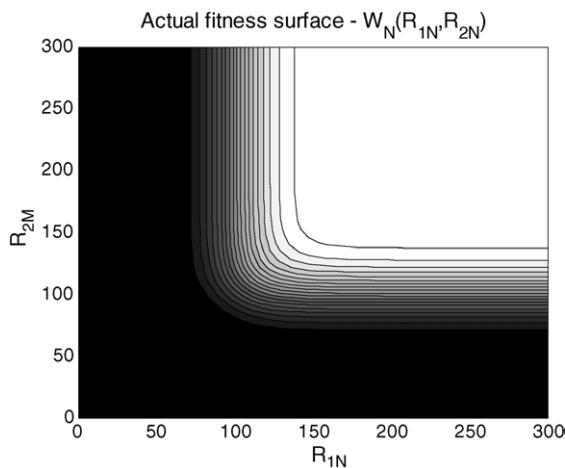


Fig. 1. Fitness surface for one species as a function of availability of the two resources. The vertical axis (height of surface) represents per capita growth rate.

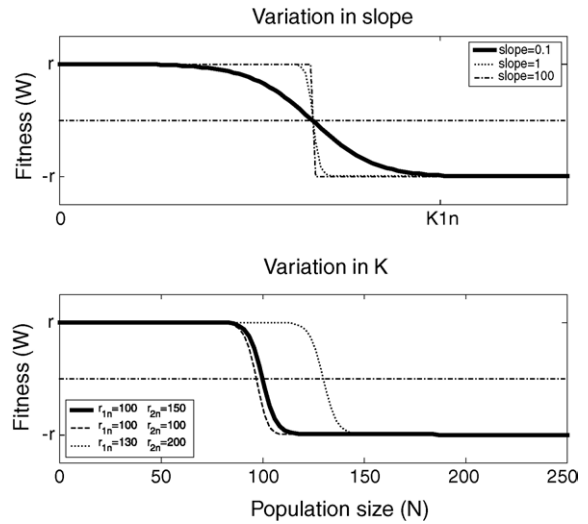


Fig. 2. Shape of the fitness function vs. population size (N). As discussed in the text, this function uses the product of two logistic functions to obtain a smoothed version of the product of two-step functions. The first figure shows how the slope parameter (c) affects the shape of the function. The second figure shows how variations in the relative availability of resources affect the function.

isocline—the zero net growth isocline—and this isocline has a sharp (90°) corner, rather than the rounded corners here. The rounding of corners here comes from the use of the logistic function rather than the step function. Tilman recognized this curvature too and called it “interactive essential resources.” This diagram also looks very similar to tests of Liebig’s law of the minimum based on crop yields (Paris, 1992), except that there the height of surface is given by crop yield rather than fitness. Also see Fig. 2 for a one-dimensional view of how varying c and R_{1N} change the shape of the fitness function.

The last step is to extend the fitness function W from that for a single population to that of two populations interacting in a mutualistic fashion. To do this, I need a few more parameters. Let p_{1N} represent the proportion of resource #1 (R_{1N}) used by species N , that species N gives up to M . Thus, $(1 + p)u$ represents the amount of resources extracted by an individual. Let p_{2M} represent the analogous proportion of resource #2 that M gives to N . Let ε represent the conversion efficiency (i.e., assume ε is the fraction of transferred resource that is actually usable by the other species). If the resource form is identical (e.g., sucrose used by both partners),

then ε might be close to 100% (minus a small percentage for transportation costs). At the other extreme, between trophic level conversion efficiencies are typically about 10%. Conservatively, I have assumed here that interspecific mutualistic conversion efficiencies ε are also about 10%. This number may be far too low if the mutualistic partner uses the nutrient in the same form as the donor species. However, this parameter has only quantitative effects on the results (sensitivity analysis run for $\varepsilon = 0.05, 0.1, 0.2, 0.3, 0.5, 0.9, 1.0$). I can now define the fitness for species N as:

$$W_N(p_{1N}, p_{2M}, N, M) = r \left[2 \frac{1}{1 + \exp[-c(R_{1N} - u_{1N}N - p_{1N}u_{1N}N)]} \times \frac{1}{1 + \exp[-c(R_{2N} - u_{2N}N + \varepsilon p_{2M}u_{2M}M)]} - 1 \right] \quad (3)$$

An analogous function gives the fitness for species M .

