

On the evolution of non-specific mutualism

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It has been argued that mutualisms are non-specific when mutualistic interactions are weak and transient, and become more specific as interactions increase in strength. However, this runs counter to the observation that there exist tightly linked mutualisms of great antiquity that are highly non-specific. Here we argue that mutualism generates positive, interspecific, frequency-dependent selection, which acts as a cohesive evolutionary force, discouraging evolution of specificity. A simple mathematical model is constructed to analyse the evolution of a community consisting of two guilds of species with mutualistic between-guild interactions, two competing species in each guild and two genetically distinct phenotypes within each species. With some simplifying assumptions, the trajectories in the neighbourhood of the only interior equilibrium point are determined analytically in terms of interactions between individuals. These show that the equilibrium is locally stable (no evolution) when there is little differentiation between phenotypes in mutualistic and interspecific, competitive interactions. On the other hand, when there is strong differentiation between phenotypes in their mutualistic interactions, the equilibrium is unstable and the community starts to evolve towards non-specificity. There are, however, two forces counteracting this tendency which, if sufficiently potent, cause evolution towards specificity. The first is generated by strong differentiation between phenotypes in interspecific competition; the second is caused by specificity which already exists between species in their mutualistic interactions. Thus, the tendency for non-specificity or specificity to evolve depends on the interplay between antagonistic and mutualistic interactions in the community. We illustrate these results with some numerical examples and, finally, survey some data on specificity of mutualisms in the light of the analysis.

KEY WORDS:—Community – evolution – mutualism – specificity – symbiosis.

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INTRODUCTION

Several recent publications have drawn attention to the tendency for interactions between mutualistic species to be non-specific, that is for a mutualist to be found in association with more than one, and often many, different mutualistic species (Schemske, 1982a; Harley & Smith, 1983: 357 *et seq.*; Howe, 1984; Law, 1985). This stands in contrast with the high levels of specificity characteristic of certain kinds of antagonistic interaction, notably those of hosts and parasites (Price, 1980: 19 *et seq.*; Thompson, 1982: 13). The contrast is especially clear between mutualistic mycorrhizal and pathogenic fungi; there is no evidence of absolute specificity of a mutualistic mycorrhizal fungus to a single host species (usually many species can be infected), whereas specificity is found even at the level of the genotype in pathogenic fungi such as rusts and smuts (Day, 1974: 96–97; Harley & Smith, 1983: 369).

At present, if any view prevails among evolutionary biologists, it is that the evolution of specificity depends in some way on the continuity, intimacy and interdependency of species in mutualistic association. For example, Real (1980) pointed out that evolution of specificity of pollinators to particular plant species requires that the food reward donated by the plant should be constant through time; in the absence of this, continuity of the association cannot be retained. Thompson (1982: 91) distinguished between 'parasite-like' and 'grazer or predator-like' mutualists on the basis of how tightly linked the species are; he argued that specificity is to be expected as the evolutionary outcome of intimate, parasite-like associations (but not of transient, grazer or predator-like ones), although this would be ameliorated by selective forces in their hosts increasing their availability to potential mutualists. In an analysis of ant/plant mutualisms, Schemske (1982a) argued that differences in specificity result from differing degrees of dependency of the ant on plant resources. Wheelwright & Orians (1982) noted that plant/pollinator mutualisms are sometimes more specific than plant/seed-disperser ones; they attributed this, in part, to the advantage for a plant of a tightly linked pollen vector which is absent in seed dispersal because of the uncertain distribution of suitable sites for germination. Howe (1984) suggested that interactions between species are too diverse and transient for specific interactions between mutualists to evolve.

Clearly, there is a level at which the evolution of specificity does depend on continuity and intimacy of the association, for there must come a point at which the association is too ephemeral for it to bring about observable evolutionary change. However, this argument would seem to apply with as much force to antagonistic as to mutualistic associations and, therefore, does not resolve the problem of why mutualism should often be less specific than antagonism. It is towards features peculiar to mutualism that we need to turn in order to find explanations for their relatively low levels of specificity (Vanderplank, 1978: 151; Thompson, 1982: 91–92; Law, 1985).

In this paper, we consider the role that positive, interspecific, frequency-dependent selection, generated by mutualistic interactions, could play in restricting the evolution of specificity. The mechanism involved is as follows. Suppose that there are two guilds of species (A and B), each species from guild A being mutualistic with each from guild B. In every species there is a set of phenotypes which differ in their 'success' with phenotypes of species in the other guild ('success' incorporating both the capacity to find and the benefit derived from phenotypes in the other guild). Assume that these phenotypes are genetically distinct and, for simplicity only, that the set of phenotypes in each species within a guild is the same. Suppose that one phenotype, say α , in guild A occurs in greater numbers than any other phenotype (this number being the sum of the densities of α in *all* species in the guild). Then, in guild B, the phenotype, say α' , which is most successful with α , has the greatest fitness and consequently increases in frequency in each species of guild B. A direct consequence of the mutualistic interaction between guilds is that as α' increases in frequency, the fitness of α in guild A becomes greater. Thus, if α' is sufficiently common, the fitness of α in guild A will be greater than that of any other phenotype and it will increase in frequency still further. The process then 'snowballs' so that the community becomes increasingly dominated by whichever phenotype starts most common, culminating in fixation of the same phenotype within each guild (in this case α and α'). In such a community, a species from one guild would interact with equal facility with any species in the other guild; that is, the mutualism would be non-specific.

In common with some other features of coevolution, the evolutionary mechanism above has a high dimensionality which cannot be reduced to a manageable system of equations without loss of the mechanism itself. Faced with this dilemma, we have adopted a somewhat unorthodox analytical method, requiring certain symmetries to be present within the system of equations. These symmetries represent both the strength and weakness of the method. The strength is that the behaviour of the system in the neighbourhood of an interior equilibrium point can be completely specified in terms of general parameters for interactions between the organisms. Thus, we can build up an understanding of how the interactions control the evolutionary process without becoming lost in a forest of simulation. The weakness is that in no real biological community would the requirement for such symmetries be exactly satisfied. However, matrix perturbation theory (Stewart, 1973: 289 *et seq.*) indicates that results from the analysis do not depend on the existence of exact symmetries; in effect the method opens up a 'window' through which to view an otherwise opaque system. Thus, we argue that the method below, notwithstanding its obvious limitations, sheds some light on the evolution of non-specificity.

We start by outlining a simple model of a community in which different patterns of specificity can evolve. The community has a single, feasible, interior equilibrium point (at which all phenotypes of all species are present); this is taken as the starting point for evolution. With certain assumptions about symmetries within the Jacobian matrix for this equilibrium, analytical expressions for the eigenvalues and eigenvectors can be written down in terms of the interactions within the community. Thus, the trajectories close to equilibrium, which indicate how the community starts to evolve, are expressed explicitly in terms of these interactions. Moreover, numerical solution of the

model shows that these trajectories give a good indication of the eventual outcome of evolution. It is found that, under reasonable biological assumptions, evolution of non-specificity occurs (although this is by no means the only possible outcome). Finally, we compare the theoretical predictions with data on specificity of mutualistic interactions

MODEL

We consider a community made up of two guilds of species (A and B), each guild interacting mutualistically with the other. In each guild there are two species containing individuals which experience both intra- and interspecific, within-guild competition. For example, the community could be envisaged as a mutualistic association of two ant species feeding on the extrafloral nectaries of two plant species, there being competition between and within the two ant species and between and within the two plant species.

Suppose that, in each species, there exist two phenotypes, say, α and β in each species of guild A and α' and β' in guild B. The success of a phenotype when interacting with the other guild is assumed to be greater when the interaction is with an alike phenotype than with an unlike phenotype. For example, one could envisage an ant/plant mutualism where there are two nectary phenotypes (α and β) in the plant guild, both types being present in both species, but each individual carrying one type only. Correspondingly, in the ant guild there would be two phenotypes, a type α' which is more successful with α nectaries and a type β' which is more successful with β nectaries (again both phenotypes being present in both ant species).

Structured in this way, the model allows several different patterns of specificity to evolve. First, each species may remain polymorphic. In this case, the community evolves neither in the direction of specificity nor non-specificity. Nonetheless, since all of the species retain both phenotypes, there is a sense in which mutualistic interactions between guilds are non-specific. Second, evolution may occur in such a way that one species ends up with phenotype α (respectively α') and the other species with phenotype β (respectively β') in guild A (respectively guild B). Here evolution is towards specificity, because α and α' come to predominate in one pair of mutualists and β and β' in the other pair. Third, evolution may have the result that all four species end up with alike phenotypes (either α and α' , or β and β'). In this case, evolution towards non-specificity is taking place because, when only α and α' (or β and β') remain, each species matches both species in the other guild. Notice that, although the first and third case both lead to non-specificity, the first is non-specific because evolution has not been taking place, whereas the latter is non-specific because evolution has taken place. It is only by analysis of the phenotypic variability within the species that the difference between them will be revealed.

Suppose that the community can be modelled in continuous time, using a set of eight differential equations of Lotka–Volterra form,

$$\dot{x}_i = r_i x_i \left(K_i + \sum_j \gamma_{ij} x_j \right) \quad i, j = 1, 2, \dots, 8, \quad (1)$$

the equations being ordered (1) guild A/species 1/phenotype α , (2) A/1/ β , (3) A/2/ α , (4) A/2/ β , (5) B/1/ α' , (6) B/1/ β' , (7) B/2/ α' and (8) B/2/ β' . The

parameters r_i and K_i are the intrinsic rate of increase and carrying capacity of type i respectively, γ_{ij} is a parameter which describes the effect of an individual of type j on the per capita rate of increase of type i , and x_i is the population density of type i . For simplicity, we do not consider the complexities arising from Mendelian inheritance; reproduction is assumed to be asexual, so that the behaviour of the community depends solely on the costs and benefits of interactions between individuals.