3.2. Population dynamics

Population dynamics are given by a discrete form of the traditional equations, where a fitness (here defined as a per capita growth rate) of zero indicates no change in population size:

$$N_{t+1} = N_t + N_t W_N(p_{1N}, p_{2M}, N, M) \quad (4)$$

$$M_{t+1} = M_t + M_t W_M(p_{1N}, p_{2M}, N, M) \quad (5)$$

Equilibrium population sizes (N^*, M^*) are found when $W_N(p_{1N}, p_{2M}, N^*, M^*) = 0$ and likewise for species M . Unfortunately, these equations are difficult to solve analytically, due to the mixture of rational functions and transcendental functions. Therefore, all subsequent results are numerical solutions of the difference equations over a range of initial conditions and parameters (found by iterating the population dynamics until an equilibrium is reached). All results presented, unless otherwise stated, are for the parameters $r = 0.4, u_{ij} = 1$ and $R_{1N} = R_{2M} = 150$ (i.e., $K_{1N} = 150$, etc.), $R_{2N} = R_{1M} = 100, c = 0.08$ and $\varepsilon = 0.1$. However, except where noted, variations in these parameters have no qualitative effects on the results (Figs. 2, 3, 5 and 8).

3.3. Coevolution

Roughgarden (1976, 1983) has suggested that coevolution will evolve to the point, where equilibrium population sizes are either maximized or minimized according to a specific mathematical rule based on derivatives of the community matrix. However, it has been shown that when there is also frequency dependence, Roughgarden’s rule can produce inaccurate results (Brown and Vincent, 1987; also see Roughgarden, 1987; Taper and Case, 1992) and a game-theory based approach is necessary (Vincent and Brown, 1984, 1987). Brown and Vincent (1987) show that coevolution (with density dependence) often induces intraspecific frequency dependence, even when it does not appear to be present. I will show, shortly, that without special restrictions, this model evolves to points other than those that maximize/minimize population size, suggesting that frequency dependence is important in this model.

Frequency dependence is incorporated by looking at the fitness of an individual playing one strategy, when the rest of the members of its species play an alternative strategy (i.e., fitness is given by $W(P_{1N}, p_{1N}, p_{2M}, N, M)$ instead of $W(p_{1N}, p_{2M}, N, M)$ where P_{1N} is the strategy of an individual and p_{1N} is the strategy of its species as a whole). This is known as “playing the field” (Maynard-Smith, 1982). When the individual fitness is maximized by playing the same strategy as the population (p_{1N}) for some given strategy for the population, then that given strategy is an uninvadable and hence an ESS (Maynard-Smith and Price, 1973). However, in this particular application to mutualism, intraspecific competition is independent of the strategy chosen by others of the same species and depends only on one’s own strategy (degree of participation in mutualism) and the partner species’ strategy. In short, $W_N(P_1, p_{1N}, p_{2N}, N, M) = W_N(p_1, p_{2N}, N, M)$. Thus, the only frequency dependence is between species; there is no frequency dependence on individual variation within a species. This is somewhat unusual for adaptive dynamics models but is nonetheless biologically correct for this model. Hereafter, I will use p_{1N} to represent the individual strategy. I will also often use the variable p as shorthand for the strategy of either species $N(p_{1N})$ or species $M(p_{2M})$.

The ESS points occur for p_{1N} , where $\partial W / \partial p_{1N} = 0$ for Eq. (3) for both species and where the populations are in dynamic equilibrium (i.e., $W = 0$ as above).