In the analysis which follows, we assume that there is a single, biologically feasible, interior, equilibrium point x_i ($i = 1, 2, \dots, 8$), and that the community is at this equilibrium point, both phenotypes of all species thus being present. To determine analytically the behaviour of the community in the neighbourhood of this equilibrium, we require that the Jacobian matrix (**J**) below should have the following symmetries:

Effect of:

A	B
$\begin{array}{c} \beta & \alpha & \beta \\ \alpha & \beta & \alpha & \beta \end{array}$	$\begin{array}{c} \alpha & \beta \\ \alpha & \beta \end{array}$

Effect on:

A	B	$= \begin{bmatrix} \mathbf{C} & \mathbf{D} \\ \mathbf{D}' & \mathbf{C}' \end{bmatrix} = \mathbf{J} \quad (2)$
$\begin{array}{c} 1 \\ 2 \end{array}$	$\begin{array}{c} 1 \\ 2 \end{array}$	

where the element in the i th row and j th column is $r_i \gamma_{ij} x_j$. Elements in the first four rows refer to the effect of each type on guild A, and elements in the second four rows to the effects on guild B. In view of the definition of interactions in the community, all elements in **C** and **C'** are negative and all elements in **D** and **D'** are positive.

It can be seen from (2) that each 2×2 and 4×4 submatrix is symmetric. To obtain a biological interpretation of this symmetry requirement, we assume that, within each guild, all types of individual have the same r_i and K_i , and hence the same equilibrium density x_i . Differences between elements in rows 1-4 and differences between elements in rows 5-8 are then attributable to differences in the interactions between individuals, the γ_{ij} s of (1). There are two conditions needed to ensure that each 2×2 submatrix is symmetric. First, the effect of an

Table Eigenvalues of the Jacobian (**J**)

λ_1, λ_2	$\frac{1}{2}(a+b+e+f+a'+b'+e'+f') \mp \frac{1}{2}[(a+b+e+f-a'-b'-e'-f')^2 + 4(c+d+g+h)(c'+d'+g'+h')]^{\frac{1}{2}}$
λ_3, λ_4	$\frac{1}{2}(a+b-e-f+a'+b'-e'-f') \mp \frac{1}{2}[(a+b-e-f-a'-b'-e'-f')^2 + 4(c+d-g-h)(c'+d'-g'-h')]^{\frac{1}{2}}$
λ_5, λ_6	$\frac{1}{2}(a-b-e+f+a'-b'-e'+f') \mp \frac{1}{2}[(a-b-e+f-a'-b'-e'+f')^2 + 4(c-d-g+h)(c'-d'-g'+h')]^{\frac{1}{2}}$
λ_7, λ_8	$\frac{1}{2}(a-b+e-f+a'-b'+e'-f') \mp \frac{1}{2}[(a-b+e-f-a'-b'+e'-f')^2 + 4(c-d+g-h)(c'-d'+g'-h')]^{\frac{1}{2}}$

individual of phenotype α or α' on one of α or α' should be the same as one of β or β' on β or β' . Second, the effect of an individual of phenotype α or α' on one of β or β' should be the same as one of β or β' on α or α' . The 4×4 submatrices **C** and **C'** are symmetric if, within each guild, both species have the same intraspecific interactions and both species have the same interspecific interactions. Finally, symmetry of the 4×4 submatrices **D** and **D'** requires that, as one guild interacts with the other, the effect of species 1 on species 1 is the same as 2 on 2, and the effect of 1 on 2 is the same as 2 on 1. Assumptions concerning the relative magnitude of different interactions are given in the next section. We emphasize that, although the behaviour of the community in the neighbourhood of equilibrium can only be obtained analytically with these symmetries, matrix perturbation theory indicates that the results are not radically altered by small departures from symmetry (Stewart, 1973: 289 *et seq.*).

The eigenvalues and eigenvectors of the Jacobian are given in Tables 1 and 2, obtained by a method of V. Hutson and H. Perfect (personal communication) from Afriat (1954). Thus, the trajectories of the community in the neighbourhood of the equilibrium point are specified in terms of the interactions between individuals. In the next section, we show how local stability of the equilibrium is influenced by mutualism between guilds. The equilibrium point is locally stable when all real parts of the eigenvalues are negative and, in such cases, the community does not evolve. On the other hand, when the real part of at least one eigenvalue is positive, the equilibrium is unstable and the community does evolve. When the equilibrium is unstable, the dominant eigenvector, which gives the trajectories close to equilibrium, indicates whether the community starts to evolve towards specificity or non-specificity. Thus, we can see how interactions within the community control the tendency to evolve specificity or non-specificity.

Table 2. Eigenvectors corresponding to eigenvalues in Table 1

3	5	7
$\begin{bmatrix} +(c+d+g+h) \\ +(c+d+g+h) \\ +(c+d+g+h) \\ +(c+d+g+h) \\ +(\lambda_3 - a - b - e + f) \\ +(\lambda_3 - a - b - e + f) \\ +(\lambda_3 - a - b - e + f) \\ +(\lambda_3 - a - b - e + f) \end{bmatrix}$	$\begin{bmatrix} +(c+d-g-h) \\ +(c+d-g-h) \\ -(c+d-g-h) \\ -(c+d-g-h) \\ +(\lambda_3 - a - b + e + f) \\ +(\lambda_3 - a - b + e + f) \\ -(\lambda_3 - a - b + e + f) \\ -(\lambda_3 - a - b + e + f) \end{bmatrix}$	$\begin{bmatrix} +(c-d-g+h) \\ -(c-d-g+h) \\ -(c-d-g+h) \\ +(c-d-g+h) \\ +(\lambda_3 - a + b + e - f) \\ -(\lambda_3 - a + b + e - f) \\ -(\lambda_3 - a + b + e - f) \\ +(\lambda_3 - a + b + e - f) \end{bmatrix}$
$\begin{bmatrix} +(c-d+g-h) \\ -(c-d+g-h) \\ +(c-d+g-h) \\ -(c-d+g-h) \\ +(\lambda_3 - a + b - e + f) \\ -(\lambda_3 - a + b - e + f) \\ +(\lambda_3 - a + b - e + f) \\ -(\lambda_3 - a + b - e + f) \end{bmatrix}$		

For eigenvectors 2, 4, 6 and 8, substitute $\lambda_2, \lambda_4, \lambda_6, \lambda_8$ for $\lambda_1, \lambda_3, \lambda_5, \lambda_7$, respectively.

PREDICTIONS

To interpret the eigenvalues and eigenvectors of the Jacobian (2) listed in Tables 1 and 2, the following three assumptions are made.

(A1) Intraspecific interactions are strong relative to interspecific interactions within and between guilds. Thus for guild A, $|a|, |b| \gg |e|, |f|, c, d, g, h$ (similarly guild B). This reflects the tendency for con-specifics to have more similar niche requirements because of their greater resemblance to each other.

(A2) Interactions between alike phenotypes are stronger than between unlike phenotypes. For guild A, this means that $|a| > |b|, |e| > |f|, c > d, g > h$ (similarly guild B). Within guilds, this again reflects the tendency for more similar individuals to have more similar niche requirements. Between guilds, it embodies the assumption that mutualistic interactions are more successful with alike phenotypes than with unlike ones.

(A3) The difference between interactions of alike and unlike phenotypes is greater when the interactants are from different guilds than when they are from the same guild. That is, for guild A $(c-d), (g-h) \gg |(a-b)|, |(e-f)|$ (similarly guild B). These differences represent the extent to which phenotypes are differentiated from one another in their interactions. The assumption is therefore that, since the phenotypes are defined in terms of their mutualistic interactions, it is likely that they will differ more in these mutualistic interactions than in competitive ones.

When these assumptions hold, the largest eigenvalue is usually λ_8 for the following reason. Eigenvalues 1-4 all contain a term $a+b+a'+b'$; due to (A1) this term has a predominant influence on these eigenvalues, causing them to be negative numbers of large absolute values. However, eigenvalues 5-8 all contain a term $a-b+a'-b'$ which, due to (A3), has relatively little effect; furthermore, this term occurs with $(e-f)$ and $(e'-f')$, so that it is now the mutualistic interactions between guilds which are important. The largest between-guild term in eigenvalues 5-8 is $[(c-d)+(g-h)] [(c'-d'+(g'-h'))]$ in eigenvalues 7 and 8. An expression containing this term is negative in λ_7 but positive in λ_8 , so the largest eigenvalue is λ_8 . (There are, however, certain circumstances under which this does not hold, which we will return to below.)

Condition for evolution

Inspection of λ_8 (Table 1) shows that it increases monotonically with differentiation between the phenotypes in their mutualistic interactions. Thus, when (A3) is satisfied, λ_8 is positive, the equilibrium is unstable and the community starts to evolve away from equilibrium. On the other hand, when there is little difference between the phenotypes for one or both guilds, λ_8 is negative and the equilibrium is locally stable (as long as all other eigenvalues are also negative), so that evolution does not take place.

Evolution towards non-specificity

When there is sufficient differentiation between phenotypes in their mutualistic interactions for evolution to take place, the direction in which the

community starts to evolve is determined by the eigenvector which corresponds to the dominant eigenvalue. The eigenvector corresponding to λ_8 has a sign structure $+ - + - + - + -$. Thus, either α and α' start to decrease throughout the community or β and β' start to decrease. Whichever of these occurs, the community is starting to evolve towards non-specificity. We predict, therefore, that there will be evolution of non-specificity, insofar as the trajectories close to equilibrium can demonstrate the more general behaviour of the community (see numerical examples).

Evolution towards non-specificity follows as a direct consequence of the mutualistic interaction between guilds. Suppose, by way of contrast, that the interaction between guilds is competitive, keeping the strength of interactions unchanged, but giving them all negative signs. The eigenvalues are unaltered but the sign structure of the eigenvector corresponding to λ_8 is now $- + - + + - + -$; thus, whichever phenotype starts to decrease in one guild, the other phenotype starts to decrease in the other guild. Alternatively, suppose that there is a predator/prey relationship between the guilds, keeping the strength of interactions unchanged but giving them negative signs in one guild. The eigenvalues λ_7 and λ_8 are now a conjugate pair of complex numbers with real part less than that of the corresponding term in λ_5 or λ_6 which may or may not be real. If λ_5 and λ_6 are real, λ_8 is greater than λ_5 and the corresponding eigenvector has a sign structure $+ - - +$ or $- + + -$ within guilds. If λ_5 and λ_6 are complex, the eigenvectors are complex, but at no time have a sign structure of the form $+ - + -$ within guilds. Thus, when interactions between guilds are antagonistic, there is no time at which the community evolves in the direction of non-specificity (while close to equilibrium); evidently it is the mutualism between guilds which brings about such evolution.