Again, the analytical solutions are intractable, so I use numerical simulations based on repeated iteration of the idea of a dynamic game (Vincent and Brown, 1987; Vincent, 1990) until equilibrium in population sizes (N , M) and strategies (p_1 , p_2) emerge. Specifically, I let:

$$\Delta p_{1N} = h \frac{\partial}{\partial p_{1N}} W(p_{1N}, p_{2M}, N, M) \quad (6)$$

and similarly for species M . The parameter h controls rate of evolution and is usually related to heritability. It has been noted that strategies, which maximize fitness are not always obtainable (Eshel, 1972; Abrams et al., 1993; Vincent et al., 1996; Geritz et al., 1997, 1998), but this is avoided by using numerical methods (i.e., using the dynamics to find the ESS points).

4. Results

4.1. Population dynamics

Several things are to be noticed about the population dynamics described by Eqs. (4) and (5) in combination with Eq. (3). First, this system is highly stable. All initial conditions (with at least one member of each species present) converge to an attractor and do so quite quickly (see Fig. 3). The exact equilibrium value is always near to but often not exactly equal to $\min(K_{1N}, K_{2N})$. This is because the higher equilibrium value (say K_{2N}) has some influence on the equilibrium population, although the lower equilibrium value (say K_{1N}) largely dominates. The attractor is usually a stable equilibrium point, although the parameter, c , serves as a bifurcation parameter. Cycles of order 2 and higher

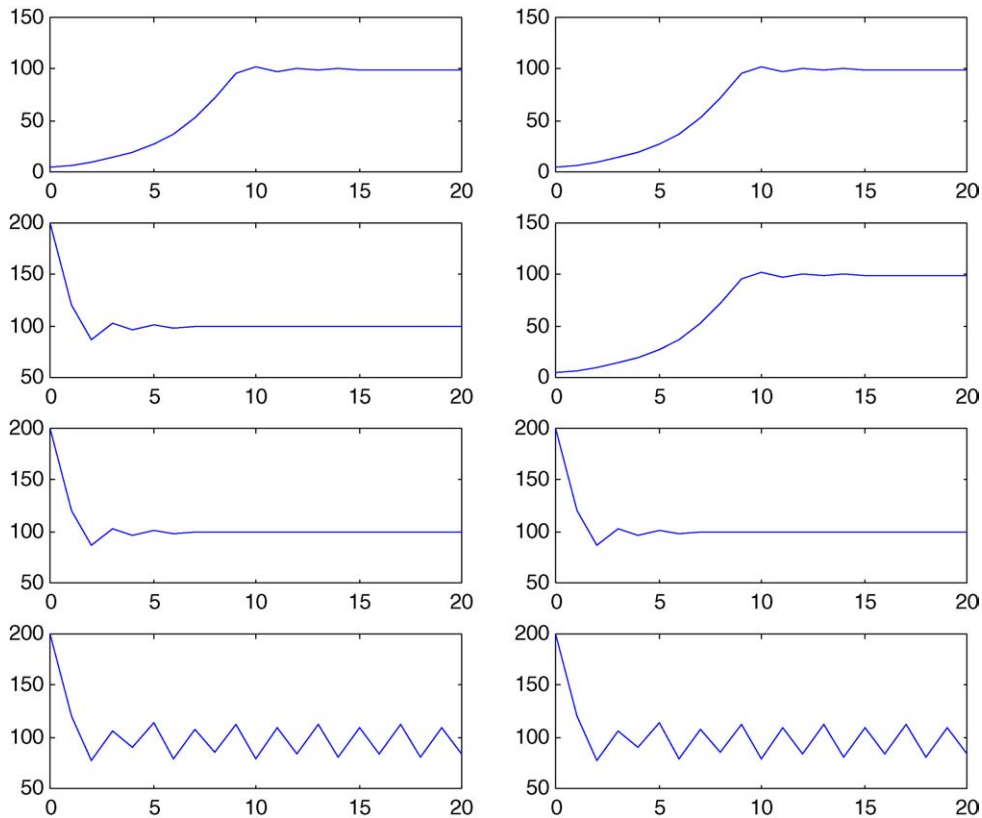


Fig. 3. Population dynamics of the system. The vertical axis is population size and the horizontal axis is time. Each row in the figure represents the dynamics for one set of initial conditions with the evolution of species #1 on the left and species #2 on the right. The fourth row changes the slope parameter, c . Although there is still a finite attractor, it becomes a two-cycle (with higher order cycles possible).