Evolution towards specificity

Clearly, the predictions above depend critically on assumptions (A1)–(A3). Altering the assumptions enables evolution towards specificity to occur. Two such cases, which are of some biological interest, are considered below.

First, consider the effect of increasing differentiation between phenotypes in their interspecific competition within guilds ($e-f$), ($e'-f'$). As the absolute value of these terms increases, holding other terms constant, there is a point beyond which λ_6 is greater than λ_8 . The eigenvector corresponding to λ_6 has a sign structure $+ - - + + - - +$ or $- + + - + - - +$ and consequently, if the equilibrium point is unstable, a different phenotype is favoured in each species within a guild. Thus, the community is evolving towards specificity, with α and α' in one pair of mutualistic species and β and β' in the other pair. Such an outcome is to be expected when the two species in one or both guilds compete strongly for the resources of mutualists in the other guild.

Second, consider the effect of making $(g-h)$ and $(g'-h')$ small. Once again, there is a point beyond which λ_6 is greater than λ_8 , the sign structure of its corresponding eigenvector being $+ - - + + - - +$. Thus, as before, the community evolves towards specificity, if the equilibrium point is unstable. The terms $(g-h)$ and $(g'-h')$ would be small if mutualistic interactions between species of the form 1-2 and 2-1 are weak, that is, if there is some specialization between mutualistic species irrespective of phenotype. We expect, therefore, that

once some specificity is present, the path towards greater specificity will not be easily reversed.

NUMERICAL EXAMPLES

To illustrate the predictions given above, some numerical results of community evolution are now given. For the sake of simplicity, it is assumed that all eight types of individual have the same intrinsic rate of increase ($r = 1$) and that the carrying capacity of all types within guilds is the same ($K = 1$ for guild A; $K = 2$ for guild B). We can then focus attention on the manner in which interactions between individuals influence the process of evolution. In addition, it is supposed that the parameters for interactions in guild B are the same as those for the equivalent interactions in guild A, simply to keep the number of parameters within manageable limits.

No evolution with weak mutualism

Table 3 (column a) lists parameter values for a community in which mutualistic interactions between guilds are very weak and in which there is correspondingly little differentiation between the phenotypes. Given these

Table 3. Numerical results

		(a)	(b)	(c)	(d)
<i>Parameters for</i>					
	Phenotypes				
Intraspecific competition	alike	-1.00	-1.00	-1.00	-1.00
	unlike	-0.98	-0.98	-0.98	-0.98
Interspecific competition (within-guild)	alike	-0.10	-0.10	-0.18	-0.10
	unlike	-0.09	-0.09	-0.09	-0.09
Mutualism (between-guild): spp. 1-1, 2-2	alike	0.02	0.20	0.20	0.20
	unlike	0.01	0.10	0.10	0.10
Mutualism (between-guild): spp. 1-2, 2-1	alike	0.015	0.15	0.15	0.015
	unlike	0.01	0.10	0.10	0.01
<i>Interior equilibrium</i>					
	\bar{x}_A	0.485	0.742	0.704	0.613
	\bar{x}_B	0.934	1.110	1.061	1.013
<i>Eigenvalues</i>					
	λ_1	-2.028	-2.648	-2.608	-2.269
	λ_2	-1.050	-1.370	-1.363	-1.260
	λ_3	-1.672	-1.990	-1.817	-1.874
	λ_4	-0.867	-1.325	-1.200	-1.036
	λ_5	-0.011	-0.055	0.017	-0.083
	λ_6	-0.003	0.036	<i>0.107</i>	<i>0.067</i>
	λ_7	-0.033	-0.164	-0.228	-0.107
	λ_8	-0.009	<i>0.108</i>	0.034	0.059

(a) A community with weak mutualism between guilds. (b) A community with strong differentiation between phenotypes in mutualistic interactions. (c) A community with strong interspecific competition between alike phenotypes within guilds. (d) A community in which there is already some specificity between mutualistic species. In each case, the parameters for equation (1) are given. It is assumed that $r = 1$ throughout and that $K = 1$ in guild A and $K = 2$ in guild B. The interior equilibrium point is then the same for all types of individual in guild A (\bar{x}_A) and all types in guild B (\bar{x}_B). The Jacobian is obtained from the interaction parameters and equilibrium densities. Using the equations in Table 1, the eight eigenvalues of each Jacobian are calculated; the largest eigenvalue is italicized.

Table 4. Jacobian matrix for community with parameter values given in Table 3 (column a)

0.485	-1.00	-0.98	-0.10	-0.09	0.02	0.01	0.015	0.01
	-0.98	-1.00	-0.09	-0.10	0.01	0.02	0.01	0.015
	-0.10	-0.09	-1.00	-0.98	0.015	0.01	0.02	0.01
	-0.09	-0.10	-0.98	-1.00	0.01	0.015	0.01	0.02
0.934	0.02	0.01	0.015	0.01	-1.00	-0.98	-0.10	-0.09
	0.01	0.02	0.01	0.015	-0.98	-1.00	-0.09	-0.10
	0.015	0.01	0.02	0.01	-0.10	-0.09	-1.00	-0.98
	0.01	0.015	0.01	0.02	-0.09	-0.10	-0.98	-1.00

parameters, the interior equilibrium point is determined as 0.485 for each type of individual in guild A and 0.934 for each type in guild B. The Jacobian may then be written down (Table 4) and its eigenvalues calculated by numerical methods or from the formulae in Table 1. All the eigenvalues are negative (see Table 3), indicating that the equilibrium point is locally stable. Thus, there is no tendency for such a community to evolve if the initial state is close to the interior equilibrium point.

Evolution of non-specificity with strong differentiation between phenotypes in their mutualistic interactions

By way of contrast with the above, consider a community in which all mutualistic interactions are increased tenfold, giving a corresponding tenfold increase in the differentiation between phenotypes (Table 3, column b). The Jacobian now has two positive eigenvalues, so the equilibrium point is unstable. The dominant eigenvalue is λ_8 and the sign structure of the eigenvector corresponding to this indicates that the community starts to evolve towards non-specificity.

Behaviour of the community further away from equilibrium is investigated by solving the system of differential equations (1). A solution is illustrated in Fig. 1, starting with a small displacement from equilibrium. We see that phenotypes α and α' increase and phenotypes β and β' decrease to extinction. Thus, the mutualistic interaction between guilds becomes non-specific, because each species ends up interacting with the same facility with both species in the other guild. This non-specificity is brought about by positive, frequency-dependent selection between guilds, favouring whichever phenotype happens to start most common (in this instance α).

Evolution of specificity with strong interspecific competition between alike phenotypes within guilds

Table 3 (column c) is an example which violates assumption (A3) in such a way that there is strong differentiation between phenotypes in their interspecific competition within guilds. The largest positive eigenvalue of the Jacobian is now λ_6 . Thus, the equilibrium point is still unstable, but the dominant eigenvector indicates that the community starts to evolve towards specificity.

Figure 2 gives a numerical solution of the equations, to demonstrate the behaviour of the community further away from equilibrium. It can be seen that,

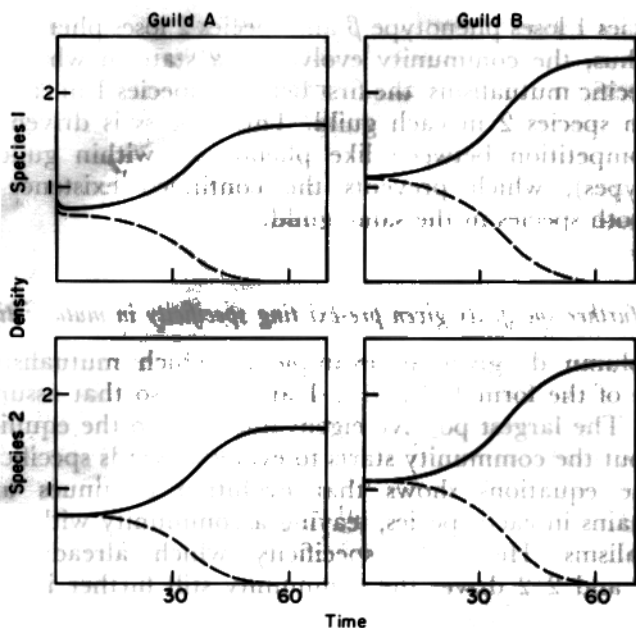


Figure 1. Evolution of a community characterized by strong differentiation between phenotypes in mutualistic interactions. The simulation uses parameter values given in Table 3 (column b). It begins with all types of individual at equilibrium except for $A/1/\alpha$, which is displaced by $+0.1$. — is the density of α and α' in guilds A and B, respectively; ---- is the density of β and β' in guilds A and B, respectively.

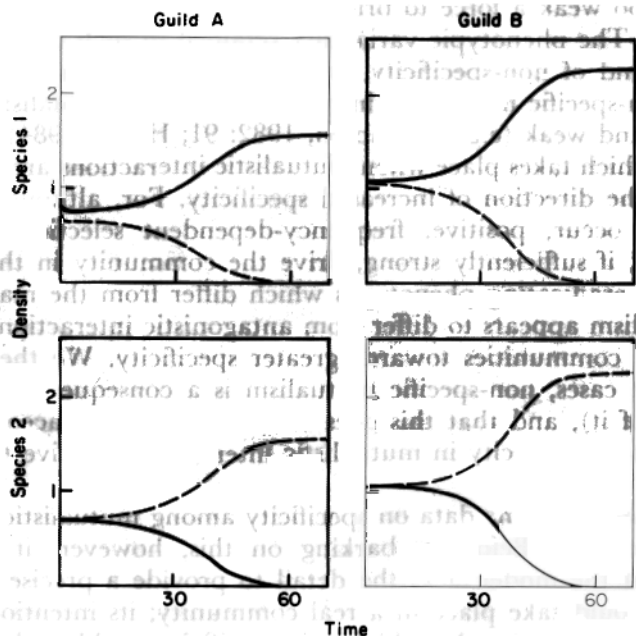


Figure 2. Evolution of a community characterized by strong interspecific competition between alike phenotypes within guilds. The simulation uses parameter values given in Table 3 (column c). Other details as in Fig. 1.

in guild A, species 1 loses phenotype β and species 2 loses phenotype α (similarly in guild B). Thus, the community evolves to a state in which there are two distinct and specific mutualisms, the first between species 1 in each guild and the second between species 2 in each guild. This process is driven by the strong interspecific competition between like phenotypes within guilds (relative to unlike phenotypes), which prevents the continued existence of the same phenotype in both species in the same guild.