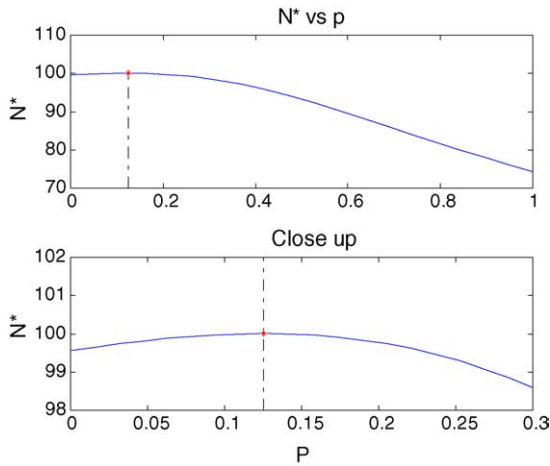


Fig. 4. Plot of the equilibrium population size vs. the evolutionary trait, p (the proportion of resources that is shared). The bottom graph is a magnified view of the region of interest in the top graph. One can see that population size is maximized for an intermediate value of p .

can be obtained with c large enough (i.e., near enough to a discontinuous step function).

Secondly, the equilibrium population densities are higher at intermediate values of rate of giving resources (i.e., p) (see Fig. 4). The equilibrium population density initially increases with p near 0, reaches a maximum and then decreases as p approaches 1. Although, as we shall see, populations do not always evolve to maximize their equilibrium population density, this finding is at least suggestive. The next section on coevolution will make this more rigorous.

Finally, if the resource availabilities change, then the optimal degree of participation in a mutualism (i.e., p) as measured by the equilibrium population size varies (see Fig. 5). If the differential in resource availability increases (say R_{1N}/R_{2N} is 150/75 instead of 150/100), then the equilibrium shifts to a higher p (greater participation in a mutualism)—here about 0.55 versus 0.125. If the resource differential decreases (say 150/150, i.e. no differential in resource availability), then the population density is highest when $p=0$, i.e. there is no participation in a mutualism.

4.2. Coevolution

The first result is that if each p (p_{1N} and p_{2M}) is allowed to evolve independently, the fitness landscape

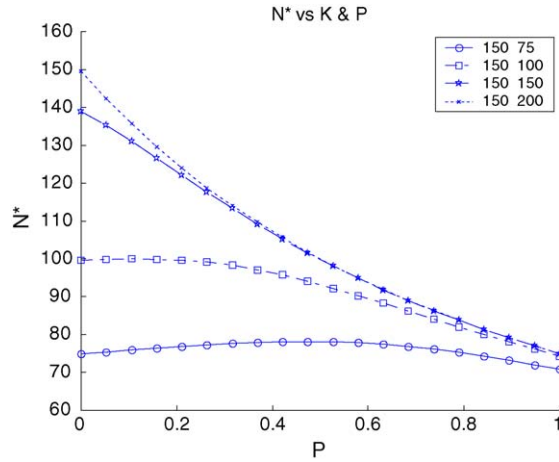


Fig. 5. The effect of varying relative resource availabilities on equilibrium population sizes. One can see that equilibrium population sizes are highest at an intermediate value of p when the traded resource is more abundant and that a zero value of p is favored when the shared resource is in equal or lower abundance.

(Fig. 6) clearly shows that the fitness for species N is maximized if its own p is minimized to 0 and its partner's p is maximized to 1. The converse is true from the point of view of M . Under the evolutionary dynamics described, the population evolves to $p_{1N}=p_{2M}=0$. In short, nobody participates in the mutualism, even though both populations would be “better-off” if they did (as measured by equilibrium population size).

This is exactly analogous to the discrete strategy matrix game commonly referred to as the Prisoner's Dilemma (Axelrod and Hamilton, 1981), where both prisoners would be better off if they would cooperate, but because defecting always increases individual fitness, cooperating is not an ESS and everybody defects. In the mutualism system under study, each population would be better off if the mutualism existed, but because the other population might take resources without giving resources, the populations coevolve to non-interaction, i.e. no mutualism.

However if the two p 's are coupled and forced to evolve in the same direction (here accomplished by setting $p=p_{1N}=p_{2M}$), then the shape of the adaptive landscape changes (see Fig. 7) and the system evolves to a point with $p>0$ (p evolves to the point where the crosshairs meet). Thus, having the degree of participation by each mutualistic partner coupled together allows for an ESS to develop. This can be thought of as enforcement of fair-trade. Note that although the im-

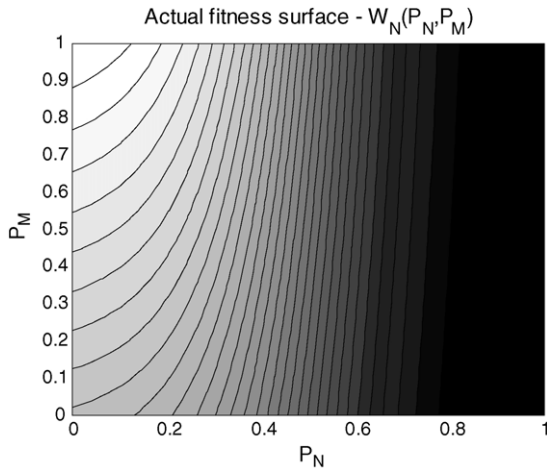


Fig. 6. The fitness surface for a species as a function of its own and its mutualistic partners strategy. Not surprisingly, we see that fitness is highest if the target species donates no resources ($P_N=0$) and the partner species donates all of its resources ($P_M=1$). This is effectively a Prisoner’s dilemma situation, even though it occurs here between species.

plementation demonstrated in the pictures is the limited special case of $p = p_{1N} = p_{2M}$, the qualitative conclusion does not change if there is any increasing, monotonic relationship between the two p ’s.

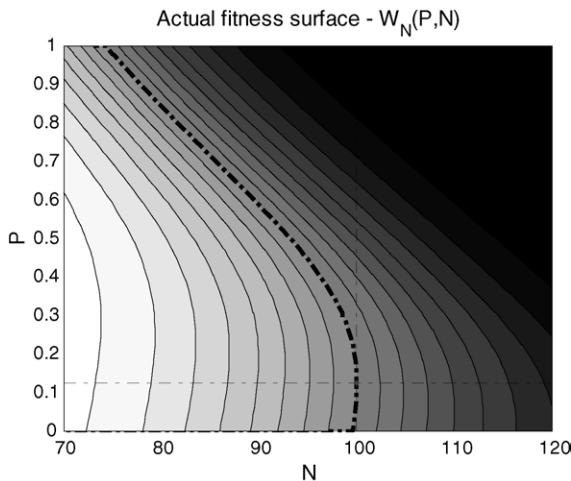


Fig. 7. A plot of the fitness surface similar to the previous figure. However, in this figure the strategies, p , of the two species are linked through some sort of “fair-trade” mechanism. The zero fitness line is shown as a thick dashed line. The evolutionary endpoint of this system is found at the intersection of the cross hairs. We can see that this endpoint occurs on the zero-fitness line at the point, which maximizes equilibrium population size.