Evolution of further specificity given pre-existing specificity in mutualistic interactions

Table 3 (column d) gives an example in which mutualistic interactions between guilds of the form 1-2 and 2-1 are weak, so that assumption (A3) is again violated. The largest positive eigenvalue is λ_6 so the equilibrium point is still unstable, but the community starts to evolve towards specificity. Numerical solution of the equations shows that evolution continues until only one phenotype remains in each species, leaving a community with two distinct and specific mutualisms. Here, the specificity which already exists between mutualists 1-1 and 2-2 drives the community still further in the direction of specificity.

DISCUSSION

The picture which emerges from the analysis above is that community evolution in the presence of mutualism depends on the interplay of mutualistic and antagonistic forces. Clearly, there are circumstances under which mutualism is too weak a force to bring about evolution of either specificity or non-specificity. The phenotypic variability retained in such circumstances itself constitutes a kind of non-specificity, and therefore supports the view that we should find non-specific mutualism in nature when the mutualistic interactions are transitory and weak (e.g. Thompson, 1982: 91; Howe, 1984). Nevertheless, the evolution which takes place when mutualistic interactions are stronger is not necessarily in the direction of increased specificity. For, although evolution of specificity can occur, positive, frequency-dependent selection generated by mutualism will, if sufficiently strong, drive the community in the direction of non-specificity, eradicating phenotypes which differ from the majority. In this respect, mutualism appears to differ from antagonistic interactions as the latter generally drive communities towards greater specificity. We therefore suggest that, in certain cases, non-specific mutualism is a consequence of coevolution (not the lack of it), and that this goes some way towards accounting for the prevalence of non-specificity in mutualistic interactions relative to antagonistic interactions.

Below, we consider some data on specificity among mutualistic species in the light of the analysis. Before embarking on this, however, it is as well to understand that the model lacks the detail to provide a precise description of events which would take place in a real community; its intention is simply to make explicit a mechanism by which non-specificity could evolve. Among the assumptions built into it, which will certainly influence the conclusions drawn, are the following.

First, the dynamics depend on the range of phenotypes present in each species within a guild. If these ranges differ, it may prove impossible for the same phenotype to be driven to fixation throughout the guild, and we would then expect to see the guild divided into subguilds sharing similar mutualistic phenotypes. There is a parallel here with co-occurring Müllerian mimicry rings (Papageorgis, 1975), although the mutualism among such mimics occurs within guilds rather than between guilds.

Second, the Lotka-Volterra equations over-simplify the dynamics of communities, and are particularly suspect as a description of certain mutualistic interactions which involve obligacy on the part of one or both interactants (Vandermeer & Boucher, 1978; May, 1981: 94; Dean, 1983). Thus, it is not possible to analyse a class of mutualism which, because of the strong interactions brought about by obligacy, would be a prime candidate for evolution of non-specificity.

Third, the analysis focuses on a single interior equilibrium point defined by the Lotka-Volterra model. This equilibrium point was chosen because it makes clear the different directions in which a community could evolve. However, it is more probable that a real community would lie at a boundary equilibrium, lacking phenotypic variation within species. Evolution would then involve invasions by phenotypes more successful with the predominant phenotypes in the other guild and/or in less direct competition with those already present in their own guild.

Fourth, analytical insights into the behaviour of the community close to the interior equilibrium point have been achieved at the cost of assumptions about symmetries in the Jacobian. Nevertheless, simulations indicate that the behaviour is not changed in a qualitative way by small departures from symmetry, as indeed one would expect, in view of the fact that the eigenvalues are continuous functions of elements of the Jacobian (Lancaster, 1969). We argue, therefore, that the technique provides a 'window' through which to look at the behaviour of a complex system, although it does remain to be seen how far beyond the window such behaviour is retained.

Non-specific mutualism

Can we tell in which of the many non-specific mutualisms in the living world has non-specificity arisen as an evolutionary outcome of mutualism? With our present knowledge, the answer is no. Nonetheless, there are criteria that indicate where it is most likely to have arisen, as suggested below.

Clearly, non-specificity of recently introduced species with weak mutualism is most unlikely to be an evolutionary outcome of their mutualistic interaction, although the traits they display may have arisen with mutualistic partners in the past. The association between Argentine ants and non-native vetches in California is a case in point (Koptur, 1979). Arguably, the characteristics of some longer-established mutualisms may also be the product of interactions with past rather than present partners. For example, Janzen & Martin (1982) hypothesized that those fruits in the New World now dispersed by animals such as horses and deer, may have coevolved with large Pleistocene herbivores that are now extinct (but see Howe, 1985).

More generally, the analysis suggests that non-specificity as a result of evolution is unlikely to be found whenever mutualistic interactions for at least one guild are weak. Many mutualisms, which are facultative for one or both partners, are likely to be of this kind. These would include, for example, mutualistic interactions between plants and ants with little reward to the ants (Schemske, 1982a), those between massively blooming, common plants and their many pollinators (Feinsinger, 1983), and interactions between fruiting trees and the casual frugivores that disperse their seed (Howe, 1984).