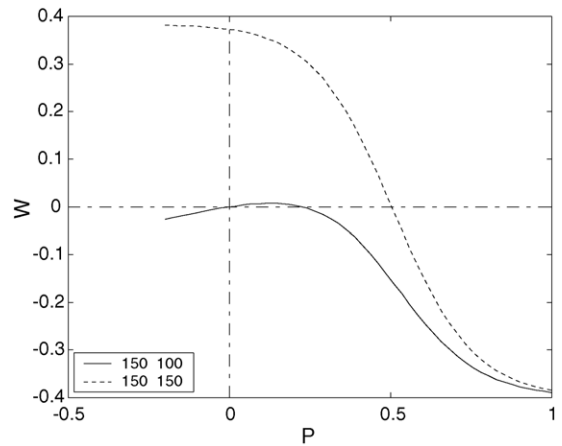


Fig. 8. This figure compares the fitness surface of the two species, assuming “fair-trade” enforcement but with resources being available either differentially or not. This diagram suggests (correctly as it turns out if we follow the evolutionary process to the end), that there will be an interior (mutualistic) equilibrium only if there is a resource differential.

The other condition necessary for a mutualism to achieve an ESS is that which was already hinted at in the population dynamics section above. There must be a differential availability of resources such that in each direction one gives what one has in excess in exchange for what one lacks. This was first shown by Schwartz and Hoeksema using the economic idea of comparative advantage (Schwartz and Hoeksema, 1998; Hoeksema and Schwartz, 2003). If the resource availability differential (comparative advantage) disappears then the ability to obtain an optimum with $p > 0$ also disappears (Fig. 8).

So far I have shown that an ESS is not possible in this model if the p ’s (degree of participation in the mutualism) are allowed to evolve independently and also not possible if the resources are not differentially available. What if these two conditions are met (p ’s coupled, resource availability different)? Under these conditions, there is a point that meets the criteria of an ESS and the system does indeed evolve to this point under the dynamical recurrence equations given above. Fig. 9 shows a one-dimensional view of fitness versus individual strategy, p . We see that a value of $p > 0$ (and hence a mutualism) is an ESS. Fig. 10 (uncoupled) and Fig. 11 (coupled or enforcement of fair-trade) show the same figure as it evolve over time. Note that the shape of the fitness landscape changes drastically as the

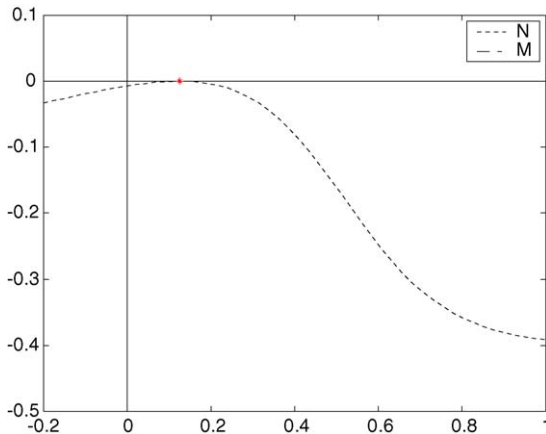


Fig. 9. This diagram shows the fitness surface for two species with “fair-trade enforced” at the evolutionary equilibrium (endpoint). We can see that the fitness is maximized and that fitness is zero at this point. Both surfaces are identical so it appears that there is only one surface.

strategies (p) and densities (N , M) of the two species change. Only when there is enforcement of fair-trade do we see that an ESS is reached. This same ESS is reached from a wide range of initial conditions and appears to be a global ESS attractor.

5. Discussion

The results demonstrate that coevolving mutualisms between species face the same challenge found in the evolution of altruism (cooperation) within a single species. This challenge takes the form of the Prisoner’s dilemma—each player (species in the case of this paper) benefits from having a cooperative partner, but always does better by cheating regardless of the partner’s behavior, leading to cheating being the optimal strategy.

It has often been assumed that coevolution of mutualisms will be similar in nature to the evolution of altruism (e.g., Szathmary and Maynard Smith, 1995). But it is not obvious that it must be so because unlike cooperating members of one species, mutualists never share any genes. Thus, mechanisms such as kin selection (Hamilton, 1964) are not viable. Even the closely related mechanism of vertical transmission does not apply to facultative mutualisms (Wilkinson, 2001). Similarly, the difference in generation times

may require great modification to the notion of reciprocal altruism (Trivers, 1971; Bergstrom and Lachmann, 2003).

A number of mechanisms first discussed in the evolution of altruism have been proposed to allow mutualist partners get over the hump represented by the Prisoner’s dilemma. Many of these mechanisms are closely related. The first mechanism is based on the idea of partner choice (Wilkinson, 2001; Ferriere et al., 2002), similar to results found in intraspecific evolution of altruism (Michod and Sanderson, 1985; Sigmund and Nowak, 1998). The closely related idea of punishment or sanctions (Denison, 2000; Kiers et al., 2003) has also been suggested (it is a fine line between choosing partners and punishing cheating partners).

This paper suggests that a third mechanism commonly identified as a source of altruism (Ratnieks, 1988) might also apply to coevolution of mutualisms, namely policing. Policing is when some external force or party enforces fair trading (i.e., no cheating). It differs from the mechanisms of partner choice and cheating punishers in that the “enforcer” is not directly involved in the interaction. In modern human societies police and the legal system perform this function. The results in this paper show that when the p for each species is linked in a monotonically increasing fashion with the p for the other species (i.e., fair-trade is enforced), then a mutualism can coevolve.

It might be hard to imagine what could be performing the policing and enforcing a coupling of the p -values. I suggest that in most mutualisms it is simple laws of physics and geometry. For an example drawn from outside bitrophic mutualisms, a pollinator has to crawl past the stamens, unavoidably performing pollination in order to reach the nectar, which is its reward (unless of course it expends the energy of eating through the flower). More specifically, within bitrophic mutualisms, the most likely mechanism for enforcement of fair-trade is simple osmosis. All of the examples given of facultative, bitrophic mutualisms live in intimate symbiotic connection and osmosis causes chemicals to flow from regions of high concentration to regions of low concentration. Most of the chemicals (e.g., sugars, mineral ions) that are traded in bitrophic mutualisms are small enough to pass through the cell wall. Hence, osmosis would indeed enforce fair-trade. If a species creates an interface to its partner that is porous enough to allow beneficial goods in via osmotic

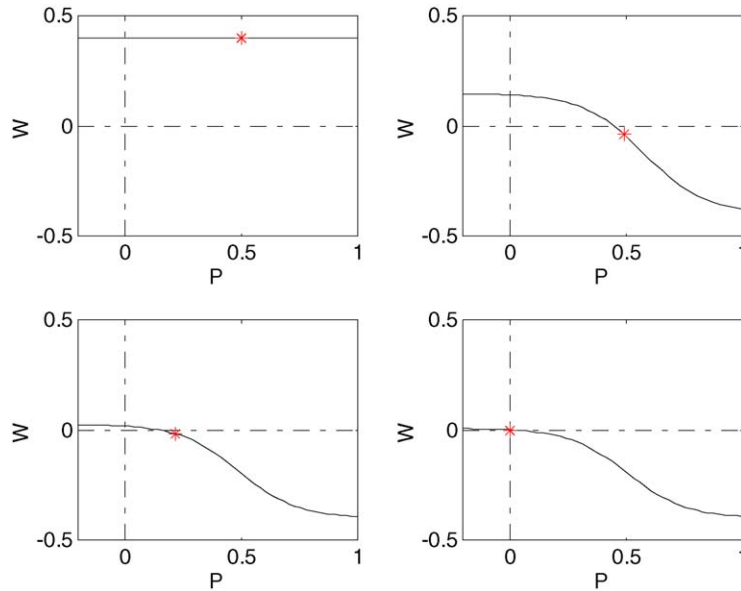


Fig. 10. This diagram shows the evolution of the fitness surface over time (with time going from left to right, then top to bottom). The asterisk represents the state of the population at each point. We can see that when the system starts at low densities the fitness surface is almost flat. Once the population grows enough for density dependence to kick in, there is a clear slope to the fitness surface and the population evolves “uphill” until it reaches a maximum. These diagrams represent evolution without “fair-trade enforcement” and the system evolves to no mutualism ($p=0$).