It is among mutualisms with strong interactions that we are mostly likely to find evolution of non-specificity (although it should be borne in mind that the strength is only important insofar as it increases the potential for differentiation between phenotypes). These would include (i) the nitrogen-fixing associations between plants and micro-organisms, (ii) several kinds of mycorrhizas, (iii) lichens, and (iv) dinoflagellates with their invertebrate hosts. The strength of their interactions is such that one or both partners often has an obligate requirement for the other so, strictly speaking, these mutualisms lie outside the scope of the model in this paper. Nevertheless, it is interesting that, although they all have features indicating a long evolutionary history of mutualistic association, the information currently available is that they are remarkably non-specific in their partners (Wilson, 1944; Mosse, 1973; Pearson & Read, 1973; Akkermans & Roelofsen, 1980; Schoenberg & Trench, 1980; Bonnett & Silvester, 1981).

Specific mutualism and within-guild competition

The model predicts evolution towards specificity when there is strong differentiation in interspecific competition between phenotypes within guilds. This could occur when species in one or both guilds compete strongly for the resources of mutualists in the other guild. For example, Levings (1982, 1983) found nests of different, tropical forest, ant species to be over-dispersed, suggesting that interspecific competition plays a significant role in such guilds. Thus, the different patterns of attendance by tropical forest ants to plants that offer extraflora nectar (Bentley, 1976, 1977; Keeler, 1980, 1981a; Schemske, 1982b; Koptur, 1984) may be influenced by competitive interactions between species.

A case in which interspecific competition evidently plays an important part in maintaining specificity is that of the acacia-dwelling ants (*Pseudomyrmex* spp.) in lowland, dry forests of Central America (Janzen, 1966). There are relatively few *Pseudomyrmex* species, although there are many other species of ant which visit plants with nectaries only in the same communities. Acacia ants are among the more aggressive ants, with active swarming behaviour and nasty stings (Janzen, 1966) and, although they are able to use other nectar sources in addition to *Acacia* (Keeler, 1981b), they exclude other species of ant from the plants that provide them with food and shelter. *Pseudomyrmex*, as the single genus of ants associated with acacias in Central America, contrasts with the wider range of ant species that occupy the domatia of *Myrmecodia* and *Hydnophytum* species in Papua New Guinea (Huxley, 1978). In this case, the ant species (from the genera *Iridomyrmex* and *Camponotus*) are less aggressive than *Pseudomyrmex*, in spite of their demonstrable plant-protecting abilities.

Interspecific competition within guilds provides a possible explanation for Schemske's (1982a) observation of increasing specificity in ant/plant mutualisms as the rewards to the ants increase (i.e. associations in which ants receive solid food and/or shelter, in addition to nectar). This trend runs counter to the prediction that non-specificity should evolve when mutualistic interactions are strong. However, if ants are predisposed to defend their resources from competitors more vigorously when the resources are more valuable, the balance between mutualistic and antagonistic interactions could be tilted sufficiently in the other direction for specificity to evolve. It is interesting in this context that *Iridomyrmex* and *Camponotus*, with relatively low levels of aggression, do not fit easily into the pattern given by Schemske (1982a).

Specific mutualism and pre-existing specificity

The model also predicts that, if some degree of specificity already exists in mutualistic interactions between guilds, evolution is likely to continue further in this direction.

The associations between hummingbirds and the plants they pollinate could be an example of this process, albeit at a broader level than the one-to-one species interactions in the model. These birds can be divided into two subguilds. The hermits are non-territorial and 'trapline', visiting the few flowers which open each day on a large number of widely separated plants (Stiles, 1975; Feinsinger, 1983); they have long, curved bills, and the flowers they visit have long, curved corollas, 'specialized' for visitors with suitably shaped bills. The non-hermits are territorial and have shorter, straighter bills that fit into a wider variety of flowers. The hermits, being non-territorial, would be the only birds likely to visit plants with few flowers, whereas the hermits would guard floriferous plants against other birds. It seems likely that this pre-existing specificity, of hermits with their few-flowered plants and non-hermits with their massively flowering plants, may have provided the impetus for evolution of further specificity in the hummingbird guild.

The clearest examples of obligate, one-to-one species mutualisms in pollination are the fig wasps and *Yucca* moths, which both pollinate and parasitize the flowers (Feinsinger, 1983). To the extent that their speciation has been brought about by the specificity of interactions, such mutualisms lie outside the scope of the present analysis. However it is worth noting that one could envisage the 'species' within guilds as conspecific populations split into two spatial regions with restricted movement of individuals between them. Mutualistic interactions between guilds in different spatial regions would then be weak and there is a possibility that specificity would evolve within regions. The drawback to this is that competitive interactions between populations within guilds would also decrease as the spatial overlap is reduced, and could prevent evolution of specificity. Clearly, it is only under rather special circumstances that the mutualistic interactions would be reduced more than the competitive ones. Nevertheless, such circumstances would be worth consideration, in view of the difficulty in finding deterministic forces which could lead to parallel speciation of plants and their pollinators (Kiestler, Lande & Schemske, 1984).

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