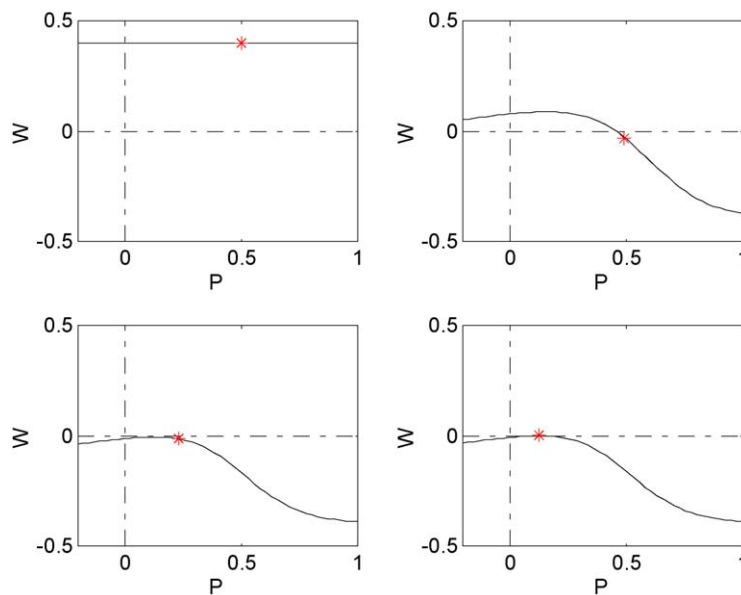


Fig. 11. Similar to the previous figure, but now the evolutionary trait, p , is subject to “fair-trade enforcement” and the population evolves to an interior (mutualistic equilibrium) which is an ESS (frequency dependent fitness maximum). Although difficult to see, in the first frame when the plotted species is low in abundance but the partner species is high in abundance, the fitness surface actually slopes up and to the right slightly (i.e., p would increase initially).

imbalance, then anything it has in excess is likely to leave to its partner through this same porous interface. Although little is known about the actual transfer of nutrients in the mutualisms I model here, simple osmosis is believed to play a central role (Smith and Douglas, 1987).

Finally, the population dynamics and coevolution model results also showed that the conditions for comparative advantage (one species having one resource in abundance that the other species is depauperate in and vice versa) appear to be necessary for mutualism to coevolve (see also Hoeksema and Schwartz, 2003). This data shows that the benefits of a mutualism are conditional on the differential availability of resources. This theoretical prediction is directly supported by experiments on both legumes/rhizobium and plants/mycorrhizae that show that the benefits of a mutualism are heavily dependent on the availability in the ambient environment of the resource that it receives from the mutualist (de Wit et al., 1966; Stribley et al., 1980). The role of productivity gradients on coevolution of mycorrhizal mutualisms has also been explored theoretically (Neuhauser and Fargione, 2004).

There are at least two methodological advances in this paper relative to many previous studies on the population dynamics and coevolution of bitrophic mutualisms. First, this paper develops a new type of mechanistic explanation based on resource limitation for stable population dynamics in mutualistic species, in contrast to papers which incorporate either a phenomenological view of resource limitation (May, 1976; Addicott, 1981; Dean, 1983; Zhang, 2003) or a mechanism based on handling times which applies primarily to resource for service mutualisms such as pollination (Pierce and Young, 1986; Holland et al., 2002). Second, this model incorporates a dynamic, game-theoretic model of evolution and deals rigorously with the fact that species may not evolve to mutually optimal strategies, while many models of the coevolution of bitrophic mutualism merely demonstrate that both species benefit from participating in a mutualism (Keeler, 1985; Schwartz and Hoeksema, 1998; Hoeksema and Schwartz, 2003).

One important limitation of this model is that it is a mechanistic description only of bitrophic, facultative mutualisms—a fairly small subset of all mutualisms. Conceptually, the model might apply to a broader range of mutualisms, but it is no longer mechanistic in nature

and it probably does not apply in any case to obligate mutualisms. The second major limitation is in the application of the ESS game theory, where it was assumed that there were exactly two species. The dynamics under conditions of a three or more species were not examined. This of course starts to blend into the models of partner choice cited earlier.

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